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Do food forests need fertiliser?



Abstract

This literature review investigates if food forests require fertilisation (with nitrogen and phosphorus) to sustain crop yields. It investigates soil nitrogen and phosphorus stocks in the temperate zones and provides insights into the potential lifespan of food forest systems that do not get fertilised. To understand the mechanisms that explain (food) forest nutrient uptake, the soil food web with all its components such as mycorrhizal fungi was described. Also, all different inputs and outputs of nitrogen and phosphorus were calculated for a (food) forest system. With the gathered data, calculations were made for a chestnut and hazelnut system (as a blueprint for a food forest). The total soil nitrogen and phosphorus stocks were divided by the annual nitrogen and phosphorus removal via nut harvests to gain insights into the time needed to exhaust soil nutrient stocks (if they were to be exhausted). Results show that several mechanisms explain natural forest nutrient uptake such as immobilisation-mineralisation reactions by soil biota, as well as mycorrhizal uptake from several different (phosphorus) pools including uptake from mineral rock particles such as apatite. Furthermore, the perennial nature of trees enables deep root networks to develop, greatly enhancing total nutrient uptake surface.

Total nitrogen and phosphorus pools vary substantially depending on soil type, topography, parent material and soil age. However, considering a 2-metre deep soil profile in the temperate zone, total nitrogen stock ranges between 7 550 and 26 440 kg per ha, while phosphorus stock ranges between 9 685 and 16 328 kg per ha. Since many of a food forest's species (mainly fruit trees) lose relatively low amounts of nitrogen and phosphorus via harvesting, the time until nutrient stocks are exhausted (without other input processes) is quite long. For chestnuts, with an annual nitrogen and phosphorus removal of 21 and 2.5 kg (with a harvest of 2000 kg DM per ha), it takes >400 years before nitrogen stocks are halved and >2 000 years before phosphorus stocks are halved in the scenarios of no inputs such as atmospheric deposition and N-fixation. In the scenarios *with* inputs, the time is increased. However, several food forest species, mainly nut trees, lose more nitrogen and phosphorus than chestnuts. Therefore, I calculated the same for hazelnuts. In the scenario of a high hazelnut harvest of 2 000 kg DM per ha, significant quantities of nitrogen are lost from the system each year due to crop harvests. Consequently, it takes only several decades to halve the soil nitrogen stock without considering nitrogen inputs. This illustrates that certain crops, specifically nut trees, should be given extra attention when designing a food forest. Including enough nitrogen-fixating species can compensate for the nitrogen losses resulting from nut harvesting.

The main question is, *what level of biomass production is supported via natural soil fertility?* There is some evidence that food forest systems can take up enough nitrogen and phosphorus to sustain high fruit or nut yields for centuries (as seen in the chestnut orchards in southern Europe). However, there are many tree species that do not give high nut or fruit yields. Many nut species allocate only a small proportion of their assimilates to fruit/nut production. Via controlled breeding, it is likely that this proportion can be increased significantly, resulting in higher nut production with the same annual nutritional uptake (so less nutrients are allocated to growth and pest resistance amongst others). For species such as apple with a long domestication history, allocation to fruit production can be higher than found in annual staple crops such as maize. It is likely that via increased focus on breeding, yields of unfertilised food forest systems can be markedly increased.

This research shows that total soil nitrogen and soil phosphorus stocks are relatively large in the temperate zone and can support unfertilised food forest' yields for several decades to several millennia, depending on crop, natural fertility inputs and yield intensity. In the case of food forests with low-nitrogen containing nuts/fruits, food forests can continue bearing fruits and nuts for centuries without considering any input. However, in certain cases such as food forests dominated by nut trees, nitrogen stocks can be exhausted relatively quickly and nitrogen inputs (via nitrogen fixing plants) should be considered to maintain high yields. Furthermore, it is not clear what kind of yield intensities can be supported by natural nutrient uptake mechanisms in food forests and future work should make this clearer.

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Introduction

The conventional annual agricultural system lies at the heart of several ecological problems such as erosion, subsequent soil infertility, drinking water competition, greenhouse gas emissions, the global biodiversity crises and eutrophication [1]. Agroforestry systems could provide some solutions to many of these problems and a steady body of evidence now indicates agroforestry is a land-use system that needs less fertiliser, increases biodiversity (compared to annual monocropping) and reduces soil erosion [2].

Food forests are agricultural systems predominantly built around tree crops, as opposed to conventional agriculture where annual crops like grains dominate the system. Food forests could be considered a form of agroforestry, although agroforestry is commonly described as “*a collective name for land-use systems and technologies where woody perennials (trees, shrubs, palms, bamboos, etc.) are deliberately used on the same land-management units as agricultural crops and/or animals, in some form of spatial arrangement or temporal sequence [3]*”. This description includes a combination of perennials and annual crops and/or animals and some food forests match this description while others do not. For example, at food forest De Ketelbroek in the Netherlands, only perennial crops (trees and shrubs) are cultivated for subsequent usage while both annual crops (except a small plot of vegetable gardens for educational purposes) and livestock are consciously excluded. Strictly spoken, such a system would not align to the abovementioned definition of agroforestry. However, in my opinion the definition of agroforestry should be broadened to include strict perennial-based systems as well, since those systems share so many features of agroforestry that it makes no sense to exclude them from agroforestry.

Food forests have been gaining popularity during the last several years in the Netherlands and new initiatives are arising almost every day. There are many well-established benefits of food forest systems compared with conventional agriculture. For example, food forest the Ketelbroek is one of the most renown food forests in Holland. Bakker (2016) compared biodiversity of the Ketelbroek with the biodiversity of nearby conventionally managed pastures as well as with a nature reserve. The results showed Lepidoptera (nocturnal butterflies) biodiversity (Shannon-index) was almost as high in the food forest as in the nature reserve [4]. The Carabidae (beetles) biodiversity was even higher in the Ketelbroek than in the nature reserve [4]. Other studies on agroforestry systems clearly confirmed these findings and showed enhanced biodiversity in agroforestry systems compared with conventional agricultural systems [2],[5],[6].

Though, there are several issues regarding food forest systems that need more scientific research to provide an answer. Production capacity (can it compete with conventional agriculture?), economic feasibility (high labour costs?), and nutrient management (do food forests need fertilisers?) are three of the key issues. This paper focusses on the latter one.

One of the highly-debated topics around the sustainability of food forests is the concept of nutrient balances. In conventional agricultural education, students learn that nutrients flowing into the system must equal nutrients flowing out of the system to prevent negative nutrient balances and subsequent soil nutrient mining. Some food forest proponents like Wouter van Eck (owner of food forest the Ketelbroek) have the opinion that there are copious amounts of nutrients in the soil and that there is no need to provide nutrients to the system, even after decades of harvesting (and, hence, nutrient outputs).

Many agriculturally educated and highly knowledgeable scientists regard this thinking as radical or ‘too-good-to-be-true’. Conventional agriculture, they argue, is only so productive because of the high soil nutrient levels, especially the high nitrogen and phosphorus levels. According to them, using unfertilised systems would severely reduce agricultural output and threaten world food security.

Food forest proponents often react by stating that *annual* agricultural system knowledge cannot directly be applied to the concept of perennial systems and most agronomists, though not all, work

with annual plants. Furthermore, they point out that natural forests have never been fertilised in their hundreds of millions of years of existence on this planet

This paper aims at evaluating both camps' claims and aims at providing an overview of the existing evidence concerning this nutrient-question. I try to find out if there is any evidence for the claim that food forests can function properly without the addition of regular fertiliser applications (in any kind of form, e.g. compost, inorganic fertilisers etcetera). I believe there are certain critical differences between food forests and natural forests that might strongly influence this nutrient-debate.

However, I also recognise that many of the people educated in agriculture are principally educated in *annual* agriculture and therefore they apply their knowledge of annual production systems to perennial systems, which are fundamentally different in their innate nature and performance.

Therefore, I am content to be in a position where I have obtained knowledge in conventional annual agriculture, agroforestry, biology, and ecology. The latter is crucial when trying to find the truth concerning the nutrient question. A food forest resembles more a natural ecosystem than a strongly disturbed agro-ecosystem, which means understanding ecological interactions, both in soils as above-ground, can be helpful during this research.

Of course, every researcher is biased in a certain way, often only noticeable in subtle details.

However, the fact that someone works on a topic like agroforestry or food forests is a result of a personal interest in the topic and the reason why someone gets interested in such a topic, is because he or she sees the opportunities or solutions provided by the topic. Therefore, although doing research on a certain topic is per definition a biased choice, the choice to invest much time in doing the research often results from a genuine belief in the power of the topic to transform or solve certain issues, especially if the research is done in fields where money is no likely motivation. In my case, this reasoning can be applied as well. I learned about all the ecological problems associated with conventional agriculture and learned about potential solutions like agroforestry, agroecology, restoration agriculture and permaculture.

However, though I am a proponent of most of these alternative agricultural systems because I see the potential ecological, social as well as economical contributions these systems could make, I am aware that there are plenty solutions manifested by proponents of these agricultural systems that are not supported by science.

The most important issue concerning these alternative agricultural systems is to provide a solid scientific base because our current society, with high rates of secularisation, has adopted science almost as a substitute for its former religion. Of course, there are still people who do not value science, but in the Netherlands, for example, science is the institution with the highest reliability (more than jurisdiction, trade unions, journalism and politics [7]).

Therefore, society only embraces new discoveries when it has a solid scientific base, though processes and persons like Donald Trump are changing this unfortunately). Research into alternatives like permaculture and food forests, mainly done by students as part of their thesis, has been increasing in the last few years in the Netherlands. I believe these contributions are crucial because some of those students will become researchers at renowned scientific institutions later in their life and will contribute to new researchers done on these subjects they got interested in during their study.

For this paper, it is critically important for me to be *as unbiased as possible*, because I believe only with objectively presented findings I can convince or at least reduce the objections of conventionally educated agronomists against the theory of no nutrient inputs *or* convince the food forest proponents that nutrient additions are needed to compete with conventional agriculture. Therefore, I try to be as open as possible in my reasoning in this paper. All the assumptions that I make to do the calculations are explained and weaknesses and shortcomings in data are mentioned.

As mentioned before, I have been educated in different fields such as ecology, (conventional) agriculture, biology and agroforestry and therefore, I am in a key position to perform an interdisciplinary research to this program as I am not constrained by just *one* of the fields most people, unfortunately, tend to be educated in. In this paper, I combine and synthesise research done in the fields of forest management, agriculture and ecology to the topic of food forests. I aim to make clear where the research stands, what data is lacking and what we can conclude from existing research

in relation to the nutrient (fertilisation) additions to food forests. The **research question** of this paper is the following one:

- “How large is the soil phosphorus and nitrogen stock available to food forests situated in temperate zones, and how long can these stocks sustain food forest nuts/fruit production before they are depleted?”

By answering this research question, evidence is provided to help answer the question “*do food forests need to be fertilised to sustain high production?*” This question is very complex and multi-faceted. Therefore, it cannot be fully answered within the confines of this internship. However, with the choice of the aforementioned research question, I try to provide a solid base in order to get to the solution to this question within the limits of this internship. I believe answering this research question provides two key insights necessary to answer this complex question. First, it provides insight into the order of magnitude of the potentially reachable nutrient stocks. Second, it shows the potential lifespan of food forest systems without fertilisation and indicates whether it is even possible to continue producing for decades or centuries. This research will form a base to, *in combination with other* (future) research on this topic, provide the answer to the question whether food forests need to be fertilised to sustain high production.

Of course, there are plenty of different nutrients, but I chose to focus on the two most often plant production limiting nutrients: nitrogen and phosphorus. Those macronutrients are almost always included in fertilisers and are taken up in large quantities. Therefore, if plants can take up enough of those nutrients, normally plant production is high. If food forests can take up sufficient nitrogen and phosphorus, a high productivity is very likely. That is why I focus on the uptake of those two nutrients in this paper: it serves as a proxy for high plant productivity.

The structure of this review is as follows. First, I explain the methodology used in this literature review. Then, I will review basic soil nutrient provision mechanisms to summarise the known methods that provide nutrients to food forest systems. Some recent findings in soil biology and the importance of soil biology on natural system nutrient provision will be summarised as well. The soil biological processes have been gaining popularity over the last decade but are still underrepresented in conventional agronomic nutrient-fertilisation recommendations.

After showing the status of soil nutrient provision, I will provide an overview of all the different inputs and outputs influencing nitrogen and phosphorus balances. Then, to be able to answer the research question, I will estimate total soil nitrogen and phosphorus content in temperate ecosystems.

Last, I will calculate the annual nitrogen and phosphorus output for two important temperate food forest crops: hazelnuts and chestnuts. These crops are representative of the nutrient outflows of most food forests based on nut and fruit trees. With the collected data on total nutrient stocks, I calculate how long it takes before nutrient pools are depleted and nutrients need to be added (via fertilisation). These calculations answer the second part of my research question and show if it is possible (and in which cases) for food forest systems to keep continuing without receiving inputs.

A conclusion that answers the research questions and summarises the findings follows the discussion section.

Methodology

This literature review collects evidence on soil nutrient (nitrogen and phosphorus) status of temperate ecosystems. It reviews studies done in the fields of ecology, lithology, agriculture, forest management and biology on this topic. However, the different fields of research applied this nutrient research to their own fields only. For example, the nutrient status of forests and the effect of clearcutting on future wood production was applied to the production of wood. However, I applied the findings of such research to the field of interest of this paper: food forests. Because food forests are a relatively new topic in Western scientific research, there is not much research done to this topic. Some of the fields that touch upon it are agroforestry and ecology. A lot of research has been done in these fields and I selected those studies that could be applied to the concept of food forests.

Before answering the research question, I investigated the mechanisms that explain natural ecosystem nutrient uptake. The first part of the body of this paper summarises the new insights into nutrient uptake. Especially the biological aspect receives special interest as recent research shows a more prominent role of this component than previously believed.

After reviewing the mechanisms of food forest nutrient uptake, this paper reviews the literature findings on nutrient stocks. One of the biggest problems encountered when reviewing the nutrient stocks of soils, was the shallow measurement depth used in the studies. Both agricultural research, but even forest research often failed to include the deep soil layers (>100 cm), while these layers are of importance for food forests. Therefore, it was quite challenging to find the right data.

After finding several studies which estimated soil nutrient stocks, I summarised the most important ones in the body of this paper to show the range of values reported in literature. With the obtained findings in soil nutrient stocks, calculations could be made on the time needed to exhaust the soil nutrient stock via crop harvesting. Several assumptions needed to be made. These assumptions are described in this paper to inform the reader about the assumptions that led to a certain calculation outcome.

From the summarised nutrient stock studies, I had to choose which ones I would include in the calculations. The arguments underlying these choices are also presented in this paper. After obtaining the results for this calculation, the research question could be answered in the conclusion.

Besides reviewing the literature, I used expert knowledge to push me into the right direction. I interviewed Thom Kuypers from the Soil Biology chair group and Gerwin Koopmans from the Soil Quality chair group at Wageningen University. They gave me insights into the possible explanations for century-old chestnut production in unfertilised systems. These insights were important because they offered new themes/directions to take into account while doing the literature review such as the very low phosphorus content of chestnuts.

So, the combination of expert knowledge and literature review provided me with the answers needed to answer my research question.

Last, this review focuses on food forests and their nutrient stocks and uptake. However, for the simple reason that there has not been done ample research on nutrients in relation to food forests, I had to work with simplified food forest systems. Therefore, this research worked a lot with agroforestry systems and tree crop systems such as the Dehesa system. One could consider these as very simplified food forest systems or even as a blueprint for food forests.

However, it is clear that the power of food forests lies in its diversity and complexity. This characteristic is extremely important and improves disease resistance, production level and even nutrient uptake. The combination of deep- and shallow-rooting trees and shrubs enables a process called resource partitioning in which different soil layers are used by the different plant species. This reduces competition between adjacent trees and improves the total system performance.

So, there is a difference in functioning between the simplified food forest systems used in this review and well-designed complex food forest systems. However, as mentioned earlier, these simplified

systems are the ones that best resemble food forest systems (as can be found in the literature) and are therefore used in this review.

Soil nutrients

Soils provide the basis of plant nutritional requirements. Only leaf deposited nutrients can be taken up above-ground. To understand the key differences between annual and perennial systems, and to answer my research question, it is needed to establish a base knowledge of soils and nutrient uptake. Soils are formed as a result of biological, chemical and physiological weathering and are a mix between rocks, mineral soil (very small rock particles) and organic matter resulting from plants, microbes and animals. Soils differ in their ability to support plant production and can be constrained by many factors like soil moisture content, sand : silt : clay ratio, topsoil thickness, temperature, precipitation, pH and plant-available nutrients.

Sediment type

The three sediment types are sand, silt and clay. The size of the particles is used to separate the three types. Clay particles have the smallest size as they are smaller than 0.002 mm. Silt particles have a size of 0.002-0.05 mm, and sand particles are the largest ones with a size of >0.05 mm [8]. Sand can be grouped even further in categories like 'fine sand' and 'coarse sand' based on their sizes. These three types of particles determine the soil type of a specific place (Fig. 1).

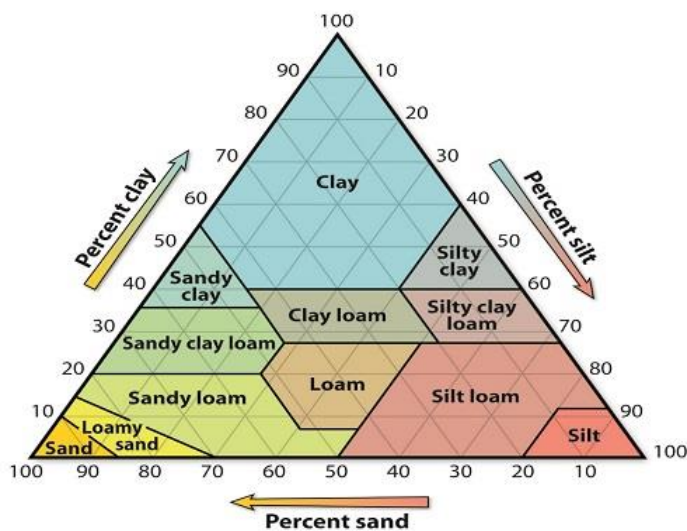


Figure 1. Varying sand, clay and silt percentages determine soil type. From: [8]

Clay soils are characterised by a high clay and low silt percentage and therefore tend to be easily water-logged. The small clay particles hold large volumes of water and therefore, especially in combination with compaction, drain slowly. This is a challenge for farmers, especially during wet springs. They can work the fields with the machines to prepare the soils and plant the seeds, but they risk severe compaction, potentially influencing the production of that soil for years to come. However, if they choose *not* to plant seeds on the wet clay field during a wet year, it will cost them a lot of money and most farmers work with very low margins so they cannot afford to do this too often. Even in relatively dry conditions, plant roots might still have trouble penetrating the heavy clay soils, especially in combination with compaction, and therefore, agriculture on soils high in clay content can be very challenging.

The opposite situation is a soil very high in sand and low in clay particles like loamy sand. Those types of soils are described as 'poor' referring to the restricted nutrient holding capacity, high risk of nutrient leaching and low water holding capacity. Sandy soils drain very quickly, posing the risk of drought to plants growing on these soils. The benefit of the drainage is a low soil compaction potential, and low risk of waterlogged conditions which are detrimental for most agricultural crops.

The summer of 2018 showed the difference in soil types in the Netherlands. The east of the country, characterised by sandy soils on a slight elevation, was plagued with drought. Even forests, with deep-rooting perennials, suffered a lot in this part of the country, whereas the lower western part of the country, with soils higher in clay content suffered less.

Historically, human societies thrived in places where soils contained a large silt content. Agriculture thrived in river deltas where annual river-derived silt replenished fertility year after year. The Nile River Delta in Egypt has been one of the most fertile regions in the world and has been one of the only places where agriculture has been sustained for millennia, mainly due to the yearly fertility replenishment from the river.

Different plants thrive in the different soil types, but for most agricultural (annual) crops, loamy soils are regarded as the best soils, since they have a good proportion of sand, clay and silt, and subsequently have the benefits of the three different particles (like the water holding capacity of clay and the good drainage of sand).

Plant nutrient uptake

Plants take up nutrients from the soil solution. The soil solution is the same as the soil pore water, which is the water that is held by the small particles of soil. Since sand particles are relatively large, sandy soils can hold less water and hold it for only a relatively small period of time, in comparison with clay soils where the small clay particles hold water for much longer. Nutrient uptake can be via mass flow or via diffusion. Mass flow uptake indicates uptake of dissolved nutrients as plants absorb water for transpiration. Diffusion is the movement of nutrients from the soil solution to the root surface via a concentration gradient. This concentration gradient is actively maintained by the plant (so it uses energy) and ensures adequate uptake of nutrients like phosphorus and potassium [9].

Plants need to take up both macro- as well as micronutrients. Macronutrients like nitrogen, potassium and phosphorus are some of the most important ones needed in large quantities because they serve as building blocks for many proteins involved in cellular processes. Micronutrients are needed in much smaller amounts. Iron, zinc and copper are examples of micronutrients and they are often required as cofactors for enzyme activity [10].

Nutrients can be present as cations or anions. Examples of cations are K^+ , Ca^{2+} , Mg^{2+} , NH_4^+ and Fe^{2+} . Because cations are positively charged, they react with negatively charged particles. Negative particles in soils are clay particles and organic matter (OM) (in a certain pH range) and form the substrate of nutrient adsorption to their surfaces. The cation exchange capacity (CEC) is a measure of the amount of nutrients a soil can hold and release into the soil solution. A high CEC usually indicates a high percentage of clay in the soil and a high OM content. A high CEC value indicates a high capacity of the soil to hold cations, which is both beneficial and disadvantageous. It means nutrients will not leach easily, but at the same time, as they are strongly bound to negative particles, the nutrient soil solution concentration might be low and plants might struggle to obtain enough nutrients [11].

A low CEC indicates that fewer nutrients can be held by the soil due to leaching of nutrients to deeper soil layers. This poses a specific risk of nutrient limitations on annual crops because normally do not root deep enough to reach the leached nutrients [11].

Nutrients can be unavailable in sufficient quantities to the plants and therefore limit growth. Plants use several mechanisms to obtain nutrients when they are not available in sufficient quantities.

- Root architecture changes
- Rhizosphere acidification
- Nitrogen-fixing bacteria associations
- Mycorrhizal associations

Root architectural changes, such as root elongation, lateral root growth and root hair elongation enable the plant to meet its nutrient requirements by increasing the absorptive surface area. In very poor soils, root networks tend to be larger than plants grown in rich soils because the plant can sense it is growing in a poor soil and therefore needs to search for nutrients over a larger surface area.

Another way to reach limiting nutrients is by rhizosphere acidification. Iron, for example, typically forms insoluble complexes in soils with a high pH. Therefore, it is not available in the soil pore water and plants cannot take up sufficiently via mass flow or diffusion. Plants can pump protons into the rhizosphere, thereby lowering the pH. This solubilises ferric ions into the soil solution and plants can meet their iron requirement [12]. Under certain conditions, plants use the same trick to solubilise phosphorus from precipitated source [12].

Nitrogen and phosphorus are the two most growth-limiting nutrients for plant productivity in most terrestrial ecosystems. Two principal reasons explain this phenomenon. They are both needed in large quantities as they are major building blocks of several plant tissues. Especially nitrogen is used in large quantities.

The second reason is the low mobility of phosphorus in soils. It tends to react to several mineral surfaces and disappears from the soil solution. Therefore, different plants have evolved mutually beneficial relationships with soil-born micro-organisms which are better equipped in acquiring difficult-to-obtain nutrients. The association of certain plant species (especially from the Fabaceae family) with nitrogen-fixing bacteria, mainly from the genus *Rhizobia*, is a well-known example. Many pioneering species have developed an advantage in colonising recently disturbed sites with low levels of available nitrogen by forming an association with *Rhizobia* bacteria. Root nodulation enables a close contact between bacteria and plant. As N-fixation is an energetically expensive process, the plants supply the bacteria with a carbon source and the bacteria fixes the nitrogen from the atmospheric N₂ which plants cannot take up. The bacteria transform the N₂ in a plant-obtainable form and meet the N requirement of the plant. As nitrogen is the main limiting macronutrient, this is extremely advantageous for plants in early successional soils with low SOM pools and subsequently low available nitrogen stores.

Another mechanism to obtain difficult-to-access nutrients, is the formation of a mycorrhizal symbiosis between plants and fungi. More than 80% of terrestrial plants form a relationship with mycorrhizal fungi and this relationship is >400 million years old and has probably aided in the colonisation of land by the first land plants [13].

There are different types of mycorrhizal relationships but the two most common and important ones are the ectomycorrhizal (EcM) and the arbuscular mycorrhizal fungi (AMF). The difference between the two types is the mechanism in which they colonise the plant roots and the plant species they bond with. The AMF penetrate the cortical cells of the plant roots whereas the EcM forms a sheath around the root cap. They are both important in the acquisition of different nutrients and I will not describe the differences between the two in detail here.

Mycorrhizal fungi play a crucial role in nutrient acquisition and are involved in the uptake of many nutrients, like cesium, copper, zinc, nitrogen, phosphorus and potassium [14].

In boreal as well as many temperate forests, about 80% of the nitrogen and phosphorus content obtained by the trees, is delivered by EcM [15]. In nutrient-poor forest ecosystems, as much as 90% of the nitrogen and phosphorus can be acquired via mycorrhizal fungi and N-fixing bacteria [16]. This suggests the pivotal role that micro-organism-plant interactions play in nutrient acquisition in natural ecosystems.

The fungi have different mechanisms to take up and deliver the nutrients to the plants:

- Organic matter decomposition. Plant residues like roots, leaves and branches can all be degraded by fungi. Plant roots themselves take up inorganic nutrients from the soil solution. However, many nutrients like nitrogen and phosphorus are present in an organic form in this organic matter. Therefore, the plant needs partners which can turn the organic nutrients into inorganic ones. This is where mycorrhizal fungi come in. Mycorrhizal fungi secrete numerous exoenzymes that cause the breakdown of plant material from which the fungus can take up nutrients [17]. Subsequently, the fungi can deliver the nutrients to the plants in the plant-available form in return for carbohydrate exudates [17].
- ‘Rock eating’ ectomycorrhizal fungi making pores in minerals and bedrock. Researchers found tunnels in different rocky materials like feldspar minerals that perfectly matched the width of fungal mycelium, suggesting that ectomycorrhizal fungi make tunnels inside bedrock

and rocky material to weather the material and increase nutrient inputs to the ecosystem [18], [19].

- Increasing the root's absorptive surface. Plants are limited by the depletion zone they created themselves for nutrient uptake. Mycorrhizae can reach beyond these depletion zones and extend the absorptive surface, enhancing nutrient acquisition [14].
- Solubilise adsorbed P (and likely other nutrients as well) that is tightly bound to aluminium-, iron-hydroxides and calcium-phosphate-oxides. Fungi secrete organic acids which can accelerate mineral dissolution [12], [19].

The living soil: plants as master regulators of the soil food web

I briefly presented the basics of soils and nutrient uptake. Many soil scientists traditionally focused on soil chemistry to explain plant production. Over time, they realised that the biologic component of soils plays an important role as well, besides chemical soil reactions. Especially in natural unfertilised systems, biological soil processes are crucial to ensure adequate nutrient availability for plants. Conventional management has, to a certain extent, bypassed this biological component (although not completely). Phrases like ‘the soil is dead’ are not literally true, as agricultural soils are still teeming with bacteria and other organisms.

However, some truth can be found in this statement, as many agricultural soils are out of balance due to the frequent disturbances such as tillage. Natural plant communities largely depend on this natural biological soil component to survive, but due to heavy fertiliser applications agricultural crops reduced their dependency on the biological aspect of soils for their nutrient acquisition. Some call agricultural crops ‘lazy plants’ to stress the dependence on agricultural inputs and the reduction in active participation with the below-ground soil food web to obtain adequate nutrients. Before directly addressing this paper’s research question, I provide an overview of the importance of the living soil to illustrate the potential role that the biology can play in feeding the plants, both in annual agriculture as well as perennial (food forest) systems.

The soil is a very vibrant ecosystem with large numbers of micro-organisms per unit of soil, especially in the rhizosphere. Many people tend to think that plants work by themselves, for example when taking up nutrients with their roots. Decades of investigation of the below-soil interactions with fungi, bacteria, nematodes, protozoa and many other animals resulted in an increased recognition of the importance of the living soil (as a collective name for all the biotic actors in the soil) in plant production. I will present here how plants in natural situations obtain their nutrients with the help of the soil food web.

Plants are in control of the soil food web. They produce carbohydrates via photosynthesis and secrete exudates via the roots into the rhizosphere. How much of the total photosynthesised assimilation products are given away as exudates differs between different plant species and different environmental conditions. In general, estimates range that most perennial trees allocate at least 20% of the assimilates to mycorrhizal fungi (so ignoring other soil food web exudates) and several species are known to allocate 50% or even more to mycorrhizal fungi [15],[20]. Plants produce a wide array of exudates. They can be mixtures of organic acid anions, phytosiderophores, sugars, vitamins, amino acids, purines, nucleosides, inorganic ions (e.g. HCO_3^- , OH^- , H^+) gaseous molecules (CO_2 , H_2), enzymes and root border cells [12]. These exudates are goal-oriented and attract the right micro-organisms needed to carry out the job. Why does the plant provide so much of its energy to the rhizosphere? If it could use this energy for photosynthesis, it would be able to invest more in reproduction, thereby increasing its fitness.

The reason why plants do this, is that plants have a higher survival and fitness when they use micro-organisms living in the rhizosphere (in natural situations). Micro-organisms can reach nutrients and water much better than plant roots can because they produce a wide array of exoenzymes, organic acids and chelates that are capable of dissolving nutrients and converting and weathering minerals. Most ground-dwelling micro-organisms, though not all, are energy-limited which explains the importance of carbohydrate plant exudates [12].

By providing exudates, the plant enables bacteria and fungi to thrive. These organisms then mineralise organic nutrients from organic matter, take up minerals from primary nutrients like apatite by weathering minerals and increase solubility of nutrients [12]. However, bacteria and fungi (except mycorrhizal fungi) do not *just* give some of their nutrients to the plant. Like in above-ground food webs, predators are needed to control the prey populations and to feed the plant again. Nematodes and protozoa are two of the most important groups of animals feeding on bacteria and fungi. After digesting them, some of the nutrients are released again (via the faeces) because no animal can achieve 100% nutrient uptake efficiency. The nematode and protozoa faeces contain all the nutrients

needed by the plant and since the plants attracted the bacteria and fungi close to its roots (the rhizosphere), the nutrient release takes place close to the plant roots as well. Close enough for the plants to take the minerals up. The nematodes and protozoa are at their turn controlled by larger organisms like worms and mites [21].

This food web is crucially important for plants *in natural situations* where inorganic nutrients are not available in sufficiently large quantities for plants to thrive. However, in annual conventional agricultural systems, due to heavy inorganic fertiliser application, soil disturbance and pesticide use, plants allocate less energy to feeding the soil food web [12]. This can be explained by the fact that the plant is not limited in macronutrients such as nitrogen, phosphorus and potassium anymore due to the fertilisation. Under natural circumstances, however, plants *need* this soil food web to take up adequate nutrients to sustain productivity. This plant-exudate-micro-organism-faunal grazer pathway is called ‘the liquid carbon pathway’ by some researchers indicating that carbon molecules flow in a liquid form (as exudates) from the plant to the soil. It is in fact a crucial pathway, but tends to be underestimated by many scientific researchers. Its main functions are:

- soil structure by creating stable soil aggregates
- increasing stable humus molecules and storing carbon
- obtaining necessary nutrients
- maintain a healthy balance of soil organisms

Creating soil aggregates

Soil aggregates exist in two forms: micro- and macroaggregates with the latter simply being several microaggregates glued together. Aggregates consist of clay particles and organic matter glued together by organic sugars like polysaccharides and have pores between them [22]. These soil aggregates therefore, can hold a lot of water in its pores and provide a favourable environment for many micro-organisms and plant roots to grow. The formation of aggregates occurs via different pathways. The most important one is the liquid carbon pathway. As plants excrete exudates into the rhizosphere, bacteria and fungi will consume them and secrete substances like polysaccharides that glue soil particles together into aggregates. A range of biological activity occurs in aggregates. Free-living nitrogen fixing bacteria and archaea, a larger group than previously believed, settle in these aggregates and contribute to plant nitrogen requirements. The problem with conventional annual agriculture is the fertiliser application and the tillage. Due to the abundance of inorganic nitrogen and phosphate, plants reduce the liquid carbon pathway activity thereby strongly reducing the aggregate-forming rate. This results in a lack of free-living N-fixing bacteria, mycorrhizae and other useful food web components, making the plant dependent on the fertiliser, ending up in a vicious cycle [15].

Increasing humus content and soil organic carbon

In natural ecosystems, plants often allocate 20% or more of their assimilates to the soil food web via exudates [15]. This is a significant proportion and is critical in building up soil organic carbon levels during succession. The only reason that the Earth has a thick topsoil layer supporting vigorous growth is because years of growth and soil organic carbon inputs to the soil have steadily increased soil organic carbon levels. Bare rock can hardly support plant life to flourish, but over time, with enough input of organic matter, enough precipitation, the formation of a topsoil layer is initiated. Fertility will increase, supporting even more plants to grow and to produce even more biomass. At the end, soil organic matter decomposition will equal soil carbon inputs and a steady state will be reached. This is how all the productive ecosystems in the world were built. Instead of seeing the Earth as an entropic system, one could argue that it resembles more a syntropic system; the sun’s energy in combination with the photosynthetic activity of plants results in a build-up of life and energy in the ecosystem as soils are fuelled by the liquid carbon pathway, soil organic matter levels are increased, nutrient mineralisation is increased as a result of the increased soil organic matter decomposition, and biomass production is increased [23].

The soil liquid carbon pathway plays a crucial role in increasing soil organic carbon content. Organic matter addition on top of the soil can increase the SOC content of the top 30 cm, but these additions do not result in significant subsoil organic matter increases, while subsoil carbon tends to be decomposed much more slowly, hence, contributing to a stable organic matter pool. As described

earlier, exudates will be used to produce microbial biomass in the soil. As this biomass turns over, some of the carbon contained by this pool is transformed into stable, difficult to break down, humus molecules. One could see this below-ground microbial population, living on plant exudates, as an extension of the biomass of the plant. So, as a below-ground equivalent to the above-ground leaves for example. When the leaves fall in autumn, they contribute to the high topsoil OM levels of most forests. The same is true when the below-ground microbe-pool turns over; it will increase the subsoil OM pool and contribute to increased soil fertility in the next years.

Again, just like the reduced aggregate formation in conventionally managed annual agricultural systems, subsoil humus build-up is largely non-existent. Most of these systems see a decrease in total soil organic carbon until a new, very low equilibrium is reached. When native forests are turned into arable fields, SOC decreases on average with 42% [24].

Obtaining nutrients

Many nutrients occur in plant-unavailable forms. Phosphorus, for example, is highly reactive in the soil and as soon as there is any free phosphorus in the soil, it becomes fixed to another element like iron, calcium or aluminium, making it unavailable to plants. Plants have trouble obtaining this nutrient, but there is a wide range of micro-organisms capable of dissolving and mineralising inorganic and organic phosphorus by excreting certain enzymes like phosphatase that can break the bond with other minerals and release the phosphorus again into the soil solution [25].

Soil phosphorus can occur in both organic and inorganic forms. Plants can obtain phosphate, which is the main inorganic form of P. However, only a fraction of the total phosphate stock can be obtained by plants (labile phosphate) because most of the labile phosphate gets rapidly fixed in occluded forms unavailable to plants such as Ca-, Al- and Fe-phosphates [25].

To reach the insoluble phosphate pool, plants make use of the solubilising power of micro-organisms. A large number of soil bacteria, from the genera *Pseudomonas*, *Enterobacter*, *Bacillus penicillium*, *Aspergillus* as well as many soil fungi, are able to solubilise insoluble phosphate from Al-, Ca- and Fe-phosphate complexes and, hence, increase the plant available inorganic phosphate pool [12]. The mechanism involved in the microbial solubilisation of P is the production of organic acids and the release of protons to the soil solution [12].

This mechanism is intriguing as it might offer a way for plants to reach P pools that most agronomists consider inaccessible (mainly P-Al or P-Fe complexes). Inoculations with the right micro-organisms to liberate those P pools might become a standard practice in future agricultural systems to enhance the phosphorus uptake.

Furthermore, bacteria and fungi can release protons to decrease the soil pH. At slightly acidic pH, phosphate availability is highest and at higher pH it precipitates with Ca minerals, while at lower pH it precipitates with Al and Fe minerals, making it unavailable to plants [26]. Plants can decrease the pH themselves as well by dumping protons in the rhizosphere [12].

Plants cannot obtain nutrients from organic matter directly (except some amino acids). They need the work of bacteria, fungi and faunal grazers to mineralise the nutrients contained by, for example, fallen leaves. In natural ecosystems, most of the nutrients are bound in organic molecules and are largely unavailable for plants. However, recent evidence shows that plants can take up amino acids such as glycine directly from organic matter decomposition, by-passing the microbial mineralisation processes [27]. Still, plants need the machinery of microbes to mineralise most nutrients since microorganisms can depolymerize and mineralise the organic forms of nutrients like N, P and S. As described earlier, the content of the microbial cells is released through protozoic predation or cell turnover. This process liberates inorganic P, N and S forms into the soil solution. These nutrient forms can be taken up by the plants again and this process is of crucial importance in natural systems to provide the plants with the nutrients they need [28].

Mycorrhizae are well-known to be involved in the translocation of P to the host plants and can be considered a 'biofertiliser'. They can obtain P from organic matter and transfer it to the plant.

Furthermore, ectomycorrhizal fungi can exude organic anions like oxalate and citrate, which can even weather feldspar minerals thereby providing the plant with phosphate that it would not have been able to obtain itself [29]. Feldspar minerals are one of the most common minerals on Earth and many rocks

contain a high percentage feldspar. They are an important nutrient pool. For example, about 90% of potassium in soils exists in the structure of primary minerals. Other nutrients like Ca, Na, Si, Cu and Mn are also present in feldspars [29].

It is worth noting that this discovery of mycelium tunnels inside mineral grains means that ectomycorrhizal fungi can provide an input of nutrients like P into the soil by mining the rocks and bedrock layer deep into the soil and it is very likely that ectomycorrhizal fungi would thereby contribute to ecosystem influx of nutrients and the formation of soil formation [18]. I will describe the consequence of this action to food forests later in this paper.

There is also evidence that micro-organisms solubilise nutrients like potassium from minerals and even from potassium-bearing rocks. This can be achieved by a range of different mechanisms including acidolysis, chelation, and the production of different substances like oxalate, lactate, citrate and gluconate [30].

Micro-organisms living further away of the plant are equally important in nutrient acquisition. Organic matter is the fuel that feeds the microbes and enables them to decompose the dead organic matter. As bacterial and fungal populations increase, predators come in and control their populations. They excrete some of the consumed biomass and this contains nutrients in inorganic forms, ready to be taken up by the plants again. This process is called mineralisation. First the bacteria and fungi immobilise the nutrients meaning they decompose the organic matter and ingest the nutrients held by it, making it unavailable for the plants. Then, as the predators feed on the bacteria and fungi, some of the minerals are liberated again into the soil solution, and become potentially obtainable for plant roots.

Those two processes (mineralisation and immobilisation) are crucially important, especially the balance between the two. When immobilisation occurs at a high rate, it can pull nutrients out of the soil pore water leading to nutrient unavailability for plants. This situation occurs for example when nitrogen-poor, carbon-rich material is buried into the soil. When sawdust is worked into the soil, microbes decomposing the material need a nitrogen source to do this. They will extract nitrogen from the soil solution, reducing the amount available for plants. After a while, predators eat the bacteria and fungi and the nitrogen gets released again, restoring the nitrogen situation and enabling plant growth again. However, timing is very important here. The immobilisation phase cannot occur during stages of fast vegetative plant growth, otherwise plant growth will be severely reduced.

In forests, immobilisation and subsequent mineralisation explain why after thousands of years of leaf fall, litter layers higher than trees are never observed.

Critically important for an adequate delivery of nutrients is the presence of the different groups of organisms in the correct ratio. For example, Alaskan forests grow very slow and litter layers can be quite extensive compared to forests at lower latitudes [21]. The principal reason for this (except temperature and light differences) is the lack of large shredding organisms [21]. Shredding organisms are crucial as they transfer organic materials deeper into the soil. Also, they break down large surfaces into smaller particles, increasing the surface area and speeding up decomposition by bacteria and fungi. Earthworms, other worms, and millipedes are some of the larger shredding organisms occurring in many forests around the world. In coniferous Alaskan forests, however, no macroshredders are present at all. Only springtails and small mites are responsible for the shredding of the organic matter. As a consequence, decomposition is very slow and nutrient immobilisation dominates the nutrient flows resulting in very slow growth rates [21].

The ratio bacteria : fungi is important as well and determines which plant species will easily grow on a specific soil. This is explained by the different forms of nitrogen, nitrate and ammonium, that the bacteria and the fungi, respectively, prefer. Fungal-dominated soils occur under woody vegetation, like forests, while bacteria-dominated soils occur in sites with a lot of disturbance. Agricultural, tilled soils have high bacteria : fungus ratios due to low fungal abundance resulting from the annual mycelium-damaging tillage.

Furthermore, the presence of nematodes and protozoa as the principal predators of the bacteria and fungi, needs to be balanced as well. There are many types of nematodes such as bacterial-feeding, fungal-feeding, nematode-feeding and plant-root-feeding. If the bacterial-feeding nematodes are (virtually) absent in a certain soil, bacterial overgrowth could occur. This entails that mineralisation is

reduced because the bacteria accumulate many nutrients in their cells and the population can grow exponentially. Plants would suffer from (temporary) nutrient deficiencies and growth would be reduced.

In an experiment, researchers compared the plant growth on different media containing no micro-organisms, only bacteria or fungi and bacteria, fungi, bacteria-feeding nematodes and fungus-feeding nematodes. With the presence of the faunal grazers, the plant biomass was significantly increased compared to the absence of faunal grazers. This was due to the increased mineralisation rate of nitrogen. Without faunal grazers, plants could take up only the limited available N while little or no N was mineralised. However, with the addition of the nematodes, more N was mineralised than the plants could take up, even though these plants grew faster [31].

Conclusions:

- Plants use many different strategies to obtain the nutrients they need. Plant roots themselves show different mechanisms to obtain rare nutrients like lateral root growth, root hair elongation and rhizosphere acidification.
- However, in natural unfertilised ecosystems, plants alone cannot obtain sufficient nutrients to promote their growth. Therefore, they use micro-organisms by allocating a significant proportion of their photosynthetic assimilates to the rhizosphere in the form of exudates.
- Mycorrhizal fungi are some of the most widely distributed organisms enabling plants to obtain the nutrients they need. As much as 80% of the P requirements are met by the mycorrhizal delivery of P [15]. Furthermore, other nutrients like zinc, copper, magnesium and nitrogen are delivered to the plant by the mycorrhizal fungi in exchange for carbon-rich material [15].
- Besides mycorrhizal fungi, bacteria are also key in providing the plant with nutrition. Bacteria ingest nutrients and after predation by protozoa and nematodes, some of the nutrients are released again in a plant-available form. The recycling of nutrients in organic matter is controlled by the processes of immobilisation and mineralisation performed by micro-organisms and faunal grazers/shredding organisms, respectively.
- Due to the extensive machinery of many micro-organisms, precipitated nutrients can be dissolved, mineral grains can be weathered and solution-dissolution reactions equilibria can be favourably changed. This can increase the plant nutrient uptake rate and, hence, sustain production.
- The liquid carbon pathway is crucial in maintaining a biologically active soil by increasing soil aggregation, microbial activity, soil carbon sequestration in deep soil layers and by preventing harmful organisms to take over. In conventionally managed annual cropping systems, this liquid carbon pathway is inhibited and soil biology tends to be out of balance. This might make the plants more dependent on nutrient additions via fertilisers and reduces the soil carbon content of the soil.

Nutrient flows in forest systems

The key difference between natural forest ecosystems and food forest systems is that the former is a more or less closed system while the latter is not. Considering nutrient flows in natural forests, plants obtain nutrients from the soil and allocate them to their branches, leaves and reproductive organs. When these components die, the nutrients are recycled via the micro-organisms as described earlier. However, when animals eat the fruits or nuts of a tree, and move to another place, they take the nutrients with them away. The direct environment of the tree where the animals just ate the fruits becomes nutrient-poorer. However, due to the animal faeces and the eventual death of the animal, the nutrients get released again via decomposition by microbes. For the forest as an entity, few nutrients exit the forest via the described pathway and the nutrients that are deposited somewhere in the forest, are redistributed again via the mycorrhizal fungi to the plants in low supply. Therefore, forests can be considered as relatively closed systems.

However, food forests are not closed systems. Just like annual agricultural systems, harvests result in nutrient outputs and over time, soil nutrient levels will be reduced if not replenished.

The question is, are the nutrient inputs to *unfertilised* food forests the same as for conventional annual unfertilised agricultural systems or are other mechanisms involved resulting in greater nutrient inputs to food forest systems? I just described the countless mechanisms that have been shown to increase nutrient availability in natural relatively undisturbed ecosystems, largely resulting from below-ground interactions. What is the impact of all these processes on nitrogen and phosphorus availability in food forests?

Just like in human nutrition, it is not what you eat, but what you *absorb*. This is also true for agricultural systems. As I will show later, total phosphorus and nitrogen pools are relatively large, however, annual crops still need to receive annual nutrient additions via fertilisation to sustain high crop production. In those conventional annual systems, nutrient *availability* is not sufficient to support high crop production without fertilisation inputs. The question is if this same way of reasoning holds for food forests as well. Since several below-ground mechanisms exist and contribute up to 80 or even 90% of forest N and P acquisition [15], (food) forests might have higher natural N and P availability than disturbed annual systems. To find out what role all these processes might play, I reviewed all the different inputs and outputs for (food) forest systems.

Nitrogen is a macronutrient that is exceptionally important in plant production. Globally, nitrogen limits natural ecosystem productivity in almost all ecosystems, including forests. As described earlier, especially young soils have relatively low nitrogen stocks (due to the long time needed to fix a significant amount of nitrogen from the atmosphere) and nitrogen fertilisation does increase forest growth [32].

Most nitrogen in forest systems is contained in soil organic matter. On average, 5.8% of SOM consists of nitrogen and about 58% of carbon. Therefore, annual SOM mineralisation is the main nitrogen source for trees with one ha of beech forest taking up >100 kg N each year from this mineralisation process [33].

Therefore, soil food web mediated reactions are key to the nitrogen supply of natural forest systems. The global nitrogen cycle is determined by many different processes like nitrification, denitrification, volatilisation, atmospheric deposition and N-fixation (both by men via Haber-Bosch process and (free-living) nitrogen-fixing organisms).

As mentioned before, N fertilisation generally increases plant productivity in temperate forest ecosystems. The fact that a natural forest responds to N fertilisation, despite being undisturbed, suggests that natural soil fertility is not enough to produce highest possible biomass. All described mechanisms contained by the soil food web as well as perennials themselves would likely be active in natural undisturbed forests. Therefore, the positive response of forests on fertilisation suggests that these soil biology processes do not provide *enough nutrients* to reach maximum possible biomass production.

The question is whether this finding in natural forests can be used for carefully designed food forest systems. Most food forest systems have been designed to include a certain percentage of nitrogen-

fixing plants, which might alter the situation as their annual nitrogen inputs might be sufficient to prevent N-limitation (and subsequent suboptimal biomass production) in the system. Furthermore, there are several examples of agroforestry systems that do not respond to N-fertilisation, which I will show later. First, to understand the flows of nitrogen and phosphorus in (food) forest systems, I will provide an overview of all these flows. This knowledge is critically important to evaluate the impact of harvesting (in food forests) on nitrogen and phosphorus availability and supplies.

The inputs and outputs applying to nitrogen are:

- Atmospheric deposition
- Migrating animals
- Rock weathering
- N fixation

- Leaching
- Erosion
- Gaseous emissions

Phosphorus is another macronutrient critically important to sustain high production levels. It is highly reactive in soils where it precipitates and, hence, becomes unavailable for plants to take up. Plants can take up the ionic forms H_2PO_4^- and HPO_4^{2-} directly from the soil solution. The problem is that the soil solution contains only very small concentrations of these ionic forms. Most soils contain less than 0.00005 g P per litre. Therefore, just to ensure normal crop growth, the phosphorus in the soil solution must be replenished on average about twice a day [34].

Several mechanisms mentioned earlier in this paper like rhizosphere acidification and mycorrhizal symbiosis are important to increase P uptake from soil solution in natural forest ecosystems. Besides ionic P in soil solution, P can occur in non-labile and labile forms. Non-labile phosphorus is a strongly bound form, while labile phosphorus is weakly adsorbed or bound to various compounds and clay in soils (the soil solid phase). This non-labile source is the primary phosphorus source that supplies P to the soil solution [26].

Several factors affect the equilibrium reaction between labile and non-labile P and, hence, determine the potentially available P in soil solution. The most important factor is pH of the soil solution. At high pH, most phosphorus is bound to calcium compounds making most P unavailable for plant uptake. At acidic pH values, phosphorus is fixed to hydrous oxides of iron and aluminium making most P unavailable to plants. This situation is frequently observed in mature oak forests on sandy 'poor' soils in the Netherlands. These soils are vulnerable to acidification as a consequence of acidic rain containing nitrogen molecules. At a certain point, low P availability can become damaging to the trees and pose a threat to their health and functioning. Maximum P availability occurs at a soil pH between 6.5 and 7 [26].

Food forests, however, could slightly acidify former agricultural soils due to the litter decomposition of certain species. A study on different plant species planted on the same acidic soil found interesting results. Coniferous plants had no further effect on the low soil pH, but most deciduous species actually increased pH. Especially maple (*Acer* spp) and lime (*Tilia* spp.) trees had a profound effect on soil pH, increasing it steadily. The main explanatory variable was the calcium content of the leaves. Lime leaves are known for their relatively high calcium content, fast decomposition and fertility enhancing effect. Conifer leaves are low in calcium and tend to acidify the soil. Especially on 'poor' soil sites, it would be worth investing in species known for their pH increasing effects like lime [35].

As mentioned earlier, a large group of soil bacteria and (mycorrhizal) fungi can solubilise these insoluble phosphates from Al-, Ca- and Fe-phosphate complexes and increase ionic soil solution concentrations [12]. These soil food web interactions are crucially important in natural ecosystems where soil solution ionic concentrations are not artificially elevated with fertiliser applications. Also for food forest systems, those microbial-mediated processes are likely a major source of nutrient provision.

Furthermore, minerals like apatite or feldspar provide phosphorus to the system via weathering. As mentioned earlier, ectomycorrhizal tunnelling in these mineral grains was observed suggesting that (under P limiting conditions), mycorrhizal weathering can increase plant P supply [18].

New phosphorus inputs to the soil only occur via rock weathering. Most bedrocks contain large phosphorus stocks and can support plant production for millions of years (coupled with efficient recycling as occurs in natural ecosystems). There is no atmospheric P-fixation pathway, as there is for nitrogen. Only tiny amounts of P can enter the system via atmospheric deposition (of sand particles for example). Therefore, the inputs and outputs applying to phosphorus are:

- Atmospheric deposition
- Migrating animals
- Rock weathering

- Leaching
- Erosion

I will now describe these inputs and outputs mechanisms in more detail.

Atmospheric deposition

Atmospheric deposition occurs via fine sediment or via wet deposition. Dry and wet deposition of N molecules has been very high in densely-populated areas such as north-western Europe over the last decades. Despite initial reductions in deposition rates due to stronger regulation and the adoption of car catalysts, the reduction has halted over the last few years but the deposition rates remain high. The average N deposition in Flanders, Belgium in 2016 was 23.4 kg N per ha, strongly passing the considered safe upper limit of N deposition for natural ecosystems [36].

In Europe there is a large variation in atmospheric N deposition, ranging from almost no to about 25 kg N per ha per year (with some regions even exceeding 25 kg) [37]. There are several consequences of this deposition for natural forests.

First, it is clear that biomass productivity in most forests in temperate climates is limited by nitrogen availability. One study looking at the feldspar rock weathering effect of mycorrhizal fungi in a forest in Sweden, looked at a fertility gradient with a slope. The upper part of the gradient consisted of small bush vegetation and the lower part consisted of trees mixed with a rich understory vegetation. Plant production and foliar nitrogen concentrations increase gradually going downslope in the gradient, probably resulting of the downslope leaching of nitrate and subsequently limiting nitrogen availability at elevated positions [38]. The study found that (mycorrhizal) feldspar weathering was increased higher up the slope compared to the lower end of the gradient as indicated by an increase in tunnels within the feldspar minerals. The authors explain this by the fact that under N-limiting conditions it makes sense that plants and fungi invest more energy in dissolving mineral N from feldspar rocks to overcome the deficiency.

Nevertheless, it shows that nitrogen is an important limiting factor in plant productivity in natural forests [38]. A large review article of ecosystems around the world, concluded that nitrogen limited net primary productivity (NPP) of temperate forests, tropical forests, temperate grasslands tropical grasslands, wetlands, and tundra [39].

This nitrogen limitation under natural forests has important consequences for food forests and I will later describe several mechanisms to potentially overcome this N limitation.

Second, the high atmospheric nitrogen levels probably resulted in the increased European forest growth observed over the past decades. However, increased nitrogen deposits have had serious negative implications for the composition of forests. Biodiversity declines strongly when high nitrogen availability occurs [40]. Plant species specialised at growing in situations of high nitrogen availability outcompete slow-growing species thriving in low-nitrogen environments.

Furthermore, acidification of soils has major implications for other nutrient availabilities like calcium, as noticed by decreased bird fecundity in sandy soils like the Veluwe area in Holland [41].

Groundwater pollution is another drawback of the atmospheric deposition [40].

Phosphorus, in contrast to nitrogen, does not enter the system in large quantities via atmospheric deposition. Atmospheric deposition of P across the United States averages 0.77 kg of P per ha per year [42]. Compared to the nitrogen inputs this may seem like a low value. However, since phosphorus requirements are lower than nitrogen requirements, this input value might still play an important role. Especially in highly weathered, very old soils, as can be found on some of the Hawaiian Islands, atmospheric P inputs might well be an important factor in maintaining site productivity. Land-derived phosphorus originating from central Asia, 6 000 km away, has played an important role in sustaining plant productivity in some of the oldest Hawaiian Islands. By wind, fine sand particles containing phosphorus, crossed the Pacific Ocean and ended up in Hawaii, ensuring sustained productivity even in old highly weathered soils [32].

Migrating animals

Most animal species live in a certain habitat, for example a forest, and tend to stay in this habitat because they can only thrive there. Some species, however, switch habitats from time to time, and can enter and leave a forest ecosystem. Examples are migratory birds and fish.

Some islands in the Pacific have accumulated considerable deposits of guano, bird faeces, from sea-fishing birds. After decades of birds nesting on these islands, a thick white layer accumulated on the island's rocks. This guano layer is rich in phosphate and was collected by humans to be used as a fertiliser in agriculture.

In a similar manner, forests can accumulate nutrients from bird castings from migratory birds. Bird castings can be an input of nutrients like N and P from outside a (food) forest system. Anecdotal evidence from Mark Shepard (pioneering agroforestry farmer in Wisconsin), shows that planting a food forest-like system in the middle of a conventionally managed annual agricultural system region can attract vast numbers of birds up to the level that he cannot sleep properly in certain periods of the year as a consequence of the noise made by the birds. Researchers found that parks in Japan received annual N inputs of 0.4-3.5 kg N per ha and annual P inputs of 0.07-0.5 kg of P per ha [43].

Food forest systems surrounded by conventional agriculture could well receive these inputs as they attract birds from far away. Like Shepard's agroforestry site, food forest de Ketelbroek acts as a magnet for birds. Many birds hunt outside the food forest, hence, translocating nutrients from outside the food forest into the system when they return to their nest/roosting sites. Therefore, food forest systems surrounded by conventional agricultural habitat likely receive significant phosphorus and nitrogen inputs via bird droppings.

Besides birds providing nutrient inputs to (food) forest systems, salmon migration is another important and even larger input. Salmon spend some time (ranging from several months to years depending on species) in the ocean and then return to the creeks where they were born. After having accumulated nutrients in their body in the ocean, salmon return to their birthplace and after they mated, they die. The creeks used by the salmon cross temperate forests and the forest ecosystem depends on this salmon run. Grizzly bears, black bears and other animals eat copious quantities of salmon to gain fat mass to get through the winter months. Due to the abundance in salmon, bears tend to eat the fish only partially, and dump the remaining carcasses alongside the river.

These carcasses are eventually decomposed and nutrients are taken up by the tree roots, mediated by mycorrhizal transport. The contribution of this bear-mediated ocean nutrition can be eminent to meeting the annual nitrogen requirements of the trees. One study found that bear-induced nitrogen accumulation alongside a 2.3 km long creek ranged between 10 and 150 kg N per year [44].

Another study found that adjacent to the main salmon spawning area, where salmon carcass densities were highest, significantly higher annual tree growth was observed [45].

Other studies on the annual growth of Alaska Sitka spruce (based on basal area) that grew adjacent to salmon streams, found that these trees grew at *more than three times the rate* of trees at reference sites above waterfalls of unknown distance from the salmon spawning areas and that the salmon-derived nitrogen formed on average 23% of the foliar N in these trees [46].

These findings provide a critical understanding of the role of nitrogen to natural forests and food forests. They show that nitrogen additions via migrating fish can indeed increase the tree growth rate.

This implies that food forests (except in regions with very high levels of atmospheric deposition like Holland) will probably be limited in their biomass production due to nitrogen shortage. Certain strategies (like including nitrogen-fixing trees) exist to overcome this issue without needing to import fertilisers from outside the food forest system and I will cover these strategies later in this paper.

Rock weathering

Soils are built by the weathering of rock over time. Rocks fall apart in smaller particles eventually resulting in sand, clay or silt particles and secondary minerals. The wide variety of rocks determines the particular texture of a soil. Weathering is thought to be an extremely slow process. Some harder rocks, can take over 500 years to form one centimetre of soil [47]. However, some periods of time were characterised by fast breakdown of rocks, most notably the last Ice Age, in which large amounts of rocks were broken down which speeded up the process of soil formation [47]. There are three types of weathering: chemical, physical and biological.

- Physical weathering is the influence of abiotic processes such as freezing and thawing, wetting and drying on rocks, leading to breakdown into finer particles.
- Chemical weathering is the breakdown of rocks via chemical processes such as dissolution and acidification.
- Biological weathering is the effect of living organisms on the breakdown of rocks. Several mechanisms like root carbon respiration can lead to the formation of carbonic acid which can chemically attack rocks and turn them into soil. Other examples of organic weathering are mycorrhizal and bacterial degradation of rocks to dissolve nutrients contained by them via several mechanisms like acidification, exoenzyme release and chelation [47]. Living organisms are key in speeding up soil formation. When primary succession started with bare rocks, the first colonisers of these rocks tended to be lichens. They started the biological weathering cycle of the rocks which was continued through mosses and later on through the roots of grasses and/or trees. Via acidification of the root environment and through penetration of cracks in the rocks, biological processes increased soil formation and slowly but steadily built topsoil.

The rate of weathering is hard to measure because rock minerals cannot be isotopically labelled. Therefore, nutrient balance studies generally allocate the difference between all the inputs and outputs to weathering. Nitrogen ecosystem inputs have traditionally been explained by nitrogen-fixing microorganisms. Therefore, young soils and ecosystems are often low in nitrogen due to the long time required for microorganisms to fix a significant amount of nitrogen [48]. However, new insights raise the possibility that nitrogen inputs via rock weathering may be an overlooked but significant source of nitrogen input to terrestrial ecosystems underlain by N-rich substrates. Globally, sedimentary rocks contain about 10^{21} g of fixed nitrogen, which is more than the 10^{19} g of nitrogen in the total biosphere [49]. Interestingly, this rock-contained nitrogen originally derived from the burial of organic matter (millions of years ago) in marine sediments, where it became incorporated into rocks as organic nitrogen or as ammonium in silicate minerals [49]. New research points out that up to 26% of the nitrogen in ecosystems is sourced from rocks [50]. These findings mean that textbooks must be rewritten to include the new information [48], [50].

Due to differences in rock properties and the huge variety of rocks, sedimentary rocks contain between 200 and 1 200 mg N per kg [49]. Morford and Houlton and Dahlgren (2011) compared the forest growth characteristics of two different sites, one site underlain with Mica schist rocks high in N (682.5 mg N per kg, from here on called HIGH) and one site underlain with Diorite-gabbro rocks low in N (55.6 Mg N per kg, from here on called LOW).

The HIGH conifer tree needles contained 50% more N per needle than the conifers on LOW. Conifer needle biomass was about 70% higher on HIGH compared to LOW, suggesting major biomass gains on sites underlain by N-rich rocks. The researchers concluded that at sites underlain by high-N rocks, 30-100% of ecosystem N inputs can be contributed to rock N sources, which is comparable to uplift models and weathering experiments showing critical contributions of rock weathering to ecosystem N

pools. They concluded that rock weathering inputs at sites underlain by N-rich Mica-schist, ranges between 3 and 10.9 kg per ha per year via weathering [49].

The total nitrogen content of bedrock can be substantial. I calculated the nitrogen content of a metre-deep bedrock layer consisting of Diorite-gabbro and Mica-schist, like in the aforementioned study. The results show that nitrogen-rich bedrock (Mica-Schist) is a large reservoir of nitrogen, while nitrogen-poor bedrock has only a relatively small contribution to total ecosystem nitrogen stocks (Box 1).

Box 1. Nitrogen content of two types of bedrock

I calculated the total N pool of a metre deep layer of both bedrocks by using bulk density value of 2.7 g/cm³ for Mica-schist and 2.9 g/cm³ for Diorite-gabbro [51].

1 ha containing a 1 metre potentially accessible Mica-schist bedrock layer contains: 10 000 m³*2700 kg/m³=27 000 000 kg rock. 682 mg N per kg rock* 27 000 000/1 000 000 = 18 414 kg N.

1 ha containing a 1 metre potentially accessible Diorite-gabbro layer contains: 10 000 m³ * 2900 kg/m³ = 29 000 000 kg rock. 55 mg N per kg rock * 29 000 000 / 1 000 000= 1 595 kg N.

Rocks are the major input of phosphate for natural ecosystems as phosphorus cannot be fixated from the atmosphere. As described earlier, rock weathering rates are hard to measure, and as the research on N-containing rocks shows, inputs could well be higher than previously believed. Research performed in 1995, estimated annual P inputs in temperate ecosystems of 0.05 to 5 kg per ha, while stating that 5 kg would already be quite a high value [52]. Back then, biological soil processes received significantly less attention than the last ten years, hence, I expect even higher P weathering rates could be possible given the recently discovered mineral weathering mechanisms.

Nitrogen fixation

Nitrogen cannot be taken up directly by plants from the air, even though atmospheric N₂ concentrations are relatively high. Most plants take up NH₄⁺ (ammonium) and NO₃⁻ (nitrate) from the soil solution (although direct amino acid uptake has been reported [27]) and are therefore dependent on other organisms to increase ecosystem nitrogen content, especially in young ecosystems/soils. Several organisms can increase nitrogen content of forest ecosystems, among which nitrogen-fixing plants and free-living nitrogen fixing micro-organisms are the most important ones. Many plants belonging to subfamilies of the large Fabaceae family such as the Papilionoideae, Mimosoideae and Caesalpinioideae can associate with Rhizobia bacteria resulting in nitrogen fixation. Other species that do not belong to these subfamilies like Alder trees are also able to form a symbiotic relationship with Frankia alni, an actinomycete N-fixing bacteria. N-fixing plants form symbiotic relationships with N-fixing mutualistic bacteria and provide energy to the bacteria in the form of carbohydrates. The N-fixing process is an energetically expensive process and that is why plants allocate part of their assimilates to N-fixing symbionts who are energy-restricted. These relationships can increase soil nitrogen content very quickly; one hectare of alder trees can accumulate up to 780 kg of N in 5 years with conservative estimates [53].

As I will show later in this article, food forests can compensate for the nitrogen output from harvesting by including a certain proportion of nitrogen-fixing species like alder.

The second important group of N-fixators are the free-living nitrogen fixating bacteria and archaea. Many of the free-living N-fixating species require soil organic matter as an energy source (in contrast to living plants in the symbiotic N-fixator relations) to fuel the energy-expensive N-fixation process. Therefore, biologically balanced, aggregated soils are crucial in hosting these useful micro-organisms. A practical example to illustrate the importance of this group of micro-organisms comes from experiments performed on mango orchards in India. Researchers found a significant positive relation between fruit yield and *Azobacter* spore count (a free-living N-fixing diazotroph) and concluded that inoculation with this species would be beneficial for mango growers to reduce external N inputs [54].

Free-living N-fixing microorganisms' contribution to food forests can be significant. Studies found that they can fix 20 kg N per ha per year in *wheat* fields in Australia. Estimates in temperate and

Mediterranean regions range from 10 to 30 kg N per ha for *annual crops* [55]. I expect that in undisturbed, well-aggregated, high OM soils as can be found in food forest systems, the contribution could be even higher. As I will show later, N outputs can be partly compensated by the N inflow from these free-living N fixators.

Leaching

In general, forest ecosystems are characterised by lower leaching rates than annual cropping systems. However, over time leaching can take its toll. For example, in very old highly weathered soils as can be found on Hawaii, many of the cations have leached out of the topsoil and are (partly) unavailable for plants. Very old ecosystems can reach a terminal steady state of irreversible depletion of rock-derived elements. Ecologists think it is mainly the leaching of phosphate that triggers the eventual inevitable collapse of ecosystems on very old soils [32].

In a study on the limiting factors for net primary production, researchers compared different Hawaiian Islands with markedly different soil ages, their substrates ranging from 300 to 4 100 000 years of age. They looked at the concentrations of available cations and nitrogen and phosphorus and the relation with primary productivity. Results showed that the young sites had little available N and P, the intermediate-aged sites had more N and P, and the oldest site had low P but high N availability [32]. The reason for low nitrogen availability in the young sites was the lack of nitrogen in the substrate and the long time needed to accumulate a substantial pool of nitrogen from the atmosphere.

Interestingly, the relation of this nitrogen and phosphorus availability matched the net primary productivity very good. The NPP peaked in the relatively fertile intermediate-aged sites. Fertilisation experiments showed that nitrogen (and not phosphorus) limits forest growth in the young sites, whereas phosphorus (and no other element) limited forest production in the oldest site [32].

Conclusions from this work are:

- Young soils contain high levels of phosphorus and are not restricted in forest growth (due to high uptake capacity via mycorrhizal activities) by the phosphorus content. Young soils forest productivity is restricted by nitrogen availability. Therefore, in early successional phases, nitrogen fixing plants dominate such soils. In much of the temperate zone, frequent intervals of glaciation resets soil development. Therefore, soils are maintained at young developmental stages in which weathering is a substantial source of most elements.
- Over time, phosphorus can leach from the soil and can become the main limiting factor regarding forest production. The consequences of this might be that food forests on very old soils (which is uncommon in the temperate zone) could quickly lose productivity once the remaining P is exported out of the system via harvested products. In such situations, sustaining production can only be realised by additions of phosphorus.
- Nitrate is prone to leaching. However, due to the endless availability of N in the atmosphere, forest N pools can be eternally replenished, which is not the case for P which mainly comes from weathering rocks.

Nitrate leaching is a process with negative consequences, not only for the ecosystem, but also for humans as it contaminates drinking water sources. N leaching in unfertilised (food) forest systems is low, primarily because most nitrogen exists as ammonium and not as nitrate. In olive orchards in Spain, for example, N leaching is about 2.2-2.9 kg of N per ha per year [56].

N leaching in natural forests is also low, except when high levels of human-induced inputs such as atmospheric N deposition surpass the annual N threshold [57]. In German forests, N leaching ranges between 0 and 26.5 kg N per ha per year and the difference with the Spanish olive orchard can be explained by the increased N-deposition rate in north-western Europe compared to Spain [58]. In regions with low atmospheric N-levels and, hence, low N-deposition, N-leaching is insignificant at deposition rates <9 kg N per ha [59].

Phosphate leaching rates are even lower than nitrogen leaching rates in forest ecosystems [60]. The principal reason for this is the low mobility of P in the soil as most of it is strongly bound to the soil

solid phase. However, looking over millennia (of soil development), P stores available for plants reduce in size due to acidification of the soil. Only occluded P and OM associated P is left [60]. Therefore, the P status of soils after thousands of years of (food) forest growth are largely unknown. Has the reduction in accessible P forms become production-limiting? Or are the numerous microbial reactions capable of maintaining adequate P provision to the trees? These questions are largely unanswerable.

In this paper, I will focus on food forests in the temperate zone characterised by relatively young soils [61]. Most of these soils (though not all) have relatively high total soil phosphorus content and, hence, this Hawaiian example does not apply to this situation. In the calculations shown later, I assumed low P leaching due to the relatively young state of the soils.

Erosion

Undisturbed forest ecosystems are known for their very low erosion rates, generally less than 0.053 mm per year, whereas conventional agriculture loses up to 3.939 mm per year, and generally more than 1 mm per year [62].

This erosion rate has (had) major consequences for human civilisations. Average soil production and geological erosion rates have been estimated of <0.2 mm per year. With the >1 mm per year rates under arable agriculture, the time required to erode through a layer of an initially decimetre- to metre-thick topsoil is in the order of a few hundred to a few thousand years [62].

The fact that most agricultural-based civilisations existed for 500 to several thousand years before collapsing matches the time needed to erode the topsoil completely. As Montgomery (2007) writes: “*it was not the axe that cleared forests but the plow that followed that undermined many ancient societies*” [63].

As mentioned before, *undisturbed* forests have low erosion rates, but disturbed forests have high erosion rates and reduced productivity. For example, roads can increase water-runoff and reduce forest productivity while fires reduce organic matter content thereby reducing water and nutrient content of the soils leading to reduced tree productivity. Compaction (as a consequence of tree felling with large machines) can dramatically reduce tree growth (up to 50% in height growth) by reducing water infiltration [64].

These findings are important when evaluating the effects of research conducted on agroforestry practices. Most agroforestry experiments were designed as duo-plantings: one row with trees and one row of annual crops. The poplar-wheat agroforestry system from France is a famous example [65]. It might well be the case that the production of the trees would have been significantly higher when heavy machines would not have been used to compact the soil. Also, experiments comparing rows of perennials with other rows of perennials might have reached different conclusions. One could imagine that in this kind of experiments in which soils are minimally compacted and disturbed due to the exclusion of annuals, site productivity could be significantly higher than in the conventional duo-agroforestry experiments.

Unfortunately, I am not aware of well-designed perennial-only ‘agroforestry’ trials, and therefore I can only speculate about the effect. It is well worth noting that the best-known food forest in the Netherlands, food forest the Ketelbroek is designed in a way that compaction is minimised; only a few paths cross the forest, no large machines are used and the site-management consists of interfering as little as possible. This practice could therefore, result in significantly increased tree growth and production as compared to a control site with the same species structured in rows and intercropped with annuals.

For the calculations, I assume nitrogen erosion as negligible because erosion rates are so low in undisturbed (food) forest ecosystems. Also, the erosion of nitrogen is disproportionately small compared to all the inputs from atmospheric deposition and nitrogen fixation. In the case of phosphorus, I include the erosion rates. Annual phosphorus losses due to erosion from natural undisturbed forests are very low as well, even in logged sites. Studies in the United States found rates of 0.03-0.06 kg P per ha per year [66]. However, since total phosphorus flows are much smaller than nitrogen flows, these low erosion rates might not be negligible and to be on the safe side, I include them in the calculations.

Gaseous emissions

Gaseous emissions only apply to nitrogen and not to phosphorus. The nitrogen cycle consists of several processes. I will not describe it here, but will explain the essentials later when I describe the N and P pools of forest systems. The key process responsible for gaseous N emissions in forests is denitrification by denitrifying bacteria. Most are facultative aerobic heterotrophs that switch from aerobic respiration to denitrification when oxygen as an electron donor runs out. Therefore, natural ecosystems characterised by high denitrification emissions are ecosystems that experience yearly flooding which creates anaerobic conditions.

In (food) forest systems, with well-aerated soils, denitrification rates are low, especially in sites that receive low atmospheric deposition of nitrogen. Over half of the forests used for denitrification studies in the literature, have denitrification rates of less than 1 kg per ha per year with an average of 1.9 kg N per ha per year [67]. In this paper, I will use a low value of 0 kg N and I will use the 1.9 value as a high value because I will later calculate the nutrient outputs and inputs for low atmospheric deposition situations with subsequently low denitrification rates. Emissions occur in the form of NO, N₂O or N₂ with the former two being greenhouse gasses. Ammonium volatilisation is another gaseous emission that can occur.

However, this emission is mainly found in agricultural systems receiving manure inputs. In forest systems ammonium volatilisation is virtually absent [67].

Perennial plant advantages in obtaining nutrients

The critical difference in terms of nutrients between a natural forest ecosystem and a food forest system is the rate of outflow of nutrients. In natural forests, the main nutrient outflow pathways are leaching and erosion and those are both marginal. In food forests, another pathway can be added and that is the *yield* of the fruits/nuts/wood/leaves/flowers produced by the perennials.

The question is as follows: *does the nutrient output via yields pose a threat to the site productivity, hence, does the outflow of nutrients result in nutrient limitations and subsequently reduced yields?* In other words, do food forest need to be fertilised?

In the previous section, I described the common pathways for nutrient inputs and outputs in natural forest systems: atmospheric deposition, leaching, erosion, migrating animals and rock/mineral weathering. Now, I will show the different evolutionary developed strategies to obtain soil nutrients in perennial systems. I covered some of these strategies earlier, but they applied to all plants. Perennial plants have several mechanisms absent in annual plants to acquire nutrients and I will show some of these mechanisms in the following paragraphs.

Later, with the collected nutrient pool data, I will show examples of different perennial systems and the effects of nutrient additions, harvesting and recently discovered strategies to obtain nutrients. I will also provide calculations that I made of some theoretical perennial (food forest) systems concerning this nutrient question and investigate whether the input processes can keep up with the output of nutrients.

Deep soil nutrient uptake

(Food) forests have some principal advantages over annual agricultural systems when considering nutrient acquisition. First, trees can reach deep soil layers that are inaccessible to annual plants. One of the famous mechanisms of agroforestry is the ‘nutrient pump’ effect of trees. Many trees have both superficial as well as deep roots. These deep roots extend to deep soil layers where nutrients could have leached to (like nitrate). Annuals cannot access these nutrients anymore, but the trees can. They can even increase nutrient availability for annuals via leaf fall. Via mineralisation, these initially unavailable nutrients for shallow-rooting plants are made available (Fig. 1).

This nutrient-pump effect is a consequence of water uptake and the water pump effect called hydraulic lift: water movement from deep to upper soil layers by roots. Part of the water is released again in the upper soil, increasing the water availability for shallow-rooting plants. In temperate and semi-arid environments, this mechanism can contribute 17-81% of total water transpired and can help with nutrient uptake. Nutrients (e.g. K and P) released from weathering of bedrock, can be dissolved within the deep water reservoir and can subsequently be transferred up via the water uptake, resulting in the addition of otherwise unavailable nutrients [68].

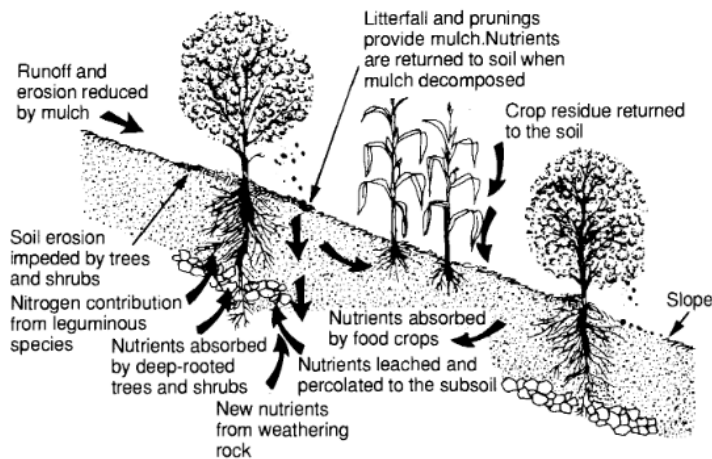


Figure 1. Agroforestry practices can recycle leached nutrients by pumping them up from deep soil layers which are out of reach for shallow rooting annual crops. From: [69].

To which depth trees root depends on species and more importantly, location. Mediterranean and desert ecosystems harbour some of the deepest rooting plants ever recorded. For example, in Tucson, Arizona, an extreme example was found. Mesquite (*Prosopis* spp.) roots were found 60 metres below the soil surface [70]. This shrub was able to fulfil its reproductive cycle even during long-lasting droughts because it could tap into the deep soil water reservoir.

Also in temperate zones, countless tree species are deep-rooted. For example, *Pinus sylvestris* can root to a depth of 9 metres. Even early on, at a young age, 4-year old stand of Douglas fir were observed to reach 3.7 metres depth [71].

Walnuts (*Juglans* spp), one of the staple crops of temperate agroforestry systems can be deep-rooted as well. In an agroforestry experiment in Montpellier, France, walnut roots were observed 5 metres deep [72]. Previous belief was that root (hair) distribution in the deeper layers was low and almost insignificant; most scientists assumed that most mineral and water uptake could be found in the topsoil layer. However, this walnut experiment showed that annual root length growth between 2.5 and 5 metres was about 50% of the total root growth (so including the shallow layer root growth) and the authors concluded that deep roots are likely an important contribution to alleviating water stress, as well as a way to obtain more nutrients [72].

Besides soil nutrient acquisition, nutrient uptake also occurs from rocks, although it is difficult to provide insights into the importance of this pool since minerals in weathering rock cannot be labelled [73]. As I described earlier, ectomycorrhizal fungi are capable of degrading feldspar mineral rocks thereby increasing the (available) nutrient pool of the ecosystem. They transfer some of the obtained nutrients to their symbiotic partners, the trees, to meet their nutritional requirements.

However, besides mycorrhizal weathering of rocks, trees themselves can weather rocks as well. Annual plants require soil to grow, trees do not. Most people have observed trees growing on bare rocks. If we would measure the available nutrient concentrations in those rocks, the outcome would be very low. Of course, the total pool of nutrients in that rock is high, but they are not available for uptake... unless you are a tree. Trees can increase rock weathering by acidification of the root rhizosphere via respiration. They can also attract micro-organisms (via root exudates) capable of solubilising rock minerals [74].

These innovative findings that soil nutrient and water uptake occurs much deeper than previously believed could have major consequences for nutrient balances of natural forest systems, as well as for climate change models. Current climate change models are mostly based on the IPCC model using 0.3 metres for carbon sequestration. However, carbon is sequestered much deeper in perennial systems. In Australia, it was found that 50-75% of SOC occurred within 0-5 metres, indicating that current 0.3 metres models significantly underestimate the total soil carbon pool [75]. Although topsoil contains

indeed the highest soil organic carbon levels, deeper layers can have significant contributions as well, especially when extrapolated on a global scale [70].

Many temperate forests are characterised by their low pH. Because of this acidity, a major part of the inorganic nutrient pool is entrapped in soil minerals and, hence, not accessible to tree roots.

Therefore, the role of mycorrhizal fungi in nutrient acquisition is very important. Mycorrhizal fungi have been shown to release phosphorus and potassium from apatite and biotite, two frequently-occurring minerals, and deliver this to the host plant [76].

Other micro-organisms have received considerably less attention. However, they play an important role in nutrient acquisition from difficult-to-access nutrient pools. Surrounding the mycorrhizal complex, complex bacterial communities have been observed. They likely play a role in plant nutrition. For example, populations of *Pseudomonas fluorescens* associated with the Douglas Fire (*Laccaria bicolor*) symbiosis showed significantly more efficient iron and phosphorus extraction from inorganic nutrient stocks compared with *P. fluorescens* isolates from the surrounding soil.

Also, the number of bacteria capable of weathering biotite and extracting iron and phosphorus was significantly higher in the mycorrhizosphere of a forest symbiotic fungus suggesting that bacteria in exchange of something, probably exudates, aid the trees in requiring the nutrients they need [76].

Other non-mycorrhizal fungi such as *Aspergillus amstelodemi*, *A. awamori*, *A. candidus*, *A. foetidus*, *A. fumigatus*, *A. japonicas*, *A. niger*, *A. tamarii*, *A. terreus*, *A. terricola* and *Sclerotium rolfsii* have been shown in lab studies to excrete organic and inorganic acids (mainly oxalate) which solubilise sparingly soluble phosphates [77]. In fact, it is now estimated that up to 40% of the culturable population of soil microorganisms are able to solubilise P [78].

Besides phosphorus, potassium is another macronutrient crucial for optimal plant production.

Multiple micro-organisms can solubilise K from insoluble forms like micas, illite and feldspar by producing organic acids, siderophores and capsular polysaccharides [78].

Concluding, perennial woody based agricultural systems can tap into nutrient pools unavailable for shallow-rooting annual plants. The deep rooting characteristic of many tree species enables them to find nutrients not only in the topsoil, but also in the subsoil and even in bedrock. Besides passive adsorption via mass flow and diffusion, trees can increase mineral weathering by root respiration and by altering the environmental conditions such as lowering the pH (to increase phosphate dissolution reactions). Besides the trees, many micro-organisms can solubilise nutrients from rocks and minerals. Several mechanisms exist among the wide diversity of organisms living in the world's soils. The question is *whether these processes can occur at a sufficiently high rate to provide the food forest trees and shrubs with enough nutrients to ensure high productivity competitive with conventional fertilised annual systems*. I will later present some real-world examples of the effects of P and N availability and fertilisation on (food) forest response and present a theory about nutrient requirements of food forests.

First, I will review data on *total* nutrient pools in forest ecosystems. These data will later be used to estimate how long perennial systems can continue to bear fruits and nuts while assuming that the trees are able to acquire the nutrients from the total pool.

Ecosystem phosphorus and nitrogen stocks

I described several mechanisms that are being used by plants and microorganisms to make nutrients available from hard-to-obtain pools like mineral, rock and organic pools. Agronomists hardly consider nutrient stocks contained by deeper soil layers (>0.3 metres) but it would be a mistake to exclude these deeper layers when analysing food forests. I reviewed data on P and N pools in different forest ecosystems around the world and at the end of this chapter, Table 4 summarises all the examples presented here.

In a study on different forests on different soils in the Netherlands, total N and P stores were measured in the litter layer, 'higher soil' and transition zone. Unfortunately, the exact depths are not mentioned in this study because they used data from several other studies that all worked with different measurement depths. However, they do classify the soil horizons with the deepest included layers (the transition zone) being a combination of AC+B+BC. Layer C is not considered and consists of loose parent material, while the layer below this one is referred to as the R layer consisting of intact weathered parent material [36].

Based on my knowledge of soil depths in Dutch forest, I estimate that this study did not look at layers deeper than approximately 70-100 cm. The authors mention that the nutrients contained by the 'lower soil horizons' are of importance because nutrients can become available due to weathering. However, they argue, the rate of available nutrient release is strongly dependent on the root penetration of this compartment [16].

As I described previously, several temperate food forest plant species easily root a few metres deep and do penetrate this compartment. Collaboration with microorganisms may therefore release significant quantities of nutrients from this lower soil layer, not included in this study. The problem is that it is hard to measure the rate of these processes and therefore, to estimate the meaningful contribution of this layer. It is important to note this because the N and P stores found by this study, tell something about the top metre maximally, and a food forest has a much larger potential pool of nutrients.

Nonetheless, the study found that the nitrogen total pool ranged between 2 900 and 7 600 kg per ha, depending on soil type and location. Total phosphate pool ranged from 180 to 1075 kg per ha.

Another study on phosphorus levels in the soil of heathland and agricultural abandoned soil, found comparable phosphorus levels (in the case of heathland). Due to the annual surplus of P (via fertiliser inputs), P levels can build up rapidly in agricultural soils in the Netherlands. However, phosphorus reacts quickly with mineral particles and becomes hardly available for plant roots. Therefore, farmers keep adding P each year, despite the large accumulated reservoirs of potential P. *If* the plants would be able (with the aid of micro-organisms for example) to dissolve the bounded P again into H_2PO_4^- and HPO_4^- , many agricultural soils could support decades (or more) of crop outputs without the need of added P. After abandonment, agricultural soil is often phytomined for P to make it suitable for a diverse nature system to develop. Therefore, the longer a site is abandoned, the lower the soil P levels. I will present the highest and the lowest soil P value here. The study looked only at the top 95 cm of soil, so the numbers are an underestimation of the total reachable pool of nutrients for a food forest. It found values of 70 mg/kg soil (lowest value in heathland) and 640 mg/kg soil in the recently abandoned field [25]. I converted these values into mass values per hectare and this results in 951 kg P per ha (lowest) and 8 694.4 kg P per ha (highest) for the top 95 cm. The highest value is a result of the decades-long fertilisation.

Tropical soils have, in contrast to many temperate zone soils, very high phosphorus binding capacity, especially tropical oxisols. Tropical forests are known for their low soil nutrient concentrations. Most of the nutrients are in the biomass and therefore, clear-cutting a tropical forest on a specific nutrient-poor soil to do agriculture there, is extremely unsustainable. After one or two years, those soils do not support conventional agriculture anymore, but when the farmers abandon the piece of land again, it may take hundreds of years for the forest to restore due to nutrient limitations and very low soil organic matter levels.

However, it is fascinating to see how much biomass a forest *can* produce on extremely poor soils. In Table 2, different tropical forests are classified by aboveground biomass, root biomass and total soil nutrients (N and P). What is striking is the enormous biomass production on the phosphorus-poor sites. For example, the moist forest in Panama with only 23 kg of P available in the soil per ha, has a biomass of 326 tons/ha which is higher than the site in Venezuela with larger soil P stores, probably due to the fact that this forest grows on oxisols, known for their difficult-to-obtain phosphorus. The same is true for the Dipterocarp forest in Malaysia with an astonishing 475 tons of aboveground biomass per ha and only 44 kg of soil P per ha, beating the lowland rainforest site in Costa Rica which has 7 000 kg P per ha in the soil [79].

Table 2. Nitrogen and phosphorus content in both the soil and biomass of tropical rainforests in different places around the world. Note the extremely low soil phosphorus content of some sites but the high biomass production. From [79].

	Amazon, Venezuela	Oxisol forest, Venezuela	Evergreen forest, Ivory Coast	Dipterocarp forest, Malaysia	Lowland rainforest, Costa Rica	Moist forest, Panama
Aboveground biomass (tons/ha)	268	264	513	475	382	326
Root biomass (tons/ha)	132	56	49	20	14	11
Total soil phosphorus (kg/ha)	36	243	600	44	7 000	23

These examples indicate that soils do not need to be phosphorus-rich to support a lush plant growth. Factors such as precipitation, radiation and temperature (as found in the tropics) are probably more important in determining net plant productivity (NPP).

Another tropical example, is cocoa production. Cocoa agroforestry can be a very sustainable type of agriculture, especially when combined with higher canopy trees. In this case, they really are an example of a (relatively species-poor) food forest system. Studies on soil nutrient levels show relatively high nitrogen contents in cocoa agroforestry systems in different tropical countries. Results indicate a soil N-content in the top 40 cm of 4 800 –18 750 kg N per ha in cocoa agroforestry systems [80].

Yanai (1992) provided a detailed partitioning of the phosphorus over the various mineral soil and forest floor compartments of a northern hardwood forest. He estimated total soil P pool of a 60 year old hardwood forest (which we can consider as a food forest) of 1 685 kg P per ha [81]. However, interestingly he only looked at soil particles <2 mm, while he explicitly mentioned that “the rate of P accretion in the mineral soil by weathering of rock fragments and parent material...is unknown. Since soil is defined as the <2 mm fraction of material in the zone of biological activity and weathering, it is possible that living biomass, organic matter, and soil, so defined, could all be accumulating P, *at the expense of the underlying parent material and rock particles >2mm*” [81].

The mineral soil averaging 54 cm of depth in this study provided the largest reservoir, containing 1 600 kg P per ha. The forest floor averaged 85 kg P per ha (5-7 cm deep) and together these formed the total P stock of the soil. As I argued earlier, most studies underestimate nutrient stores because they only focus on the top layers and this study did this too. The total soil depth including the forest floor was only 60 cm deep.

Other studies that included deeper soil profiles found higher soil P and soil N values. Phosphorus pools in long-term agricultural fertilisation experiments had values much higher than the one reported above. In a plot that had *not* received P fertiliser, phosphate content ranged between 3178 and 8328 kg per ha in the top 100 cm [82]. In a study on soil P content of rich loess soils in China, researchers found forest P stocks of about 16 000 kg phosphorus per ha to a depth of 200 cm [83]. Loess soils are

known for their high fertility level and can support high agricultural production. Therefore, this 16 000 kg P per ha is likely on the high end of the spectrum. As I will show later, I will not use this value in the calculations on system lifespan. However, this study also indicated the P content of the 100-200 cm soil layer (about 8 000 kg P per ha) and this value will be used for the calculations because it is the only study that clearly showed the total P content of this soil layer.

For nitrogen, the same issues were encountered. Most studies did not look over the entire soil profile within reach of the trees' roots. However, the three studies looking over the largest soil profile I could find, showed the following nitrogen stocks.

The first study investigated soils of sites not fertilised with N for a long time. It showed high N levels in a soil profile up to 100 cm depth with N values ranging from 3 050 to 21 940 kg per ha [82].

Northern hardwood forests have high nitrogen stocks as well, although stocks vary substantially depending on site. Researchers investigated the Pacific Northwest forests in the United States. They considered total N pools of these forests and specifically, deep N pools. They found that Douglas-fir trees rooted up to 3.7 metres in a 4-year old stand and up to 10 metres in a mature stand [71].

Therefore, they concluded that the assumption that nitrogen that leached deeper than 1 metre is lost to the ecosystem is deeply flawed [84].

A study looking at 200 cm deep soils in China's loess soils found nitrogen content of about 9 000 kg N per ha [83]. This finding, despite being on rich loess soil, matches other studies findings reasonably well. Many studies on temperate forests estimate nitrogen contained in the first metre of soil is several thousands of kilograms per hectare.

The aforementioned studies only looked at *soil* P and N levels, but not at rock content. As described earlier, natural ecosystems harbour a wide array of micro-organisms that can weather rocks to unlock their contained nutrients. Tree roots themselves can do this as well to a certain extent. It is very hard to investigate how high these weathering rates can be and whether they are relevant, but because many locations (especially in mountainous areas) contain stones or even a bedrock layer relatively close to the surface, it is worth mentioning the total content of these rocks that could *theoretically* be accessed by deep-rooting plants. I want to emphasise that it is unknown if this pathway would make a significant contribution to food forest nutrition, but as I will show later, some nutrient outflows in food forests are relatively low and therefore, this pathway might be significant.

Table 3. An overview of the different phosphorus concentrations of several lithology categories. From [85].

Lithology categories	Composition	Global coverage %	Bulk density (g cm ⁻³)	P concentration (ppm)
Precambrian basement (PR)	60% granodiorite + 30% granite + 10% basalt	11.6	2.6	792
Carbonate rocks (SC)	Pure carbonate	10.4	2.3	484
Siliciclastic sedimentary consolidated rocks (SS)	70% shale + 30% sandstones	16.3	2.3	528
Basic and intermediate volcanic rocks (VB)	75% basalt and 25% andesite	5.8	2.6	1364
Mixed sedimentary consolidated rocks (SM)	15% carbonates + 60% shales + 25% sandstones	7.8	2.3	528

Researchers found P concentrations for the different lithology categories existing on earth [85]. The values given are in ppm (Table 3), and I converted these values into kg per ha. I assumed a bedrock/stone layer of one metre thickness as being available for deep-rooting trees, and calculated the P contents of this layer for Precambrian basement (PR) and Carbonate rocks (SC) which are some of the most common types of rocks (Box 2). Furthermore, they comprise the range of values that can be found in different bedrock materials.

Box 2. Calculation of phosphorus content contained in two different bedrock types (Precambrian basement and Carbonate rocks).

In 1 m of PR there is $792 \text{ (P conc. in ppm)} / 1\,000\,000 * 2600 \text{ (bulk density rock)} * 10\,000 \text{ (volume soil 1 ha)} = \mathbf{20\,592 \text{ kg P per ha.}}$

In 1 m of SC there is: $481 / 1\,000\,000 * 2300 * 10\,000 = \mathbf{11\,132 \text{ kg P per ha.}}$

What I want to illustrate by summing up these studies is the influence of soil types, measurement methods and depths and global locations on N and P levels. Later I will make some calculations with nutrient balances and therefore, I need to have both low and high estimated nitrogen and phosphorus values in soils. To make it more structured, I summed up all the studies in Table 4.

It shows an average value for phosphorus and nitrogen of 5 402 and 10 437, respectively. These values simply indicate the average total store for a variety of studies using varying soils and different measurement depths. Later, I will explain which values listed in this table, I will use to calculate the nutrient balances. Furthermore, I want to mention that the studies listed in this table, indicate the total N and P stocks. Only a certain percentage can be obtained by the trees in a food forest. As I have shown earlier, the mechanisms to take up nutrients from plant-unavailable sources are there in food forest systems, as described extensively above. The question is *at which rate this nutrient-provision happens in food forests* and whether it is sufficiently high to compensate for the loss of nutrients via crop harvest.

Table 4. The varying P and N pools found by different studies looking at different soil depths. Low and high estimations found by these studies are listed for different ecosystems, ranging from heathlands to tropical rainforests.

Study	P values (kg/ha)	N values (kg/ha)	Type of soil	Pools	Depth measured (cm)
[16]	180-1 075	2 900-7 600	Varying temperate zone	unknown	+/-100
[25]	951-8 694	-	Poor heathland-recently abandoned agricultural soil	All	95
[79]	23-7 000	785-20 000	Varying tropical soils	All	Unknown
[80]	-	4 800-18 750	Wet tropical	All	40
[81]	1685	-	Temperate forest	All	Unknown
[84]	-	2 660-26 600	Temperate forest	All	350
[85]	11 132-20 592	-	Bedrock (Precambrian basement and Carbonate rocks)	Mineral	100

[49]	-	1 595-18414	Bedrock (diorite and mica schist)	All	100
[82]	3 178-8328	3 050-21940		All	100
[83]	16 000	9 000	Forest on loess soil	All	200
Average soil	5 402	10 437			

I will now present some practical examples of perennial systems which one could consider extremely simplified food forests. These examples illustrate the effect of fertilisation and nutrient removal on site productivity. They suggest that, at least to a certain extent, perennial systems can acquire the necessary nutrients without fertiliser inputs.

Olive trees

The olive tree is one of the most cultivated tree crops in the world, dominating agro-ecosystems in the Mediterranean region. Olive trees can live for more than a millennium and still bear fruit. For example, in Corsica we can find two of the oldest olive trees of about 1 250 and 1 500 years of age. Both trees still yield close to 300 kg of olives per tree [86]. This is educative because it shows that a tree can yield hundreds of thousands of kilos in its lifetime without receiving major nutrient inputs. Olive trees are known for their ability to grow even in poor, rocky soil, hence, the crop was traditionally cultivated in rain-fed agriculture associated with low productivity. This low productivity was mainly caused by the lack of irrigation water (hence, rain fed) during summer. Because olives were grown without irrigation, the tree's extensive root system formed symbiosis with mycorrhizal fungi. Therefore, P deficiencies in olives are rarely seen and P fertilisation is not typically recommended [87].

The principal reason of the increased olive productivity over the past three decades has been the intensive, irrigated, high density orchards. Especially irrigation seems to increase olive tree production significantly [87]. Researchers observed up to 200% increased yields in olive tree plantations that were transformed from rain-fed into irrigated orchards [88].

To find out the impact of nitrogen fertilisation, fertilisation experiments have been performed in Spanish olive tree orchards. Spanish researchers investigated the effect of N fertilisation on olive trees. One plot of olive trees received an annual nitrogen fertiliser treatment and a control treatment did not receive fertiliser at all. After thirteen years, foliar nitrogen concentrations were measured and the results showed that they did not drop below 1.2% after the thirteen years, even in the unfertilised plot [87].

The researchers wondered how it was possible that the trees did not show nitrogen deficiencies and concluded other sources of plant-available nitrogen must have increased the soluble nitrogen fraction in the soil. First, the losses of nitrogen were low. Leaching losses ranged from 2.2 to 2.9 kg N per ha, compared to leaching rates from 14.1 up to 117.4 kg N per ha for the fertilised plots [87].

Interestingly, losses via yields were equal between the two treatments, showing that *N fertilisation did not increase olive yield* in this thirteen year period. N removed by yield was about 9-18 kg N per ha. Ammonia volatilisation was almost insignificant in the unfertilised plots and nitrogen fixation accounted for 7 - 28 kg N per ha per year input. Therefore, biological N-fixation might have compensated already for the outputs (take the average value of 7 - 28, 17.5 kg per ha per year and the average yield N output of 9 - 18, 13.5 kg per year). Input - output = 17.5 - 13.5 = a surplus of 4 kg N per ha per year. However, it is likely that not all the N from this process is available for the olive trees and therefore the authors suggested that another N input could play a role: mineralisation of organic matter [87].

I described earlier how organic matter builds up during succession due to the continuous input of dead organic materials (from plants, animals, and microbes). Micro-organisms break down part of the organic matter and this results in a yearly organic matter turnover rate. Depending on temperature, humidity and organic matter inputs, a certain turnover rate is established for each different ecosystem/region. In the tropics, due to the high temperature and humidity levels, organic matter pools are relatively small because of the extremely high decomposition rate by microorganisms. In

boreal forests, SOM stocks are very high due to the low temperatures and subsequent low microbial decomposition activity. In each ecosystem, a certain equilibrium value will be reached once a system has matured. This value is determined by the input (via dead plants roots, leaves, etcetera) and the decomposition rate. In most temperate ecosystems, about 1 - 3% of the total organic matter pool is mineralised each year, meaning that the nutrients contained by the organic matter are released in the soil solution, hence, available for plant uptake. This process is key in the productivity of forest systems all over the world.

Connecting this to the olive tree study, the researchers estimated that nitrogen mineralisation of organic matter contributed to 44.8 - 69.6 kg N per ha per year. Even if only half of this mineralised N could be obtained by the tree, it was more than enough to compensate for the N outputs (leaching 2.2 - 2.9 kg + fruit yield 9 - 18=11.2 - 20.9 kg). Therefore, the researchers concluded that this organic matter mineralisation could explain why leaf nitrogen concentration did not drop below 1.2 % after 13 years in the unfertilised plots, and that in fertile soils (e.g. have relatively high organic matter content), annual applications of nitrogen fertilisers are not necessary for good olive yields. Important to note is that soil organic matter decomposition and the subsequent nutrient input is no real system input as it does not enter the system from outside. The nitrogen that ends up in the organic matter comes from decomposed leaves which obtained their nitrogen via soil nitrogen uptake by the tree. I will explain this decomposition pathway in more detail later.

The most important conclusions from the olive tree examples are:

- Nitrogen fertilisation has no result on olive yield in soils with appropriate soil organic matter content
- Irrigation is more important for biomass production in olives than nutrient additions in most situations
- Phosphate deficiencies rarely occur in olive tree orchards
- Soil organic matter plays a key role in perennial system nutrient provision via microbial mineralisation

Dehesa

The Dehesa system located in Spain and Portugal is a classic in the agroforestry world. It consists of a parkland landscape with low-density planting of oak trees (mainly *Quercus ilex*) with an herbaceous layer in between the trees. Pigs feed on the acorns in certain periods of the year and other animals graze the vegetation between the trees. Furthermore, it is a biodiversity hotspot harbouring species like the extremely rare Iberian Lynx.

The Dehesa system is characterised by poor soils, low in available nutrients, and long periods of drought and high temperatures. Therefore, it is a hostile environment for most trees. Some trees like oak (*Quercus* spp.) survive here and can even produce a crop (of acorns used to fatten the pigs). Water availability is the main limiting factor in this system, but nitrogen comes next. Many of the trees are several centuries old, have never received external fertilisers, and still produce acorns, showing that it is possible to continuously harvest products from a 'food forest-like' system. Production levels vary a lot between years, areas and individual trees. Lack of selection on high-yielding individuals resulted in sub-optimal acorn production levels in the Dehesa system (from an economic standpoint).

Coefficients of variation over 100% between individual trees or plots are common in the bibliography. Within one plot, it is possible to find trees with zero annual production and trees producing up to 300 kg acorns per tree [89]. On a plot level, Dehesa systems seldom produce more than 600 kg of acorns per ha per year [89]. This shows the tremendous importance of breeding programs for tree crop plants to select those varieties capable of yielding much more than their wild counterparts.

Due to the poor soil status of the Dehesa system, researchers investigated whether fertilisation would increase acorn production [90]. They compared to different sites; one with *Quercus ilex* trees and nitrogen-fixing deep-rooting bushes: *Retama sphaerocarpa*. The other site had no N-fixing bushes, but instead of *Retama* bushes, it was covered with *Cistus ladanifer*. Both sites were fertilised with N fertiliser and foliar N concentrations, as well as leaf DM were determined. As can be seen in Table 5, the site containing the N-fixing shrub *Retama*, was not affected by N-fertiliser. *Leaf N concentrations*

were similar in the fertilised and unfertilised sites. The leaf dry mass was even higher in the unfertilised plot, although the difference was just insignificant ($P=0.056$) [90]. However, in the site containing the Cistus shrubs, N fertiliser increased foliar N concentrations (12.3 mg/g compared to 10.7) and increased leaf dry mass as well from 0.35 g per shoot to 0.53 g per shoot [90].

This experiment shows that N-fertilisation in nutrient-poor, low SOM systems, can increase biomass production and shows that the inclusion of nitrogen-fixing plants in the design of food forests (at least in places with low SOM and nitrogen availability) can raise crop yields (at least of oaks) with the same value as artificial fertiliser can. However, it shows that N-fertilisation has no effect on tree biomass production when enough nitrogen is already provided to these trees (via N-fixation).

Table 5. The effect of N fertilisation on nitrogen, potassium and phosphorus content in the leaves of *Quercus ilex* on two sites; one with N-fixing *Retama* bushes, and one without N-fixing bushes (*Cistus*). From [90].

Site	Fertilisation treatment	Leaf dry mass (g shoot ⁻¹)	Concentration N (mg g ⁻¹)	Content (mg shoot ⁻¹)
Retama	Fertilised	0.540	10.900	5.900
	Unfertilised	0.660	10.400	7.000
	<i>P</i> value	0.056	0.384	0.195
Cistus	Fertilised	0.530	12.300	6.400
	Unfertilised	0.350	10.700	3.700
	<i>P</i> value	0.003	0.007	<0.001

Organic matter nutrient mineralisation and immobilisation

I have already described the mineralisation pathway in (agro)forest ecosystems and the significance of this pathway in succession and forest nutrient provision. As organic matter levels build up over time during succession due to the annual increasing biomass inputs until a mature forest system has been reached, annual nutrient mineralisation increases the available nutrients each year, supporting an even more abundant biomass production, enforcing the loop.

Planting a food forest on a degraded site low in organic matter can be compared with the succession from heathland to climax-state oak-beech forests in central Europe. Heathland is characterised by low aboveground plant biomass and low available nutrient levels in the soil solution. However, during succession, litter input by far exceeds decomposition rates resulting in the increased thickness of the O-horizon of the soil. At the end of the succession, decay rates increase and organic matter levels plateau to a steady state level.

The question is, how can a nutrient poor ecosystem (the heathland) supporting only marginal biomass production, transform itself into an ecosystem that supports a 34 times larger total above ground biomass (the climax-state beech-oak forest) and its contained nutrients [91]?

The accumulation of nutrients seems to be controlled by the rate of organic matter accumulation. During the succession, nitrogen, phosphorus, potassium, calcium and magnesium concentrations increases up to 375% in the organic horizon [91]. See Table 6.

Not only is the total nutrient pool of the organic horizon increased, higher nutrient concentrations in the soil solution are also observed for the end-state of the succession. Particularly, Ca^{2+} , NH_4^- and PO_4^{3-} were significantly higher, which is important as plant uptake depends on availability of nutrients, not only on total potentially obtainable pools.

Table 6. Size of the element pools in the organic soil horizon in heathland (early pioneering state), birch-pine forest (late pioneering state) and oak-beech forest (climax-state) relative to heathland values. Note the increasing nutrient concentrations as ecosystem state moves from pioneer towards climax-state vegetation. From [91].

	C %	N %	P %	Ca %	Mg %	K %
Heathland	100	100	100	100	100	100
Birch-pine forest	230	203	146	240	207	198
Oak-beech forest	293	315	185	375	312	336

Besides soil nutrient increases, nutrients accumulate as well in above-ground biomass. These increases are even more pronounced than the changes seen in the soil with increases up to 19 times the initial biomass content. See Table 7.

This example indicates a vicious cycle; increasing nutrient supply allows the growth of high-nutrient demanding species such as beech. At the same time, these late-successional species have a higher biomass productivity and a higher nutrient stock contained in their biomass. Due to increased litter production, a larger part of the nutrients becomes available for microbial decomposition processes and this system is characterised by a lower residence time of nutrients in the soil as compared with the heathland situation.

This suggests that nutrients are becoming available during succession as a consequence of the increased biomass production and food web fuel (via larger photosynthetic surface of vegetation).

Table 7. Size of above-ground plant biomass nutrient pools in heathland, birch-pine forest and oak-beech forest, relative to heathland values. From [91].

	C %	N%	P%	Ca%	Mg%	K%
Heathland	100	100	100	100	100	100
Birch-pine forest	809	583	711	544	377	432
Oak-beech forest	3 465	856	1110	1930	808	980

Studies on tropical forest succession came to the same conclusions. During succession, calcium held by the above-ground vegetation increases as well, but no sign of reduced soil exchangeable calcium over time is observed, indicating that soils were adequately replenishing immobilised calcium from *unavailable* forms [92]. This phenomenon was also observed for phosphorus.

What is interesting about these increased nutrient concentrations with succession, is that the annual *requirements* also increase, not only the total pools. For example, 1 ha of broad-leaved European beech forests requires more than 100 kg N per ha per year, which is similar to many agricultural systems. Even on so called ‘poor’ sandy soils, beech forests with a standing above-ground biomass of > 200 tons per ha can still grow.

The question is, where do they get their nitrogen from? The key seems to be the microbial community. Microbial mineralisation-immobilisation turnover is about fivefold larger than tree N uptake and releases more nitrogen (about 500 kg N per ha per year) than the tree needs. A large part of this is again immobilised by microbes, but sufficient N (>100 kg) can be taken up by the trees, meeting their nitrogen requirements [33].

These examples show that during succession, nutrients accumulate in the living plant biomass, microbial biomass and the dead (plant+microbes) organic matter. Due to the nutrient cycling process performed by the soil food web, nutrients become available to meet the demand of the trees. Most nutrients in forest systems are contained in the organic pool. Particularly nitrogen, due to its mobility (as nitrate mainly) is firmly incorporated into organic matter and organic matter forms the major N storage of forest ecosystems, with total levels of several thousand kg N per ha.

The key difference between a food forest system and a natural forest is the fate of the reproductive organs. In natural forests, reproductive organs will remain on site and contribute to the organic matter pool, while in food forests, these will be harvested and removed from the system.

The theory that came up in me after reading the previously mentioned olive study was: if SOM mineralisation liberates enough N (and likely also most of the other required nutrients) to sustain yields, *could a food forest system maintain these high OM levels (and the contained nutrient levels) even though some nutrients leave the system via outputs?*

As natural succession occurs, solar energy captured by plants and used to liberate nutrients (via the soil food web) increases the total *available* nutrient pool of the ecosystem and allows higher biomass production levels. Each year, a certain amount of nutrients is made available, translocated to the biomass (for example leaves), and becomes part of soil organic matter as the leaves fall in autumn. Imagine someone starts a food forest on a former conventional field that has low organic matter levels and a disturbed soil food web. As the trees grow on this plot, they produce a yearly biomass input to the soil, increasing its soil organic matter content over time. After approximately twenty years, serious amounts of nutrients are beginning to be extracted from the site because trees have matured and have started to produce significant amounts of nuts and fruits. A proportion of the total biomass production is now exported from the site and cannot contribute to the SOM pool.

However, since the system is still relatively young, biomass production via leaves continues to increase for a few decades probably, after which a more or less constant leaf litter fall rate will be reached. If this food forest would have been a natural forest, even more biomass would have contributed to the organic matter pool since the nuts and fruits would not flow out of the system. At a

certain point, an equilibrium between decomposition of SOM and input of SOM will be reached and SOM levels will plateau.

I wondered, how much higher would the SOM levels have been if the fruits and nuts would have decayed on site instead? I consulted the literature and found annual leaf biomass production in chestnut forests in Portugal being around 3.2 tons of dry mass per ha [93]. In these natural forests, the production of fruits was maximally 570 kg dry mass per year per ha [93].

Dutch research on oak forests came to the same conclusion: annual leaf production is about 3.33 tons DM per ha per year and fruits (acorns) about 500 kg DM per ha per year [16].

Therefore, natural, mature forests have annual biomass inputs of about 4 tons of DM per ha per year. If we would make the same calculation for food forests, we can find out the difference in biomass input due to the harvesting of products. I realise that I ignore many aspects of food forest design, like the stacking of plants in a multi-layered system, which might increase biomass production significantly compared to natural forests. However, just for simplicity, I assume a food forest to have an annual leaf production of 3.3 tons DM per ha per year (like the natural forests) and because food forests must allocate significantly more of their assimilates to fruit/nut production than a natural forest, I take a fruit/nut production of 1.5 tons DM per ha per year (so I assume total biomass productivity is higher than natural forest productivity).

I assume that due to genetic breeding, the trees used in food forest can increase their reproductive organ biomass productivity compared to their wild natural forest cousins. The total theoretical biomass input would then be 4.8 tons of DM per ha per year for food forests. Now, comparing a natural forest with a food forest, about $(1.5 / 4.8) * 100 = 31\%$ of the total biomass in a mature food forest could flow out of the system via harvesting, while 100% of the produced biomass remains on site in a natural forest. The total biomass input (3.3 tons DM per ha per year) contributing to OM accumulation would be less than in a natural forest (4 tons DM per ha per year).

This shows that planting a food forest on a soil low in OM will increase SOC levels like planting a natural forest would do. The major difference is that the expected food forest equilibrium SOC levels will be somewhat lower than the SOC levels of a natural forest because of the difference in biomass inputs (4 tons vs 3.3 tons DM in a mature system per ha per year). If I simplify this reasoning even further for illustrative purposes, one could say that food forests would reach about 21% lower equilibrium SOC levels than a natural forest would do (on the same soil). Of course, there are many factors influencing this equilibrium value and many factors influencing the biomass production of both natural as well as food forests, and therefore this reasoning should just be considered as an illustration of the situation.

Assuming a climax-forest has a soil nitrogen stock (in organic material in the top metre) of about 5000 kg per ha, a food forest would probably have less organically bound N because organic matter inputs are lower. If we take the 21% lower SOM and assume that N stock would also be 21% lower, then the food forest would have a nitrogen stock of about 4000 kg N per ha. For simplicity, let's assume a per ha tree uptake of 100 kg N per year, like in the beech forest mentioned earlier. In this system, microbial mineralisation and immobilisation is about 5 times higher than tree N uptake (about 500 kg per ha per year) so due to organic matter decomposition, enough N becomes available for the chestnut trees to cover their total N demands (including the nut production). With a good chestnut harvest, N removal via nut yields would be about 21 kg of N per year (as I will show later this paper).

So, without N inputs, the system would slowly lose all the nitrogen via outputs and after a while, organic matter decomposition rates would mineralise insufficient quantities of N to support this level of chestnut production.

However, this is not in line with the fate of the SOM pool. As I stated earlier, the SOM pool of such a system will reach a steady state level and, hence, SOM pools will not decrease once the equilibrium value is reached. According to this reasoning, N pools *cannot diminish* as N is a principal component of SOM (about 5.8% of SOM is N) so SOM levels cannot be maintained when the N balance is not neutral or positive at least.

Therefore, I would argue that the lost N outputs will be compensated by new N inputs (I will show which inputs later) to maintain the SOM pool *at least until a certain level of N outputs beyond which*

the compensation rate cannot make up for the losses anymore. If crop N harvests are above this threshold value, SOM pools will plummet indeed. According to this reasoning, food forest systems which can maintain their equilibrium SOM levels would never run out of *total* nitrogen contained by the system if input rates (like N-fixation or atmospheric deposition) would compensate for the N removal via crop harvesting.

However, since most forest systems receiving nitrogen fertilisers respond with enhanced growth, the remaining question is whether food forests would be able make available the necessary amount of nitrogen *at the right time and in the right place.*

Nutrient synlocalisation and synchronisation are terms used in agronomy to explain the importance of the place (synlocalisation) and time (synchronisation) in fertilising crops. Fig. 2 shows what could happen when a crop is fertilised only at the start of the growing season. Initially, nitrogen availability can be much higher than crop demand, making the nitrate prone to leaching, denitrification or volatilisation. However, when crop demands are high (during leaf growth), most of the nitrate might already be lost from the system and the plants could now experience N shortages which limits plant growth.

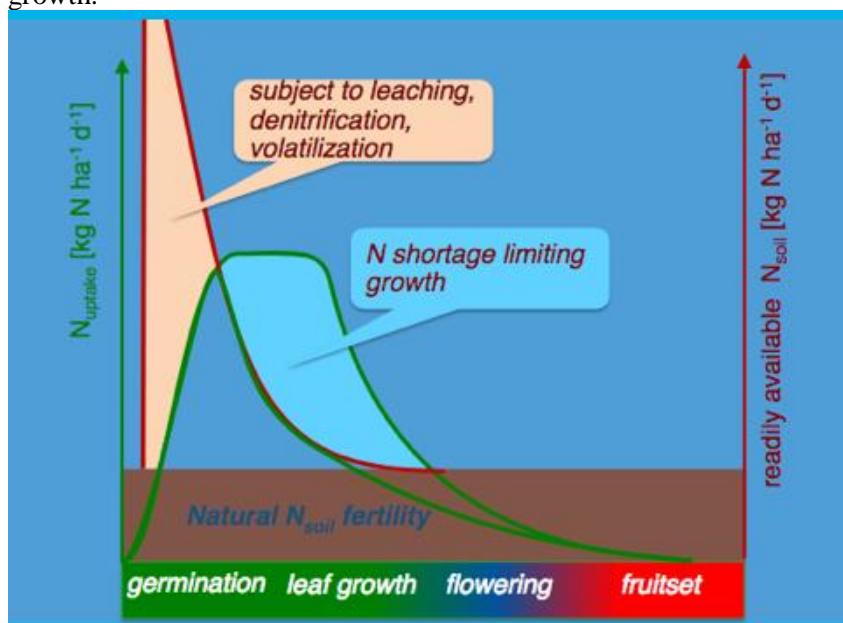


Figure 2. Crop nitrogen requirements during different phases of development and the effect on nitrogen availability of one sole nitrogen fertilisation application.

In (food) forests, fertilisers are not applied but the release of nitrogen via SOM decomposition can be considered as fertilisation. Therefore, in sub-optimal functioning systems, the release of nitrogen from organic matter decomposition might be not optimally matched with tree demand. Considering the example of chestnuts, the trees might experience N limitations, especially in dry years when mineralisation reactions of SOM are (too) low due to microbial water stress.

Also, certain litter layer mixtures might favour fast or slow N mineralisation. Lime leaves are quickly decomposed, hence, nitrogen is quickly released, while oak leaves need more time. Identifying and measuring when certain plant species in a food forest require most N and when most N is mineralised could help with optimisation of nutrient supply. For example, if chestnut trees require most nitrogen in June while via decomposition of chestnut leaves, most N would be mineralised in May (after which it quickly becomes immobilised by microorganisms if the plant does not take up the nutrients immediately), one possibility could be to intercrop the chestnut trees with trees whose litter is more difficult to decompose and from which most N is mineralised in June (when the chestnut trees need most).

This is just a theoretical example to illustrate potential issues and solutions to meet nutrient requirements of food forests based on organic matter decomposition. Sub-optimal nitrogen synchronisation might well be a major limiting factor in natural forest nutrient provision.

Conclusions about this organic matter-nutrient theory:

- Food forest systems likely have relatively high (compared to annual agricultural systems) SOM levels, albeit lower SOM levels than natural forest ecosystems where no biomass is exported.
- Microbial decomposition of SOM mineralises large amounts of nutrients which partly become available for trees. Most the tree nitrogen demand is met via this decomposition pathway.
- According to the steady state assumptions of forest SOM pools (when mature), food forests will likely also reach an equilibrium SOM value, albeit lower than a natural forest due to the lower inputs (as more biomass is exported).
- SOM consists of nutrients like carbon, nitrogen and phosphorus. Therefore, (annual) nutrient accumulation and provision rates during succession are tightly linked with increasing SOM levels. The other way around, as nutrients are lost from a food forest system via harvesting, SOM levels should decrease as well. However, due to the assumption of a steady state SOM level in mature food forests, nutrients lost via harvesting must be replenished in the soil via certain inputs (like nitrogen deposition and fixation) to comply with this steady state SOM assumption.
- Up to a certain extent of nutrient removal via crop harvesting, it is plausible that plant available nutrients are replenished to ensure continued plant biomass production and, hence, sustained litter (nutrient) inputs. This would result in a constant SOM pool which is the most likely scenario for food forests.
- However, at a certain harvest intensity, trees cannot meet former nutrient demands which will lead to reduced biomass (and hence nutrient) inputs. This will lead to reduced SOM levels and reduced nutrient mineralisation rates, hence, limiting plant nutrient uptake even further and resulting in lower yields until a new equilibrium of outputs and inputs is established.
- Many factors such as precipitation, temperature, soil characteristics and microbial food web composition all influence the process of decomposition, mineralisation and subsequent nutrient uptake. Therefore, topography has an important influence on the functioning of food forests and the level of harvest it can support without diminishing its SOM levels and nutrient supplies.

Food forest lifespan calculations

The following tree crop example shows that sustained yields without inputs are possible in the chestnut forests in France. I did my Bachelor thesis on the sustainability aspect of these chestnut forests in the Ardèche and discovered that in general, the traditional orchards on the steep sloping mountainsides do not get fertilised. Nonetheless, many of these chestnut orchards are 200-300 years old and have been giving nuts every year. The only manure that these forests receive is sheep manure from sheep directly grazing in this agroforestry system, but the sheep simply relocate nutrients as they eat the herbaceous plants on the same plot as the trees. Therefore, there is no high input of nutrients from fertilisation. The only possible inputs to this system are weathering processes, atmospheric deposition and runoff from higher areas. In the recent decade, the production of many orchards has fallen due to different exotic pests and diseases manifesting themselves in the region. Chestnut gall wasp (*Dryocosmus kuriphilus*) has been observed for the first time in the Ardèche region in 2010 and since then, some orchards lost up to 100% of their productivity. The gall wasp lays its eggs in the buds of the chestnut tree and once the buds begin to develop, galls develop and the bud cannot develop into a leaf or flower, hence, strongly reducing the tree's vigour and reproductive capacity. Most varieties are vulnerable to the insect; however, some varieties show (partial) resistance and can be used to overcome this problem in association with other solutions like introducing the gall wasp's natural predator.

Corsica is another region with centuries of chestnut cultivation history. As Russel Smith already described in the previous century, the mid-altitude of a large part of Corsica is occupied by chestnut forests which have been in place already for at least five centuries [94]. In 1850, chestnut forests covered 33 000 ha while grain agriculture covered only 14 400 ha [95]. When Corsica was under French occupation, Louis XV wanted to reduce the chestnut acreage because it was considered the cause of the islands' economic underdevelopment. Furthermore, the French kingdom considered Corsicans as lazy and reluctant to adopt civilised agriculture and modern institutions. The chestnuts were considered as a weapon because they provided food during wartime. The Corsicans resisted the imposed policies to increase grain cultivation and reduce their horto-pastoral civilisation in which money hardly existed. Therefore, chestnuts symbolised independence, freedom and resistance to the French oppressor throughout the island's history [95].

With the collected data on P and N pools of common temperate zone forest ecosystems (as listed in Table 4, I will now make calculations for the chestnut system to find out how long it takes until nitrogen and phosphorus stocks are seriously reduced as a result of harvest output. In box 3 and 4 I calculated how much nitrogen and phosphorus would have been harvested from these chestnut systems over 250 years.

Box 3. Annual and 250-years phosphorus removal via chestnut harvesting.

The farmer I worked with in the Ardèche, Francis Pierron, estimated that a single healthy 250-year-old tree can yield about 100 kg of nuts (fresh weight) which equals about 50 kg of nuts DM. One hectare can contain about 40 of such trees so total DM yield could be 2 000 kg DM chestnuts per ha. P content of dried chestnuts is about 123 mg per 100 g [96]. Annual P removal with the fruits is 2000 kg DM * 1.23 g/kg = 2460 g = **2.46 kg P per ha per year**. Assuming that over 250 years the average yield has been 1 600 kg DM per ha per year, P removal would be **492 kg of P in 250 years [96]**.

Box 4. Annual and 250-years nitrogen removal via chestnut harvesting.

For nitrogen, I make the same calculation. The protein content of chestnut averages 5.6 g per 100 g DM [96].
N content of protein is on average *amount of protein / 5.3* [97].
Per kg DM yield, 56 g is protein and this translates into 10.57 g N per kg DM.
2 000 kg * 10.57/1 000 = **21.14 kg N per ha output per year** via nut removal. Over a 250-year period, again assuming average yield to be 1 600 kg DM per ha, N removal would be 1600 * 10.57 * 250 / 1 000 = **4 228 kg of N**.

Total phosphorus removal is 492 kg and total nitrogen removal is 4228 kg of nitrogen. This latter value comes close to the total soil organic N pools of most northern temperate deciduous forests (Table 4). Therefore, if there would not have been a replenishment of the lost N, these forests would not be able to grow and produce chestnuts anymore. Also, soil organic matter levels would have dropped dramatically (without new N inputs) as nitrogen is a principal component of SOM. This has not happened, as I personally observed dark topsoil layers in the chestnut orchards in the Ardèche. This indicates that there have been annual inputs to compensate (at least part of) the N removal with crop harvests. Atmospheric nitrogen deposition cannot solely explain this as levels are relatively low in the Ardèche and Corsica. Rock weathering could explain part of the inputs, and nitrogen fixation by free-living microorganisms as well as N-fixing shrubs growing in the orchards, have probably played an important role in balancing the nitrogen balance.

To give an answer to this paper's research question, I will make several calculations that show *the time that it takes until the soil nutrient stocks of N and P are depleted by 50%* with annual harvests of nuts.

First, I provide an overview of minimum and maximum values for all the different inputs and outputs of a chestnut forest (as a blueprint for a more diverse food forest). I described all these inputs earlier in this paper. I also mentioned the different values that can be found in literature. These data are listed in Table 4.

Second, I make a nutrient balance for both the low and high values of all those inputs and outputs for both nitrogen and phosphorus. This nutrient balance provides insights into the fate of the nutrients. Negative balances mean that the soil is mined for nutrients and that it has a final lifespan for how long it can sustain productivity. Positive balances mean nutrients accumulate in the system. In this case, a system would never reach low nutrient levels. These calculations are simplified and show a wide range of possible outcomes. The goal of them is not to give a precise number, but to find out the order of magnitude that we are talking about.

Assumptions:

- Atmospheric deposition ranges from 1->40 kg in densely-populated areas. Because high N-deposition levels (>9 kg per ha per year), increase leaching and, hence, influences the input : output balance, I will only consider the situation of <1-9 kg atmospheric deposition, which is appropriate for many regions of the world and is the aim of emission reductions [98].
- Annual chestnut DM yield is 2000 kg per ha per year, resulting in 21 kg of N and 2.5 kg of P being removed via the nut harvest.
- Erosion rates are very low because of the thick litter layer and canopy, reducing the rain's impact on the soil.
- Gaseous emissions are low due to the lack of fertiliser inputs and relatively low atmospheric deposition rates.
- N-fixation via free-living micro-organisms is difficult to measure which is why different studies show a range of values. Especially the upper limit for food forest systems is unknown, but based on wheat cultivation in a conventional tilled disturbed system, at least 30 kg per ha can be expected. This value is used for the calculations, but I suspect higher values are realistic for relatively undisturbed food forest systems.
- No N-fixing plants are considered in these calculations, while in reality several of these plant species can occur in chestnut forests.
- 50% of the total soil nutrient pool can, over time, be accessed. This is merely a theoretical value, indicating that equilibrium reactions cause the dissolution of reacted phosphorus (unavailable pools) into the soil solution (available), or mycorrhizal uptake from the plant-unavailable pools.
- Even when nutrient pools are reduced, I assume that the trees are still able to acquire sufficient nutrients to sustain the 2 000 kg per ha yield.

Table 8. Input and output data, both low and high estimations, as obtained from reviewed literature on forest ecosystem inputs and outputs.

	Inputs				Outputs			
	Rock weathering	Atm. Dep.	Bird inputs	N-fixation (free living)	Harvest	Leaching	Erosion	Gaseous emissions
P	0.3-5 [52]	0.2-1.1 [42]	0.07-0.5 [43]	-	2.5	Negligible**	0.03-0.06 [66]	-
N	0-10.9 [49]	1-9 [59], [37]	0.4-3.5 [43]	5-30 *[55]	21	<2 [98]	Negligible***	0-1.9 [67]

*studies on conventional agricultural systems show upper values of 30 kg per ha. However, undisturbed (food forest) soils are likely to harbour more free-living N-fixing organisms and this process might contribute to more than 30 kg N per ha.

**phosphate leaching is negligible over the timespan of several hundreds or thousands years. Only when considering > 10 000 years, P leaching can be a significant outflow of P. Perennial food forest crops have the advantage of obtaining leached P from deeper layers, so phosphate leaching is even further reduced.

***nitrogen losses via soil erosion are considered to be negligible for food forest systems due to the superior erosion control in these systems. The reason that nitrogen erosion rates are listed (and phosphorus erosion rates not) is because the total annual fluxes of phosphorus are much smaller than those of nitrogen and therefore even small erosion rates can have some impact (which is not the case for nitrogen).

Nutrient balances show whether a system is accumulating nutrients or whether it is mining the soil for nutrients. Table 9 shows the nutrient balances for N and P for both low and high estimated inputs and outputs. These inputs are the sum of the inputs provided in Table 8. For example, nitrogen low indicated in the Table 9 is 6.40 kg (and this is the accumulation of 0 (rock weathering) +1 (atmospheric deposition) +0.4 (bird faeces) +5 (N-fixation by free-living microorganism)). On average, the system seems to accumulate both nitrogen and phosphorus. However, in the case of the low input and output scenario, nitrogen and phosphorus balances are negative indicating that it *could* be possible that the system is mining the soil for nutrients.

The reason that I include these balances is not to show the precise number because the balance is dependent on many local site characteristics like moisture, topography, etcetera) and I cannot provide *the* right number just based on literature data.

I show the best possible estimations from low to high values for the different inputs and outputs because it provides us the *potential range of scenarios* that these chestnut systems face. In appendix A, besides the low and high values for all the inputs and outputs, the average values can be found as well, in Table A1 the inputs and in Table A2 the outputs.

With both the high and low values I will show a calculation of *the time required for the chestnut systems to mine 50% of the soil's initial nitrogen and phosphorus*. This gives insights into the lifespan of perennial systems and helps answer the question whether it is necessary to fertilise food forest systems.

Table 9. Low, high and average nitrogen & phosphorus balances based on the range of input and output values summarised in Table 8. The nutrient balance indicates if nutrients are mined from the soil (negative values) or if nutrients accumulate in the soil (positive values).

	Inputs	Outputs	Nutrient-balance
Nitrogen, low	6.40	21.00	-14.60
Phosphorus, low	0.57	2.53	-1.96
Nitrogen, high	53.4	24.90	28.50
Phosphorus, high	6.60	2.56	4.04
Nitrogen, average	29.9	22.95	6.95
Phosphorus, average	3.59	2.55	1.04

In Fig. 3 I made a representation of the actual nutrient uptake situation for (food) forest systems in northern temperate regions. Of course, soil depth varies a lot as does soil type and nutrient levels. In some European countries, soils can be many metres deep while in other countries soils are no thicker than several decimetres and are underlain by a bedrock layer. Due to these difference, I came up with a generalised scenario consisting of a soil layer of two metres and a bedrock layer of which two metres can be accessed.

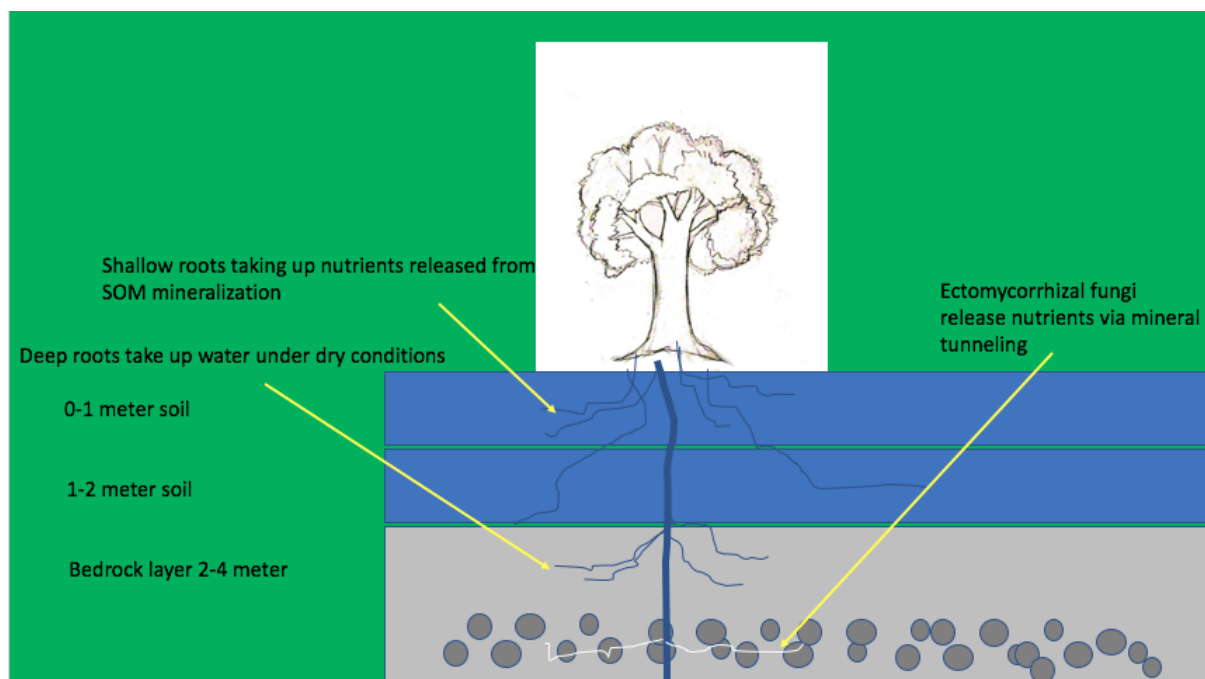


Figure 3. The designed scenario used for the calculations that follow. One ha of chestnut trees on a soil of two metres deep underlain with a bedrock layer. Plants can root down to 4 metres in this scenario, so 2 metres into the bedrock layer. In this bedrock layer, ectomycorrhizal fungi are an important coalition partner to weather the rock minerals and to release the contained N and P.

I already provided an overview of the range of phosphorus and nitrogen values found by different studies in Table 4. For the calculations based on the scenario illustrated in Fig. 3, I had to choose the most appropriate values (listed in Table 10 and 11). Therefore, from all the studies listed in Table 4, I selected the studies that were done in *temperate* regions and ignored the tropical studies (because this paper focuses on food forest systems in temperate zones).

Furthermore, I used different studies for different depths simply due to a lack of data. For example, if one study only looked until 100 cm, I chose this one for the first metre. If another study provided results for 100-200 cm, I used this one for the remaining metre of soil. In most cases, the 0-100 cm layer had ample data, so I could select both a low and a high value.

However, in the cases of 100 to 200 cm depth, due to a lack of studies investigating the total phosphorus and nitrogen stock of this depth, I chose to work with one value for both the high and low

scenario because there was only one study that indicated the content of this layer (for P and for N). Of course I evaluated the given value to find out if it was appropriate or an outlier.

The phosphorus value I used (8000 kg per ha) could be on the high end of the spectrum because it was measured in rich loess soils. This is something to keep in mind when analysing the results of the calculations. The nitrogen content seems reasonable comparable to other literature data. For the bedrock, I used the same values listed in Table 4, but doubled them because I considered a bedrock layer of 2 metres. The studies from which the values used in Table 10 & 11 were chosen are listed between brackets (reference) in Table 10 & 11.

Depending on the nutrient (phosphorus or nitrogen), I used different scenarios which are listed below.

I made the following assumptions for **phosphorus**:

- trees root until 4 metres depth, so 2 metres into the bedrock layer.
- annual P loss via chestnut harvest is 2.5 kg
- a *carbonate* bedrock underlies the soil with a P content of 11 132 kg P per 1 m layer per ha.

Table 10. Total phosphorus content of the different soil and bedrock layers. Both low and high values are listed if sufficient data were provided by literature.

Layers (m)	P content low	P content high	P content average
0-1	1 685.0 [81]	8 328.0 [82]	5 006.5
1-2	8 000.0 [83]*	8 000.0 [83]*	8 000.0
2-4	22 264.0 [85] **	22 264.0 [85] **	22 264.0
total soil P (0-2)	9 685.0	16 328.0	13 006.5
total (soil + bedrock)	31 949.0	38 592.0	35 270.5

* Only one study clearly indicated the P content of the 100-200 cm layer. That is why the low, high and average value are the same. They all come from this single study.

**as mentioned earlier, I chose to work with a given scenario that consisted of a bedrock type of carbonate in the case of phosphorus. That is why I use the same value for both low and high scenarios. However, there are several other types of bedrock that have markedly higher P content meaning that total P stock in the bedrock layer might be even higher in food forests on other than carbonate bedrock.

For **nitrogen** stores, I made the same calculations with the assumptions:

- trees root until 4 metres depth, so 2 metres into the bedrock layer.
- I used the earlier calculated N content of Mica-schist bedrock as a high N content bedrock type and the calculated N content of Diorite-gabbro bedrock as a low N content bedrock type. I multiplied the calculated values by two to get the N content for a two-metre deep layer. The reason why I chose to use two different bedrock types in the case of nitrogen, and not for phosphorus, is because bedrock high in nitrogen is much rarer than phosphorus-rich bedrock. As can be seen in Table 11, the 3 190 kg nitrogen per ha in a two-metre thick bedrock layer is a relatively low nitrogen content compared to the carbonate bedrock used for phosphorus (22 264 kg per ha) which is a relatively phosphorus-poor bedrock. Therefore, for phosphorus, the low spectrum is already a high value, and including even higher phosphorus bedrock does not add much value.
- annual N removal off site is 21 kg per ha (via crop harvest).

Table 11. Total nitrogen content of the different soil and bedrock layers. Both low and high values are listed if sufficient data were provided by literature.

Layers (m)	N content low	N content high	N content average
0-1	3050 [82]	21940 [82]	12495
1-2	4500 [83]*	4500 [83]*	4500
2-4	3190 [49]	36828 [49]	20009
total soil P (0-2)	7550	26440	16995
total (soil & bedrock)	10740	63268	37004

* Only one study clearly indicated the N content of the 100–200 cm layer. That is why the low, high and average value are the same. They all come from this single study.

Now that I showed a rough estimation (with high and low values) of P and N levels up to four metres deep in northern temperate areas of the world (Table 10 & 11), I can show the potential lifespan of perennial systems like the chestnut system described earlier. As I showed, P and N removal via chestnut harvests with a high yield of 2 000 kg DM chestnuts (about 4 tons fresh weight) are 2.5 and 21 kg, respectively. I made the following assumptions:

- above-mentioned yields are the average yields for a period of several centuries.
- *no* new P and N inputs occur.
- leaching and erosion of nutrients are negligible.
- the trees can acquire *50% of the P and N in the soil layer (0–2 m) over time*.
- *no* rock mineral weathering occurs.
- even when N and P pools become smaller due to continuous removal via harvests, trees can continue to acquire all the nitrogen and phosphorus needed to yield 2000 kg DM chestnuts.

N-lifespan would be $16\ 995/2/21=405$ years.

P-lifespan would be $13\ 007/2/2.5=2\ 601$ years

This calculation provides an insight into the magnitude of time needed to remove 50% of the nutrients from site.

To include the several inputs and outputs listed above, I calculated the nitrogen-lifespan for several situations (including the one mentioned above).

- “no inputs, harvest only”: the only output is the harvest (this is the one above).
- “5% rock weathering, harvest only”: from the bedrock layer (2–4 m) 5% of the total nitrogen contained by this layer is taken up by the trees, no further inputs and the only output is the crop harvest.
- “10% rock weathering, harvest only”: same as previous one, only difference is a 10% instead of 5% rock weathering.
- “atm. dep. & bird dep. , harvest only”: two different inputs (atmospheric deposition and bird deposition) and the only output remains harvest.
- “atm. dep. & bird dep. , harvest & leaching & gaseous emissions & erosion”: two different inputs of nitrogen (atmospheric deposition and bird deposition) and all the different outputs: harvesting, soil erosion, gaseous (N₂O&NO) emissions and nitrate leaching.
- “atm. dep & bird dep. & N-fix. (freel.), all outputs”: contains all inputs except rock weathering as well as all outputs.

I choose to calculate these different scenarios because it is impossible with the current data to come to *one* value which is *the true value*. There is significant variation in processes like rock weathering rate, N deposition and N leaching. To illustrate the order of magnitude, which is the focus of this research, (and not to come with an exact value) I show the system’s lifespan for different scenarios to prevent under- or overestimations. For example, the first ‘no-inputs, harvest-only’ scenario does not even consider the other inputs and outputs besides harvest losses of N and P. This scenario simply assumes an annual nitrogen and phosphorus removal via chestnut harvest. Therefore, this scenario can be used as an indication of the *minimum time* needed until 50% of the nitrogen and phosphorus are taken up from the soil.

For each scenario, I calculate the time until 50% of the nitrogen contained in the 2-metre soil layer has disappeared (as a reasonable estimation of the total potentially obtainable pool, probably even an underestimation) under the above-mentioned different input and output scenarios. Three different values are calculated: a low and high lifespan value and an average lifespan value. These values are based on the different (low and high) total soil and bedrock nitrogen and phosphorus values mentioned in Table 10 & 11. Note that the average lifespans in Fig. 4 are not always the mean of the high and low bars, which might be confusing. The average values are calculated by averaging low and

high N values as reported in the literature. When calculating these averages per scenario via this pathway, other values are obtained than when you would divide the two accumulated low and high values by two. This might seem strange, but it has to do with the way the calculations are made in the Excel file. The presented average values are actually appropriate means calculated by Excel in a different way and do not differ enormously with the averages one would obtain by averaging the two extremes. Hence, these presented values should be used as averages.

Furthermore, I assume that the trees remain capable of taking up sufficient nitrogen to support a 2 000 kg DM chestnut harvest, even after centuries with shrinking nitrogen pools. This is probably an overestimation of the potential uptake after a while, but to make the estimations clear yet informative, I choose to use a constant N uptake rate. The results of these calculations are presented in Fig. 4.

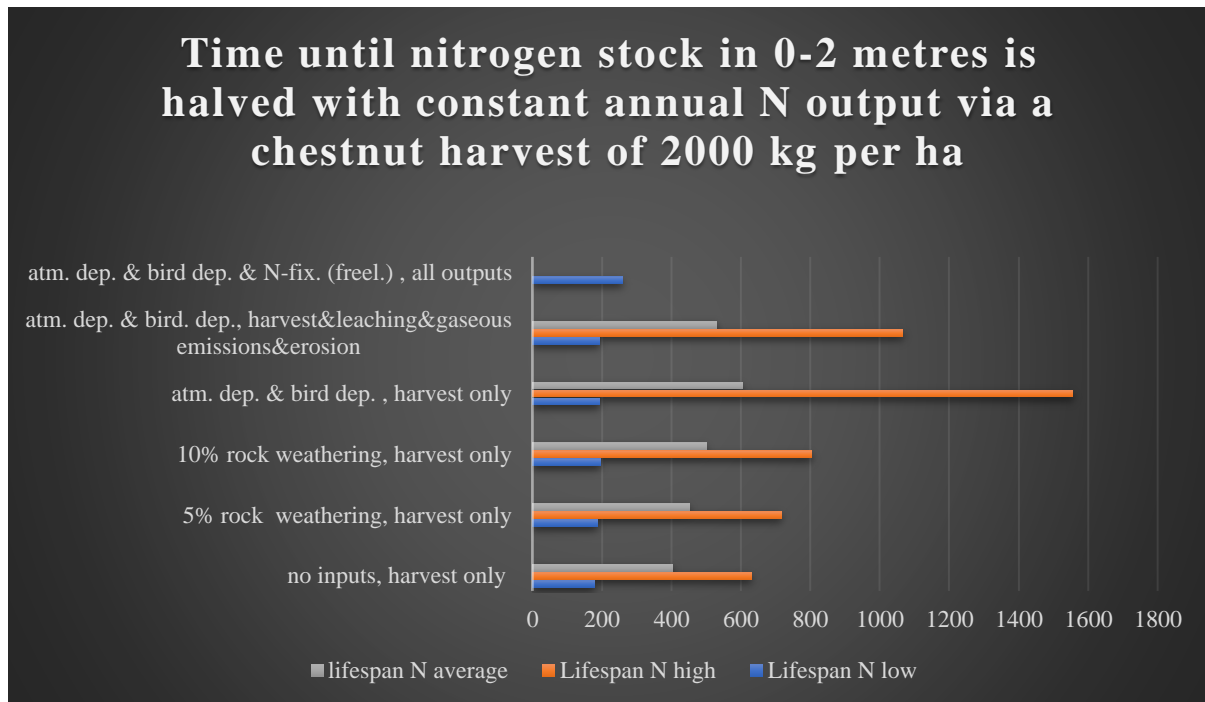


Figure 4. The time needed to reduce soil nitrogen stock by 50% for different input/output scenarios for a chestnut orchard. Low, high and mean values are reported based on the range of reported inputs and outputs as listed in Table 9 and based on the range of initial soil nitrogen stock as listed in Table 11.

In general, average time needed to reduce soil N stock by 50%, ranges between 405 and 605 years. See Fig. 4 & Appendix Table B1. The situation without inputs and only chestnut harvests as output, has the lowest mean N lifespan of 405 years. When I added rock mineral weathering as an N input to the soil, mean lifespans increased up to 452 and 500 years for the 5% and 10% weathering, respectively.

Due to the large variation in atmospheric nitrogen deposition, with reported rates higher than 40 kg of deposited N per ha per year, including atmospheric deposition as an input increased maximal N lifespan a lot. In this model, I only used a range of 1-9 kg for low and high values. I did so, because if levels are >9 kg per ha per year, leaching can increase dramatically in forest ecosystems thereby altering the outputs as well. To prevent this issue, I used maximum nitrogen deposition values of 9 kg N per ha per year, and using this number, maximal N lifespan increased up to 1 555 years.

The top graph representing the low estimation of the N lifespan is the only graph that could be made for the top scenario.

Taking the maximal or even the average values for all the inputs and outputs would result in indefinite lifespans as the N balance would be positive (Table 9). Therefore, these are not shown in Fig. 4 but it indicates that in a well-aggregated soil, free-living N-fixators might already push the balance to the positive side indicating there is net N accumulation in the system even while chestnuts are harvested.

Symbiotic nitrogen fixating plants are not included here but looking at the graphs, including them will quickly result in a positive N balance, hence, no reduction in N pools over the years.

For phosphorus, I calculated the following scenarios:

- “no inputs, harvest only”: the only output is the harvest.
- “5% rock weathering, harvest only”: from the bedrock layer (2-4 m) 5% of the total phosphorus contained by this layer is taken up by the trees, no further inputs and the only output is the crop harvest.
- “10% rock weathering, harvest only”: same as previous one, only difference is a 10% instead of 5% rock weathering.
- “atm. dep. & bird dep. , harvest only”: two different inputs (atmospheric deposition and bird deposition) and the only output remains harvest.
- “atm. dep. & bird dep. , harvest & leaching & erosion”: two different inputs of phosphorus (atmospheric deposition and bird deposition) and all the different outputs: harvesting, soil erosion and P leaching.
- “all inputs and outputs (incl. rock weathering)”: contains all inputs (but only shows the low P lifespan because the average and high lifespans could not be plotted due to a positive P balance suggesting P accumulation over time.

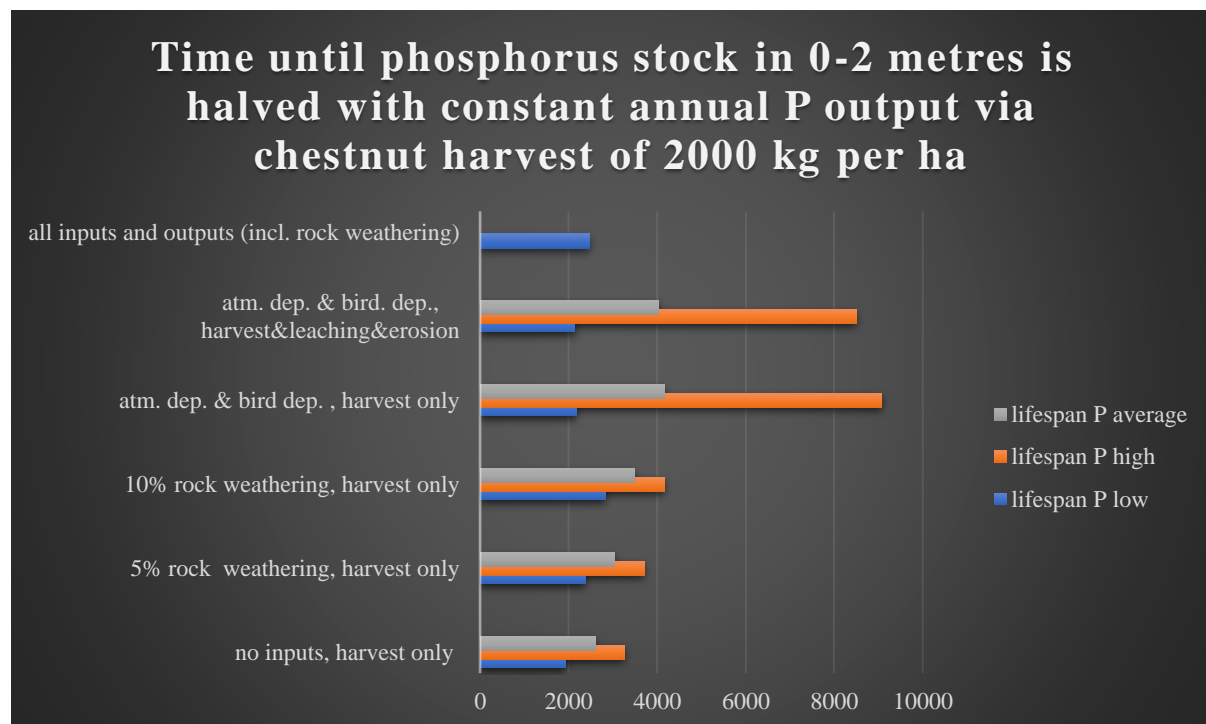


Figure 5. The time needed to reduce soil nitrogen stock by 50% for different input/output scenarios. Low, high and mean values are reported based on the range of reported inputs and outputs as listed in Table 9 and based on the range of initial soil phosphorus stock as listed in Table 10.

For phosphorus, the average lifespan is much higher than for nitrogen with the average time needed to reduce soil P stock by 50% ranging from 2 601 and 4 155 years. See Fig.5 & Appendix Table B2. Rock weathering rates of 5 and 10% increase lifespan up to a maximum of 3 492 years. However, when rock weathering is neglected but atmospheric deposition and bird faeces are included, maximal P lifespan increases even more up to 9 071 years. When all the outputs, atmospheric deposition and bird faeces are included, lifespans are slightly reduced (due to the increased losses). However, when all *inputs* including rock weathering are included, only the low P lifespan values can be displayed because the average and high values are

negative due to the positive P balance, meaning that with average and high rock inputs included, there is a slight net accumulation of P in the system (Table 9).

These results show that there is a wide range of potential outcomes considering P stocks in the chestnut system. Nonetheless, lowest P lifespans are 1 937 years which is a long period of time compared to the nitrogen lifespans.

These model outcomes explain why the centuries old unfertilised chestnut orchards of the Ardèche and Corsica have been able to continue bearing nuts. As mentioned earlier, a 250-year continuous chestnut harvest of, on average, 1 600 DM per ha per year, would result in a total P loss of 492 kg. Even when considering the smallest soil phosphorus stock listed in Table 10, without considering P inputs or other outputs, the 0-2 m soil layer would still contain $9\ 685 - 492 = 9\ 193$ kg of P. With high P estimations, there would even be $16\ 328 - 492 = 15\ 836$ kg P left in the top 2 metres of soil.

Looking at the bottom graph in Fig. 5 (without inputs and only outputs via crop harvesting as calculated in the 492 kg), average lifespan would be 2 601 years before *half* of the total P pool listed in Table 10 would be lost. Therefore, after 250 years, the system could continue to yield for more than 2 351 years (since the graph shows the calculations for 2000 kg DM yield, and the 492 kg of P is calculated for a 1600 kg DM yield average over the 250 years, meaning that yields could be sustained even longer than the calculations show).

When we take inputs like atmospheric deposition and outputs like leaching into account (while still neglecting rock weathering), the remaining P stock in the soil is even higher with an average value of $13\ 007 - 492 = 12\ 515$ kg. This would translate in a remaining lifespan of 3 789 years (assuming the 2 000 kg DM harvest) before the soil P stock would be halved.

Nitrogen shortages could pose an earlier risk of production limitations than phosphorus shortages. 250 years of chestnut harvesting (as only output) would result in a nitrogen loss of 4 228 kg N.

Considering the aforementioned average N pool of 16 995 kg N per ha and the low estimations of 7 550 kg per ha (Table 11), N pools could be significantly exhausted after 250 years of cropping. Since some Corsican orchards have been producing nuts for more than 450 years, these nitrogen outputs would result in 7 610 kg N lost which is more than the low scenario soil contains. Therefore, two potential situations are possible:

- N stocks are indeed drastically reduced after long periods of chestnut cultivation. If this would be the case, chestnut yields are likely to slowly decrease as nitrogen shortages are increasing. This production decrease is not observed so this scenario is unlikely applicable to the chestnut orchards.
- N stocks have been (partly) replenished. This scenario seems most plausible because of the relatively high SOM levels observed in these orchards. The fact that high SOM levels are still there after 250 years of cropping mean that there is still adequate N in the system to build the SOM as N is a principal component of it. Therefore, I think that N stores have been partly restored due to different inputs like atmospheric deposition and (free-living) nitrogen fixators mainly. As mentioned earlier, with relatively modest N inputs via free-living N-fixing microorganisms, N balances could easily become positive suggesting nitrogen accumulation instead of nitrogen losses. Combined with some N-fixing bushes in these orchards, biological N-fixation could replace at least to a certain extent the N lost via crop harvests.

These calculations show the time that a chestnut forest would be able to grow (while passing all assumptions stated earlier) and produce nuts before P and N soil stocks would be halved.

Furthermore, the data explain how it has been possible for chestnut systems in Corsica and the Ardèche to continuously produce a crop of yearly nuts for centuries long. The chestnut trees have been capable of obtaining the required P and N from the diminishing soil nutrient stock and, hence, show that it is possible for food forest-like systems to continue obtaining the required P and N to sustain relatively good harvests for centuries long.

The major question is what level of harvest is supported via the natural soil food web nutrient delivery pathway, but unfortunately it is impossible to accurately estimate this due to a serious lack of data for

perennial unfertilised systems. However, as mentioned before, a healthy mature chestnut tree gives about 100 kg of fresh nuts per year. With about 40 trees per ha this results in about 4 ton fresh nuts or 2 tons dried nuts. The caloric content of chestnuts is about 1880 kcal per kg fresh weight so 4 tons of fruit results in about 7 520 000 kcal per ha per year produced via the chestnuts. The world average *net* wheat yield is about 6 500 000 kcal per ha, indicating that net chestnut yield in kcal is higher than net wheat yield [99]. However, comparing the system with the *net* world's highest wheat yield of about 18 600 000 kcal per ha, shows that the chestnut system is much lower than the wheat system. This is mainly attributable to assimilate allocation to wood production (over nut production). Nonetheless, this shows that a non-fertilised perennial system (which can be considered as a blueprint of a food forest) can produce relatively high caloric food product outputs due to nutrient cycling via the soil food web.

Summing up the obtained insights considering the chestnut food forest example:

- it takes several hundreds of years before nitrogen stocks are halved considering the scenarios without N inputs and, hence, a negative N-balance (mining).
- when taking into consideration *some* relatively low inputs like atmospheric deposition and bird faeces inputs, the time until half of the N stock is gone increases with several hundreds of years up to about 600 years.
- when considering a positive nitrogen balance, mainly because of free-living N-fixing organisms, N pools slowly accumulate and nitrogen will not become in short supply.
- it takes about 2000 years before phosphorus stocks are halved considering the scenarios without P inputs and, hence, a negative P-balance (mining).
- Including some P inputs from atmospheric deposition and bird faeces, this estimation increases up to about 4 000 years.
- Including all inputs and outputs results, on average, in a positive P balance, suggesting that in some cases, P will accumulate in soils (during young soil development phases at least) and soil P pools will not become scarce.
- These calculations assume continuous adequate N and P uptake by the trees which could be an overestimation of the trees' capacities. However, there are some rare examples of perennial systems that have maintained their production rates for centuries without fertiliser inputs (like chestnut forests in Corsica and the Ardèche, as well as the famous Dehesa system in Spain) showing at least that this uptake *can be continued*.
- The first key characteristic explaining the long time required for significant P reductions of the soil stock is the low P export via crop harvesting. Most annual cropping systems remove several tens of kilos P per year, while the chestnut system only loses about 2.5 kg per year. This is characteristic for many fruit (including chestnut) trees and might be the secret to sustained yields as natural soil food web processes can keep up with the rate of P losses to compensate for it.
- The second key characteristic explaining this long time before P stocks are seriously reduced is the extensive root network combined with the interactions with beneficial organisms like mycorrhizal fungi, enabling the trees to obtain hard-to-access nutrient pools (especially useful for P acquisition).

Hazelnut system

One of the clues for this long time period is the low phosphate export via crop harvests. This is a trait we observe in most fruit trees (and chestnuts). Nut trees, on the other hand, are characterised by the high protein content and subsequent nitrogen content of the nuts. Therefore, with the same assumptions as the calculation for the chestnut system, I will now present the case for hazelnuts as a proxy for most northern nut trees. I use the data from Table 9 & 11 and substitute the crop harvest output data of the chestnuts with the crop output data of hazelnuts.

First, I consider a hazelnut system with a yield of 1 200 kg per ha (moderate yield) and later I consider a high-yield hazelnut system of 2 000 kg nuts per ha. I will only show the results for nitrogen because P contents are relatively low (about 3.48 kg P per year per ha for a DM yield of 12

00 kg and therefore P lifespans are still very high). Per ha, for a 1 200 kg yield, about 34 kg of nitrogen is exported off site with the annual hazelnut harvests (box 5).

Box 5. Hazelnut system annual nitrogen removal for a moderate yield.

Hazelnuts have a protein content of about 15 g per 100 g DM hazelnuts. N-content is thus $150/5.3 = 28.3$ g per kg DM [97]. Hazelnut yield varies between countries and I chose a fairly low value of 1 200 DM per ha per year [100]. $1\ 200 * 28.3 / 1\ 000 = 33.96$ kg N per ha per year.

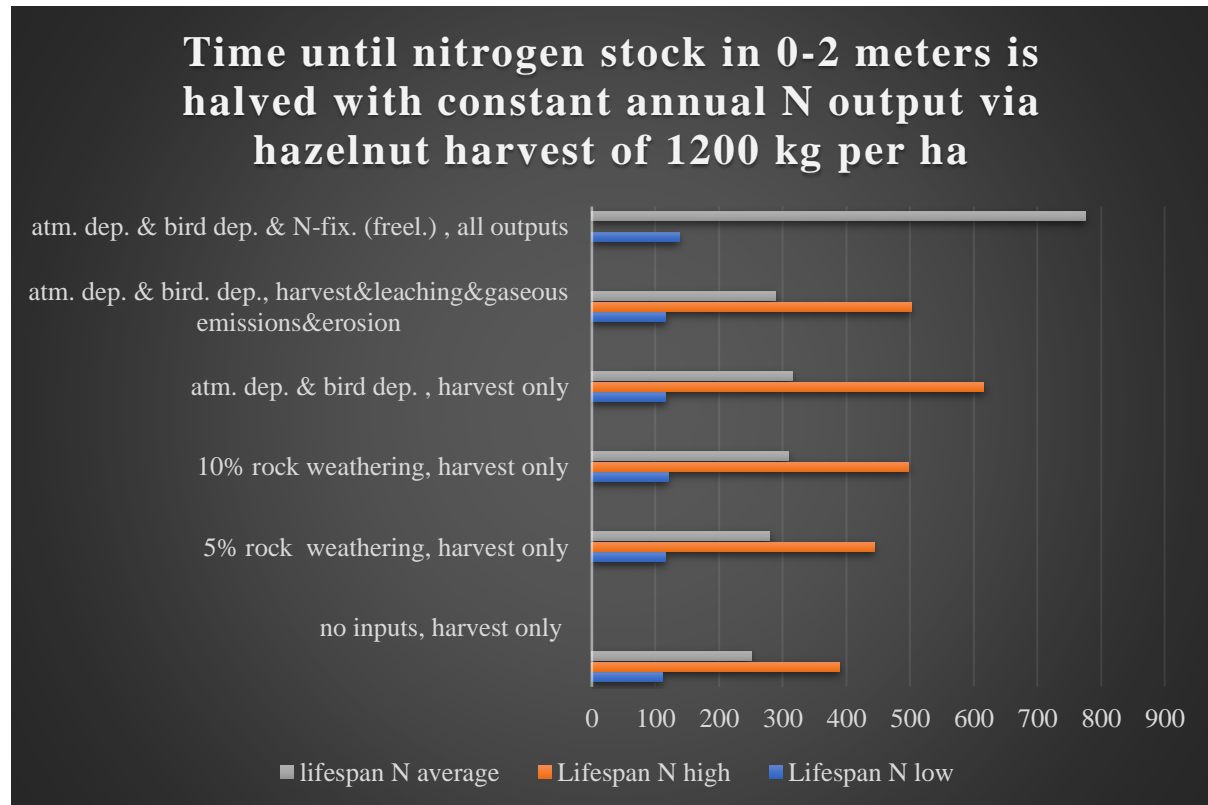


Figure 6. The time needed to reduce soil nitrogen stock by 50% for different input/output scenarios. Low, high and mean values are reported based on the range of reported inputs and outputs as listed in Table 9 and based on the range of initial soil nitrogen stock as listed in Table 11.

The hazelnuts show lower N lifespans compared to the chestnuts. The first scenario “no inputs, harvest only” shows it would take 250 years on average to reduce soil N content with 50% whereas the chestnut system would require 405 years to do this.

In the top scenario with all inputs and outputs considered, there are significant differences as well. The chestnut system’s nitrogen balance would be positive in the case of high and average calculations (Table 9), so only the low lifespan is shown in Fig. 4 of 259 years.

In the case of the hazelnuts however, besides the low value, the average value had a negative balance so could be calculated and displayed as well. This value is high (775 years). Only the high lifespans would have a positive N balance so they could not be displayed. See Appendix Table C1 for all the exact values used to create Fig. 6.

Table 12. Hazelnut nutrient balances for a system with moderate yields (1200 kg DM per ha).

	Inputs	Outputs	Nutrient-balance
Nitrogen, low	6.4	33.96	-27.56
Phosphorus, low	0.57	3.51	-2.94
Nitrogen, high	53.4	38.86	14.54
Phosphorus, high	6.6	3.54	3.06
Nitrogen, average	29.9	36.41	-6.51
Phosphorus, average	3.585	3.525	0.06

In Table 12, I calculated the nutrient balances for both nitrogen and phosphorus for the low, high and average situations. Like the chestnut system, the hazelnut system shows negative balances for the low scenarios. However, unlike the chestnut system, the hazelnut system shows negative *average* nitrogen balance suggesting that the system is slowly mining the soil's nitrogen pool. The average phosphorus balance is just positive (0.06), but can be considered 0 meaning the rates of input and output of phosphorus are equal.

These results suggest that food forest crops high in protein (like walnuts, hazelnuts and pecans) could have a tendency to take up more nitrogen and phosphorus from the soil compared to a low nitrogen and phosphorus crop like chestnuts. Furthermore, the hazelnut yield considered in this example was modest. A higher yield would definitely be necessary if a system based on perennials like hazelnuts were to compete with conventional agricultural systems. Therefore, I also made this analysis with a higher yield of 2 tons DM per ha which can relatively easily be reached with appropriate cultivars.

Nitrogen outputs per ha per year are now 56.6 kg N per year (almost doubling the 1 200 kg yield nitrogen output) and phosphorus outputs are 5.8 kg per ha. Therefore, for each scenario, the N lifespans also decrease on average by almost 50%. In this case, in many scenarios the low N lifespans are estimated as less than a century.

Furthermore, the top scenario with all inputs and outputs except rock weathering shows the low, high and average values for the first time because for all three, the N balance is negative, indicating the hazelnuts are mining the soil for N which cannot be replenished quickly enough (Fig. 7).

Time until nitrogen stock in 0-2 meters is halved with constant annual N output via hazelnut harvest of 2000 kg per ha

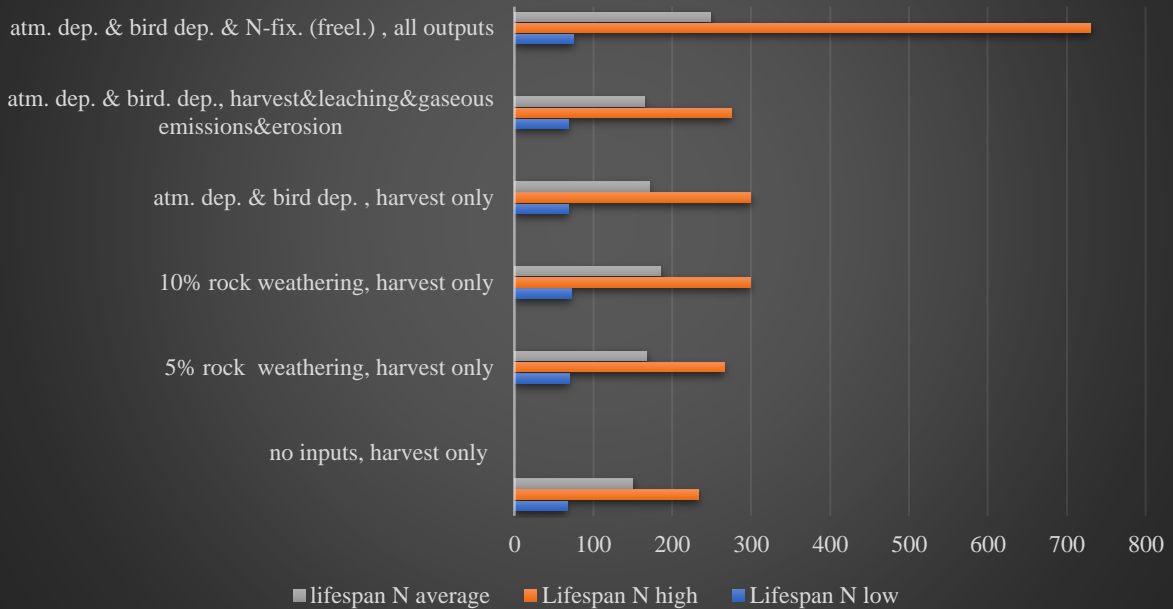


Figure 7. The time needed to reduce soil nitrogen stock by 50% in a high-yield (2000 kg per ha) hazelnut system for different input/output scenarios. Low, high and mean values are reported based on the range of reported inputs and outputs as listed in Table 9 and based on the range of initial soil nitrogen stock as listed in Table 11.

The N balances belonging to the 2000 kg hazelnut yield calculations are given in Table 13. See Appendix Table C2 for all the exact values used to create Fig. 7. The situation has dramatically changed compared with the 1200 kg hazelnut yield and especially compared with the chestnut system. The average N and P balances are both negative, and quite significantly. This indicates strong N- and P-mining of the soil which is unlikely to be compensated by inputs. In fact, the only positive nutrient balance is in case of a high phosphorus input scenario, with a balance of 1.54 kg per ha per year.

These results suggest that food forests with a high coverage of nut plants (like hazelnuts) should receive a source of nitrogen to prevent nitrogen mining and soil fertility losses. Incorporation of nitrogen-fixing trees would be highly recommendable in this case. Phosphorus deficiency is probably no problem at all in the first centuries. As the yearly P removal of 5.8 kg is about double the rate of P removal for chestnuts which have average P lifespans of more than 2 000 years, the time when P stocks of the soil will be halved will probably be about a thousand years. But still, if food forest systems are to be maintained for hundreds of years, P fertilisation could be required to sustain production after several hundreds of years.

Table 13. Hazelnut nutrient balances for a system with relatively high yields (2000 kg DM per ha).

	Inputs	Outputs	Nutrient-balance
Nitrogen, low	6.4	56.6	-50.2
Phosphorus, low	0.57	5.8	-5.26
Nitrogen, high	53.4	61.5	-8.1
Phosphorus, high	6.6	5.86	0.74
Nitrogen, average	29.9	59.05	-29,15
Phosphorus, average	3.585	5.845	-2.26

Conclusions

- Tree crops with a fruit/nut high protein content like hazelnut, walnut, and pecan need more nitrogen than low-protein fruit trees like apples, pears and chestnuts.
- Average yield calculations for hazelnuts show that N-stocks might be reduced by 50% after >100 years, which is faster than in the case of chestnuts.
- Soil P stocks decline slower than nitrogen stocks and therefore nitrogen will become the first limiting nutrient in the hazelnut system without additions.
- However, in the case of all inputs and outputs (except rock weathering which might be a significant input in certain systems underlain by nitrogen-rich bedrock), the average harvest hazelnut system might still be in a positive N-balance as indicated by the lack of high N lifespan in Fig. 6 meaning that the system would accumulate nitrogen in the soil.
- Concerning all the nitrogen inputs and outputs (N balance), the negative balances can be corrected by inclusion of some area allocated to nitrogen-fixing trees within the system.
- In the case of high-yielding hazelnut bushes, the N-balances are all negative (concerning all inputs and outputs), even the high input-output scenario. This indicates that the harvest intensity outcompetes the natural input processes of nitrogen which could lead to the 50% reduction of the soil N-stock within several decades.
- In the case of high-yielding hazelnut bushes, inclusion of tree N-fixators (or external fertilisers) are crucial to replenish the soil N pool.

Plant breeding

When the first agricultural civilisations developed thousands of years ago, the main cultivated crops were (annual) grains. The highest yielding individual grasses were selected and its seeds were planted the next growing season. Over time, this selection process improved grain yields drastically resulting in expanding cities. Now, millennia's later, most genetic breeding programs are still focused on annual crops like wheat, rice and corn. The genetic improvements translated into increased crop yields.

The most famous production improvements could well be the selection of dwarf rice and dwarf wheat varieties during the Green Revolution. Norman Borlaug, who won the Nobel Peace Prize in 1970 for his work, created a dwarf variety of wheat that allocated a larger share of its assimilates to the grains (the wheat) rather than to long stems. He basically altered the plant's energy allocation pattern. Similar work resulted in large increases in rice production. From the 1960s through the 1990s, rice and wheat yields *doubled* in Asia [101].

Genetic breeding has also created >3 metre high corn plants that beat any other food crop with a per ha calorie production of >35 million calories (in the United States), while record yields of >100 million calories per ha have been observed [102]. Part of the explanation for this yield number is the C4-photosynthetic pathway contained by corn plants and of course the high levels of fertilisation. This C4-pathway enables plants to photosynthesise more efficiently than C3 plants like wheat. Corn's ancestors were grasses native to Mexico commonly known as teosinte. Biological evidence uncovered in Mexico suggests that maize was domesticated from its wild ancestors 8 700 years ago. Teosinte shows heavy branching from the stalk resulting in tiny ears with just a few hard maize kernels. Selection of individuals with less branching resulted in individuals with a lower number of ears, but with more kernels per ear. Over time, the hard case around the kernel disappeared and the number of kernels per ear increased.

The end-product is modern-day corn which dominates the countryside and is used predominantly as feed crop and biofuel crop, rather than for human nutrition [102].

However, unlike dozens of annual crops that form the bulk of our current diet, many perennial tree crop species that are grown including walnuts, hazelnuts and pecans have undergone very few cycles of controlled breeding (if any) [103].

The problem with many perennial fruit and nut crops is the long waiting period. For many fruit species such as apple, pear and plum, it can easily take 5 or even 10 years before the tree will first fruit. Therefore, breeding improvements are much harder to accomplish compared to annual crops which perform their entire life cycle in just a few months. However, a successful example can be found in the breeding of plums at the Appalachian Fruit Research Station. Researchers isolated a fast flowering gene from Californian Poplar (*Populus* spp.) and transformed it into plum (*Prunus* spp.) resulting in a shortening of the breeding cycles from five years to only one year [103].

This technique could dramatically increase the breeding potential of perennial crops and could result in markedly improved crop yields. However, this technique is not undisputed as many people are against the use of genetically modified organisms.

There are also possibilities to breed early flowering trees via conventional breeding. Mark Shepard, a permaculture tree crop pioneer from Wisconsin, uses mass seeding to select interesting genotypes. For example, he has selected chestnut individuals which started flowering at age 2-3 instead of the more usual 8-15 years. Simply via chance events and mutations in the parent genome, deviating individuals can arise. He pollinated these early-flowering trees with pollen from high yielding chestnuts and some of the resulting seedlings contained both traits: early-flowering and high production. In this way, traditional plant breeding can also reduce the time until the first flowering event with several years for many fruit and nut species, which would greatly help with the establishment of new breeding programs for tree crops.

Probably the major reason why early human agricultural societies (and our current society as well) chose to work with annual grasses rather than perennial tree crops can be explained by the issues: reliability, fast cycle and storage.

Due to the fast cycle of annual grains, only months after sowing the seeds, harvests could begin. As I explained above, this does not apply to perennials and would therefore be a major drawback. Furthermore, annuals are more reliable as many perennials have cycles of heavy cropping and very low yields. Many nuts cannot be stored as easily as annual grains because of the high fat content. Without adequate storage, a certain part of the harvest can turn rancid, while starchy low-fat grass seeds do not experience this problem.

Many wild tree crops are already much more productive than their annual wild counterparts (which gave rise to modern wheat, rice and corn). In fact, large quantities of pecans and black walnuts grown in orchards were not the result of controlled breeding efforts but largely consist of cultivars that were developed by propagation of the best-performing trees in native forests or selected seedlings of those trees. Brazilian nuts are another famous example of a crop that has not been subjected to modern breeding efforts. Most of the exported nuts are gathered in the wild rather than in orchards. With the discovery that the Amazon is not as wild as we used to think, (early civilisations did select some perennial trees like the Brazilian nut tree and favoured them over wild ‘useless’ trees, thereby strongly affecting the forest composition of the area surrounding their settlements) we understood that there has been centuries-long genetic breeding of the Brazilian nut tree. Of course, this was not a controlled breeding program, simply a selection of seedlings of the best performing mature trees.

The same is true for other tree crops like black walnuts and pecans. The few cultivars released from recent breeding programs are mostly from first generation progenies. Although there are only a few nut tree breeding programs around the world (and most of them have been established only a few decades ago), the outcomes are promising.

However, the few breeding programs on nut crops are mainly limited to locations with breeding objectives focused on the needs of commercial industries, like the extensive walnut breeding program at the University of California. Breeding programs like this tend to neglect a large proportion of the total gene pool. For walnuts specifically, millions of Persian walnut trees are located in Eastern Europe, the Himalayas and China. Many of these places are poorly accessible (due to their remote and mountainous location in sometimes politically unstable regions). As a result, (Western) breeding efforts had limited access to the total global walnut gene pool, while traits such as fruit clusters with up to 20 nuts, precocious trees, dwarf trees, cold-hardiness and disease resistance have been observed. Including these genomes into global breeding programs has great promise for improved health and production of current orchards.

Already in the past decades, yields have increased dramatically. The average yield of walnuts in the United States in 2004 was 1.45 tons of shelled nuts per ha. However, recently developed hybrids in France like the ‘Lara’ variety could yield 5000 à 6000 kg per ha with only 8 years old trees [104]. In only three years time, from 1995 to 1998, the world average walnut tree yield increased from 1200 to 1750 kg, an increase from 46% [105]. A walnut grower in California even reached yields of > 6 000 kg per ha on irrigated land by reducing the plant-distance [106].

To give an indication of the contribution of such large per ha production, I calculated how many people could obtain 10% of their daily caloric need from just a single ha of walnuts producing 6 000 kg nuts. See Box 5.

Box 5. Per ha caloric production high-yield walnuts.

I used a caloric content of 675 kcal per 100 g dry nuts. The abovementioned 6 000 kg nuts could be dry weight, but is likely fresh weight. With an initial water content ranging between 15 and 50%, there is quite some variation. I decided to use an initial water content of 35%. After drying until 8%, weight has gone down by 27%, so total DM yield would be $0.73 * 6\ 000 * 675 = 30$ million kcal per ha [107].

If just 10% of the diet (of 2000 kcal) were to come from walnuts, then just a single hectare with 4 380 kg nuts ($29\ 565\ 000$ kcal per ha / 200 kcal per person = $147\ 825$) would provide 147 825 people with 10% of their daily dietary needs [103].

This example shows that a highly productive walnut orchard would be able (calorie-wise) with annual

staple food crops as corn (with U.S. average of >35 000 000 kcal per ha and indicates the potential global improvement via selection as well as management (irrigation, spacing, fertilisation).

Another (anecdotal) example of the difference in production between individual trees, comes from my own experience in Dutch forests. I know several chestnut trees (*Castanea sativa*) that produce exceptionally large nuts, at least the size of many commercial chestnut orchards. However, on the same soil just 50 metres further are other chestnut trees experiencing the same environmental conditions, but they have markedly lower production and much smaller chestnuts. Also, in the French Cevennes area, profound differences in nut production can be found between individual walnut trees. I personally observed a few individual (semi) wild trees with clusters of three to five nuts loaded with nuts while most trees had substantially less total nuts and nuts per cluster. Therefore, I would agree with the aforementioned articles which argue that production levels can be increased substantially through controlled global breeding programs.

Concerning the nutrient question of food forests covered by this paper, there are some promising opportunities to increase yields without increasing soil nutrient levels. The issue regarding many nut crops is that they are programmed to invest a lot of energy in height growth before, and even while producing nuts. Under natural conditions, individual trees would lose the battle for light when they would not invest heavily in height growth. Therefore, seedlings invest the first years or even decennia a lot of energy in gaining height and once they have reached a certain height, they start flowering and start producing nuts. However, in food forest systems in which nut trees do not have to compete for light (due to the design), nuts should ideally invest less energy in height growth and more in production. From the total amount of assimilates (made available via photosynthesis) a larger proportion can now go to the fruit set and nut production. There are many other characteristics that can be selected for or against to increase production levels.

Due to genetic improvements of nuts and fruit trees, food forests are expected to increase in productivity in the coming decades. However, the issue concerning the nutrients is as following: increasing production levels (due to genetic improvements) can only be realised if plants are able to obtain sufficient nutrients from the soil. One could question why under natural conditions plant production tends to be low and why under food forest conditions this would not be the case?

Natural selection results in individuals with the highest fitness, defined as the highest number of viable offspring during an individual's lifetime.

Many wild trees as well as herbaceous perennials allocate 5% of their net annual assimilation to sexual reproduction. However, several domesticated trees and palms allocate *more than 50%* of their annual assimilation to reproduction, higher than maize which is the world's most productive annual crop, illustrating the enormous transformation in translocation made possible through the process of domestication [108]. Apples can even allocate 64% of their net annual assimilates to fruit production [108].

The increased production of annual staple crops during the past century does not seem to be caused by enhanced efficiency of the photosynthetic apparatus, but from changes in carbon allocation patterns [109]. As mentioned earlier, the work of Borlaug in creating dwarf wheat varieties also altered the carbon allocation pattern; a smaller proportion of the assimilates was allocated to height growth and a higher proportion was allocated to kernel production [109].

Coming from wild trees allocating about 5% of their net annual assimilation to sexual reproduction, and ending up with domesticated trees that allocate up to 64% of their net annual assimilation to sexual reproduction shows the enormous potential that is still out there for many underdeveloped crops, especially nut trees such as walnuts, pecans and hazelnuts.

The question is, why do natural trees not allocate much more energy to reproduction to increase their own fitness and evolutionary success? There are many different reasons for this such as competition, disease resistance, light restrictions, nutrient restrictions, water restrictions etcetera. All those issues need to be dealt with and if a plant just allocates large proportions of its assimilates to reproduction, it will never claim space in the forest canopy resulting in a slow death in the dark. Other possibilities are

underdeveloped root systems, causing tree death during droughts, while the trees that invested in deeper roots will survive the dry spell and, hence, can produce more seeds in their lifetime, resulting in an increased fitness compared with the high-production, low root-investing individuals [110]. Most ecologists divide plant assimilates over three main processes: sexual reproduction, vegetative growth and plant defence. As early as the 1800s studies suggest that sexual reproduction is in competition with vegetative growth. It was noted that cutting flowers to prevent the fruit setting resulted in increased plant lifespan. The idea that reproduction, growth and defence interact and compete for limiting resources is an established principle [110].

When humans select certain individuals, enhance their reproductive allocation pattern via breeding and *take care of it*, these trees could well have enhanced fitness compared to individuals that allocate less energy to reproduction. The explanation is the fact that human care gets rid of natural constraints like shade. If a tree is planted in an orchard, there is no need to invest a lot of energy in height growth and a rare individual that starts producing fruit early on, will be selected for (and would be dead in a natural environment). The creation of these agroecosystems enabled rarely observed traits (like earlier fruit setting, less height growth) to be expressed and resulted in increased yields. Other environment-related factors like irrigation and fertilisation played an important role as well in getting the most out of the genes.

It is hard to predict, with current scientific data, what would be the role of soil nutrients in enhancing the production of (improved) varieties. The question is, does the supply of nutrients match the increase in net allocation to fruit or nut production? In other words,

- *would an individual plant that is genetically bred for its high sexual reproduction allocation pattern need more nutrients in total or does the reduction in allocation to other processes compensate for the increased nutrient demand for the sexual reproduction processes?*

In the case that the answer is ‘yes, it needs more nutrients’, then it is questionable if trees can acquire the extra nutrients. If the answer is, ‘it needs about the same total of nutrients, the key difference is simply the allocation of nutrients’, then it is likely that improved individuals produce more than a non-improved individual on the same site in the same conditions.

Some evidence for the last theory was already provided by J. Russell Smith in his renown book ‘Tree crops: a permanent agriculture’. He visited several countries with tree-crop cultivation and when he visited the *chataigneraies* (chestnut orchards) in Corsica, he observed individual trees with extremely high production levels. He saw one big tree near the village of Pedicroce with a girth of 4.60 metres and a spread of about 60 feet and the owner stoutly insisted the tree yielded 1 000 litres of nuts on average [94].

Russel Smith talked with a French Professor of Agriculture at Grenoble University, professor Grand, and he estimated that one hectare of chestnut trees would yield 1 972 kg per ha as an average value for France. Furthermore, he insisted that this was an average and said that yield would be 4 000 to 5 000 kg of nuts per ha in a year of a big harvest [94].

In the United States, he noted one Chinese chestnut tree of 11 years old bearing 40 kg of nuts [94]. One hectare planted with this grafted chestnut (say 400 trees as they are still small and young) would easily bear 16 000 kg of nuts, which is a huge production level for chestnuts. Furthermore, Russel Smith mentioned one Japanese chestnut, called the Japan Mammoth, grown in Alabama, which had very large nuts. They were 6.35 cm x 4.28 cm meaning they were the size of a large egg [94].

In food forest systems, high energetic and (nutrient) investment in height growth, radial growth and branching is not necessary. In the last decades, apple cultivation in the Netherlands has switched from large trees to dwarf trees. This was mainly done to increase the ease of harvesting. However, there are several other benefits such as early high production. Dwarf trees can already produce 10 kg at 2 years of age. Because of the high density planting (of about 3 300 trees per ha), one ha can already produce 33 tons of fruits when it is just two years old. This is much higher than tall trees produce at this age, which were planted in much lower densities (up to 100 trees per ha). Though these trees could also bear 10 kg of fruits at two years of age, the total per ha production ends up at about a thousand kg of apples at age 2. With increasing age, the difference between tall and dwarf apple orchards becomes less and after age 10, differences might be negligible, mainly because tall trees can bear about 30

times more fruit than dwarf apples. The downside to dwarf apples is a limited lifespan of about 25 years, while tall trees can remain productive for more than a century. What I want to show with these examples is that apples (both tall and dwarf, which both allocate up to 64% of their assimilates to reproduction), have high yields when they reach maturity and *growth slows down*. These tall apple trees do not allocate large proportions of their assimilates to growth, once matured.

Genetic breeding of many nut trees can change allocation patterns. For example, by reducing wood and branch growth, more assimilates (and nutrients) can be used to increase nut production. Annual per ha nitrogen uptake of deciduous temperate forests is several tens of kilos. Most of the annual nitrogen uptake is translocated to the leaves. Dutch oak forests of about 100 years old take up about 78 kg of nitrogen per ha annually [16]. The leaves get about 44 kg of N per ha annually [16]. So about 34 kg of N is used for other processes including stem growth, branch growth, root elongation, exudates excretion and sexual reproduction (flowering and nut production). Of course, all these processes are crucial, but altering the allocation pattern could increase the amount of nitrogen that can be used for nut production. In designed food forest systems, mature nut trees are allowed to slow down their investments in branching, height growth and radial increases. For example, the 34 kg of nitrogen not going to the leaves, are divided over the aforementioned processes. Imagine that due to breeding, the allocation pattern could be changed in such a way that a significant part of this 34 kg is now being allocated to sexual reproduction (in contrast to wild trees where only a fraction goes to reproduction). This would increase the amount of assimilates and nutrients that can be used for nut production and could result in nut production increases.

In natural ecosystems, plants are mainly constrained by three different issues: water, nutrients and light. By creating agro-ecosystems, humans can directly alleviate the light issues. All plants can receive optimal light. Also, via fertilisation and irrigation, plants can get (largely) rid of those constraints limiting their productivity. Unfertilised food forests can also be designed in such a way that light-interception is ideal for each plant and those systems can also increase water availability through hedges (reducing water transpiration), increased soil organic matter levels (capturing more water) and the trees themselves (with their canopy protecting the soil from the rain's impacts). So, these two constraints can be alleviated reasonably well. The effect of food forests on the remaining main constraint, nutrients, is more difficult to predict. As shown before, nutrient mineralisation levels and soil nutrient ionic concentrations are higher in climax forest ecosystems compared with heathland (which serves as a proxy for annual agricultural soils). However, these are relatively closed systems while a food forest is an open system. Therefore, making predictions is very hard.

I mentioned earlier in this paper the example of tropical rainforests scattered around the globe with widely varying soil nutrient levels. Even in soils with extremely low phosphorus availability, rainforests biomass could surpass 400 tons per ha. Many tropical rainforests are characterised by low nutrient availability due to aluminium binding of phosphorus or because most soils are highly weathered. Still, tropical forest is one of the most productive ecosystems on the world. I posed this question earlier: how is it possible to have one of the highest net primary productivity (NPP) rates while soil nutrient stores are considered as very poor? I think the answer is provided by: light, temperature and lots of rain. Enzyme activity is higher as temperature increases (up to a certain maximum temperature value), and since most tropical forests are situated around the equator, temperatures are year-round high. Light is strong and production can be sustained year-round. Water is abundant (at least during the rainy season). These three factors together are the primary reason why tropical forests, on very poor soils, exhibit very high primary productivity.

This also indicates that other factors are probably more important than soil nutrient availability in predicting primary productivity. I mentioned earlier that olive trees production increased several folds when dry systems were irrigated, showing the significance of water in olive cultivation. Therefore, my theory is that water availability is more important than soil nutrient fertility level. Of course, it is hard to separate the two as soils high in organic matter or in clay store more water, but also more nutrients.

Also, low water availability directly limits photosynthesis as it is required in the reactions to build sugar molecules. In poorer soils with adequate water, photosynthesis can build enough carbohydrate molecules that can be transformed to exudates which are subsequently released by the roots. These exudates can increase nutrient supply as described in this paper. Therefore, even in poor soils, but

with adequate water availability, trees are able to acquire (up to a certain extent) their nutrient needs simply by increasing exudate or root hair growth (which are energetically, and thus limited by photosynthesis and, hence, water, expensive processes).

Perennial woody plants can be considered intelligent living beings with hundreds of millions of years of evolution and over time, they figured out countless strategies to survive. Water availability is one of the only things (although certain mechanisms do exist such as deep root growth) that plants cannot control, while nutrient acquisition is a process that can be controlled by the plant and mainly via the soil food web (which is stimulated by the plant's exudates).

Hence, I expect that most unfertilised food forests with genetically improved varieties in most temperate soils will show increased productivity compared with food forests with genetically less favourable plant material when water availability is sufficient. Only in stressed conditions (such as a severe drought), I expect the two systems to converge as the genetically superior plants cannot invest in more productivity because their basic metabolic needs must first be covered. They simply need all their assimilates to survive instead of reproduce.

The same line of thinking can be found in gerontology and aging research. Caloric restriction (restricting daily caloric intake) is one of the interventions that can lead to marked lifespan prolongations in multiple species of animals, and probably also in humans [111].

There are several theories explaining how eating less leads to living longer that I will not cover here. I mention this phenomenon because it can teach us something about trade-offs between reproduction and maintenance which is directly applicable to the breeding of plants. Namely, one of the most important consequences of calorie restriction is reduced fertility. The body seems to decide to allocate all the available energy towards cell maintenance and shuts down all superfluous energy-consuming processes such as reproduction. In human clinical trials as well, low libido is one of the most important observed consequences of limiting calorie intake [111].

Calorie restriction is a stress-response to limited ecosystem nutrient availability and results in enhanced cell defence mechanisms via activation of stress-response pathways such as AMPK and FOXO, while lowering the insulin-like growth-pathway (IIS) as well as mTOR which are stimulated by amino acids and insulin (hence, food consumption).

Under stressful conditions, plants tend to show similar mechanisms (especially perennial plants). For example, when there is a drought, energy allocated to reproduction is limited, hence food production is reduced. Even varieties with increased sexual reproduction assimilate allocation, will reduce their assimilate allocation to reproduction and use the remaining assimilates to adapt and survive.

Therefore, it is likely that under stressful (drought) conditions, improved varieties do not live up to their potential in food forest systems. However, under less stressful conditions it is likely that, even in relatively poor soils, improved varieties outperform less improved varieties in food forests, due to higher sexual reproduction assimilate allocation.

The answer therefore on the posed question '*would an individual plant that is genetically bred for its high sexual reproduction allocation pattern need more nutrients in total or does the reduction in allocation to other processes compensate for the increased nutrient demand for the sexual reproduction processes?*' could both be 'yes' or 'no' as explained in the previous paragraphs. Even if the answer would be yes, it does not automatically mean that it is unlikely that genetically bred trees in unfertilised food forest would not live up to their potential. One of the key traits affecting productivity is nutrient uptake capacity. Via breeding, trees can be developed that outperform others due to root architectural changes like increased root hair expression. *Because of* the enhanced uptake, trees would be able to produce more fruits or nuts, so high-yielding individuals might be genetically favoured to take up nutrients.

Conclusions:

- Many perennial tree crop species have undergone very few cycles (if any) of controlled breeding (exceptions do exist, like apple and pear trees).
- Annual plants like corn, wheat and rice have been subject to breeding for millennia and subsequently produce bumper crops that most perennial crops cannot match (in terms of calories per ha).
- However, there is a large *potential* to improve the production of many tree crops, especially nut crops. Some individuals can be found that bear heavily each year, even in unfavourable conditions. Working with these outstanding individuals via controlled breeding or grafting has the potential to increase tree crop yields significantly.
- Recent evidence for this potential can be found in the production of walnuts. In just three years, the world average walnut yields increased by 46% and recently developed varieties in combination with innovative management measures have been reported to produce several times the world average walnut production. In terms of calories per ha, these high-yielding orchards can compete with annual staple crops such as corn and potatoes.
- Domestication of tree crops can increase plant assimilate allocation to reproduction a lot compared to the wild ancestors. Wild trees tend to invest about 5% of assimilates to reproductive organs, while trees with a long domestication history like apples can allocate as much as 64% of its assimilates to reproduction.
- The development of agroecosystems, places that are optimal for plant production, is the key to optimising fruit and nut production. Alleviating many constraints found in natural situations enables rare genotypes to survive and, hence, enables humans to select those individuals to start breeding programs with. One of the key questions is to what extent this increased reproductive assimilate allocation can go on until serious trade-offs begin to show off (such as increased pest vulnerability).
- Concerning nutrients in food forests, it is difficult to predict the effect of cultivating good genetic individual trees in unfertilised systems. Does the phenotype in such systems represent the genotype? The key question is whether an individual plant that is genetically bred for its high sexual reproduction allocation pattern need more nutrients in total or does the reduction in allocation to other processes compensate for the increased nutrient demand for the sexual reproduction processes? It is tempting to think that an increased production of nuts or fruits must be accompanied by an increase in nutrient uptake. However, according to an opposing theory, less nutrients are needed for other key processes such as growth and plant defence, meaning that without taking up more nutrients, more nutrients are already available for sexual reproduction.
- This latter theory is most likely to apply to food forests in relatively unstressed conditions as different varieties in the same orchard (and thus conditions) can show large differences in production.
- Furthermore, it may well be that it is not the nutrients that constrain sexual reproduction, but the annual assimilates (due to shading under natural conditions and water stress) that limit sexual reproduction. Therefore, improved varieties of tree crops grown in agroecosystems such as food forests receiving optimal light (and possible irrigation) will make sufficient assimilates to produce bumper crops of fruit or nuts in the same soil as non-improved plants (with low sexual reproduction allocation) that produce much lower harvests.
- Water availability likely trumps soil nutrient pools as different trials showed much stronger tree crop responses to irrigation than to fertilisation as outlined in this paper.

Conclusions

Different nutrient acquisition methods provide (food) forest systems with the necessary nutrients. Numerous different mechanisms exist to increase plant nutrient availability. Mycorrhizal fungi play a pivotal role in ensuring adequate nutrient supply to (food) forest ecosystems. The soil food web, with all its actors, is responsible for the yearly decomposition and mineralisation processes of dead organic matter. Plants have the capacity to influence the soil food web to meet their nutrient demands.

Total soil nitrogen and phosphorus stocks were estimated using different literature findings. The results differed substantially depending on soil type among others. However, a sense of the order of magnitude was established. With the established nitrogen and phosphorus pools, it became clear that the total *potentially* available pool was often very large. The true question is, how much of this total pool would be available to the trees and at which rate would it become available?

Perennial –based systems have the capacity to reach more nutrient pools than annuals and due to mycorrhizal uptake as well as immobilisation-mineralisation, they obtain nutrients from pools that are not available according to most soil tests used by agronomists. However, evidence clearly shows that fertilisation with nitrogen generally increases forest biomass production indicating that natural forest ecosystems are nitrogen-limited. Therefore, the question is *what level of biomass production is supported via natural soil fertility?* This question cannot be answered in this paper, but several examples are provided of systems that have relatively high production levels, though not as high as modern-day fertilised maize monocultures.

Some examples of unfertilised perennial systems that have been able to continue producing nuts or fruits for centuries, are the Dehesa system, chestnut forests and olive trees. These examples showed that, even though lots of nutrients have left the system over time via nut harvesting (as much as 4 228 kg of nitrogen in the case of 250-year-old chestnut systems), the system was still producing and, hence, the *available* nutrient pool must have been *replenished*. Numerous potential explanations for this long-term nutrient availability can be found in the described soil food web. However, it was not the purpose of this paper to find *the* explanation for this phenomenon. The focus of this paper was to investigate if there is any evidence that food forests can continue to produce without the need of fertilisation.

To find out if this was possible, I combined the obtained data on total nitrogen and phosphorus pools and the data on annual P and N inputs and outputs from agroforestry sites. Chestnut harvests removed about 21 kg of nitrogen and 2.5 kg of phosphorus per ha per year. Modelling how long it would take until 50% of the nitrogen and phosphorus in the 2-metre-thick soil layer would be removed via harvests, resulted in average N values of about 400-600 years, depending on the scenario. For phosphorus, >2000 years is needed to deplete 50% of the initial P content of the 2-metre-thick soil profile. These results indicate that the N and P stocks were large enough to support at least centuries of crop harvest before a 50% reduction in initial stock was accomplished, even in the absence of inputs, and might explain the chestnut system lifespan in Corsica and in the Ardèche.

Since chestnuts are nuts with relatively low phosphorus and nitrogen content, I did the same calculations for protein-richer hazelnuts, both for a moderate and high yield. Especially in the case of the high hazelnut yield (2000 kg DM per ha), nitrogen stores would be depleted by 50% in only several decades as compared to the 400-600 years for the chestnuts. In fact, all but the high phosphorus scenario showed a negative nutrient balance, indicating that soils were being depleted of nitrogen and phosphorus without fertilisation inputs.

Therefore, it might well be that there is a sweet spot; a certain nutrient export level (yield intensity) that is just supported by the nitrogen and phosphorus input rate of the ecosystem. This rate, and subsequently this sweet spot, depends on many factors like soil type, precipitation, organic matter level and initial nutrient stock. This concept might explain why chestnuts in Europe (not a very high nitrogen and phosphorus output) have been able to produce for centuries. This century-long production might not have been the case if walnuts or hazelnuts were picked instead of chestnuts because the nitrogen pools could have become limiting after several decades already, resulting in low production rates.

Thus, the question is if the natural nitrogen and phosphorus uptake rate is sufficient to produce crops that can compete with, or at least come close to conventional agricultural systems (calorie wise). Annual cropping systems that do not receive fertiliser (in any form, so including compost) are generally unable to compete with fertilised intensive agriculture. However, perennials have several advantages over annuals in obtaining nutrients such as their deep rooting nature, mycorrhizal symbiosis and the ability to maintain or even increase soil organic matter (and the annual nutrient mineralisation as a consequence of decomposition).

There are some indications that perennial tree crops can give relatively high yields in unfertilised systems. Chestnut forests, the Dehesa system and olive production experiments show that trees can continue cropping for centuries without human fertilisation. However, as indicated in his renown book “tree crops – a permanent agriculture”, Russel Smith suggests breeding of perennials has a long way to go to reach the level of annual crop breeding. He provides some strong arguments that the genetic potential for high-yielding trees is there and shows several examples of outstanding individuals producing bumper crops of fruits or nuts in unfertilised plots.

Considering the fact that most wild trees allocate approximately 5% of their assimilates to sexual reproduction and that one of the trees with the longest domestication history, the apple, can allocate 64% of its assimilates to sexual reproduction, it becomes clear that there is an enormous potential for trees that have not been subjected to such intensive domestication.

Many nut species such as pecans, Brazilian nuts and walnuts have not been subjected to controlled breeding programs. For Brazilian nuts and pecans, most orchards consist of seedlings from the best-performing wild tree or are the result of just a few generations of breeding. Of course, the difficulty in breeding perennials is the waiting period until trees start to flower for the first time. However, several new developments have dramatically decreased the waiting period and some fruit trees now flower at the age of just one or two years.

This greatly speeds up the development of useful high-yielding, resilient varieties. Walnuts have been bred quite intensively in certain areas of the world. The problem is that only a fraction of the total genome is used because many walnut trees are located in remote regions in political-unstable countries. But still, in just three years, world average walnut production increased by 46%. In some of the breeding programs, great successes have been made. Furthermore, several varieties currently exist that can compete with annual industrial crops (calorie wise).

Many of these new varieties are cultivated in fertilised and irrigated systems. Therefore, it is hard to predict how they would perform in unfertilised food forest systems. But, as mentioned earlier, many observations of outstanding wild or semi-wild trees in unfertilised plots suggest there is a lot of potential via tree breeding programs.

With the calculations done in this review paper, the research question: “*How large is the soil phosphorus and nitrogen stock available to food forests situated in temperate zones, and how long can these stocks sustain food forest nuts/fruit production before they are depleted?*” can be answered. Most temperate region’s soils have a large stock of both phosphorus and nitrogen consisting of several thousands of kilograms per ha (in a two-metre-deep soil profile). For crops, low in protein (thus low in P and N), such as fruit trees and chestnuts, nitrogen and phosphorus outputs via fruit harvests are relatively small, at least up to a certain extent of harvesting intensity. In several scenarios, the outflow of these nutrients can be entirely compensated with system inputs such as weathering and atmospheric deposition, meaning that there is an accumulation of nitrogen and phosphorus in the soil (due to rock weathering or N-fixation). In the case of negative nutrient balances (for example when considering low rock weathering and N-fixation scenarios), it still takes >2000 years before phosphorus stocks are halved and >400 years before nitrogen stocks are halved. Therefore, food forest systems based on this kind of crops have a sufficiently large nutrient pool to *potentially* replenish the lost nutrients. However, it is unknown at which rate nutrients can be delivered to the tree crops (especially from difficult-accessible pools) and, hence, how large the harvest level that can be supported by the soil can be.

Most nut crops can remove relatively large quantities of nitrogen from the system. Hazelnuts were used as a proxy for all nut crops in a food forests and high yields resulted in relatively large negative nitrogen balances. The time until the total soil nitrogen pool was halved, was only several decades as

compared to >400 years for the chestnut example. This indicates the importance of including nitrogen-fixing plants in the design for food forests with a high coverage of nut trees and shrubs. All in all, this review finds that soil nitrogen and phosphorus stocks in the temperate zone are sufficiently large to support low-protein tree crop system harvests at least for several centuries, while high-protein tree crop systems harvests can only be supported for several decades to several centuries in the scenarios of low nitrogen inputs (from natural processes). Furthermore, this review brings to light the most important question for future research: *at which rate can nutrients be delivered to the tree crops (especially from difficult-accessible pools) and, hence, how large can the harvest level that can be supported by the soil be?*

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Appendix

Appendix A

Nitrogen and phosphorus inputs and outputs used in the calculations of nitrogen and phosphorus lifespan for different soil and bedrock layers for chestnuts. Low, high and average values are used to make Fig. 4 & 5 to illustrate the range of possible outcomes depending on which values are used.

Table A1. The different (low to high) nitrogen and phosphorus inputs into a chestnut food forest system.

Chestnut	Inputs			
	rock weathering	atm. deposition	bird inputs	N-fixation (free-living)
nitrogen low	0	1.00	0.40	5.00
nitrogen high	10.90	9.00	3.50	30.00
nitrogen average	5.45	5.00	1.95	17.50
phosphorus low	0.30	0.20	0.07	0
phosphorus high	5.00	1.10	0.50	0
phosphorus average	2.65	0.65	0.29	0

Table A2. Different nitrogen and phosphorus outputs for a chestnut food forest system. For the columns total inputs and balance, data from table A1 (inputs) are used.

Chestnut	Outputs						
	harvest	leaching	erosion	gaseous emissions	total inputs	total outputs	balance (input-output)
nitrogen low	21.00	0	0	0	6.40	21.00	-14.60
nitrogen high	21.00	2.00	0	1.90	53.40	24.90	28.50
nitrogen average	21.00	1.00	0	0.95	29.90	22.95	6.95
phosphorus low	2.50	0	0.03	0	0.57	2.53	-1.96
phosphorus high	2.50	0	0.06	0	6.60	2.56	4.04
phosphorus average	2.50	0	0.05	0	3.59	2.55	1.04

Appendix B

Lifespan of a chestnut food forest system based on the time required to exhaust the soil (0-2 m) from 50% of its original stock for different scenarios.

Table B1. For a chestnut harvest of 2000 kg DM per ha per year, the lifespan until 50% of the initial soil nitrogen stock is extracted is displayed for different scenarios. Note that the negative values mean that the nitrogen balance is positive, indicating there is no finite lifespan.

Scenario	Lifespan N low	Lifespan N high	lifespan N average
no inputs, harvest only	180	630	405
5% rock weathering, harvest only	187	717	452
10% rock weathering, harvest only	195	805	500
atm. dep. & bird dep. , harvest only	193	1555	605
atm. dep. & bird. dep., harvest & leaching & gaseous emissions & erosion	193	1066	531
atm. dep. & bird dep. & N-fix. (freel.) , all outputs	259	negative	negative

Table B2. For a chestnut harvest of 2000 kg DM per ha per year, the lifespan until 50% of the initial soil phosphorus stock is extracted is displayed for different scenarios. Note that the negative values mean that the phosphorus balance is positive, indicating there is no finite lifespan.

Scenario	lifespan P low	lifespan P high	lifespan P average
no inputs, harvest only	1937	3266	2601
5% rock weathering, harvest only	2382	3711	3047
10% rock weathering, harvest only	2828	4156	3492
atm. dep. & bird dep. , harvest only	2172	9071	4155
atm. dep. & bird. dep., harvest & leaching & erosion	2143	8504	4039
all inputs and outputs (incl. rock weathering)	2471	Negative	negative

Appendix C

Lifespan of a hazelnut food forest system based on the time required to exhaust the soil (0-2 m) from 50% of its original stock for different scenarios.

Table C1. For a hazelnut harvest of 1200 kg DM per ha per year, the lifespan until 50% of the initial soil nitrogen stock is extracted is displayed for different scenarios. Note that the negative value means that the nitrogen balance is positive, indicating there is no finite lifespan.

Scenario	Lifespan N low	Lifespan N high	lifespan N average
no inputs, harvest only	111.2	389.3	250.2
5% rock weathering, harvest only	115.9	443.5	279.7
10% rock weathering, harvest only	120.6	497.7	309.1
atm. dep. & bird dep. , harvest only	115.9	616.0	314.6
atm. dep. & bird. dep., harvest & leaching & gaseous emissions & erosion	115.9	521.3	293.4
atm. dep. & bird dep. & N-fix. (freel.) , all outputs	137.0	negative	812.4

Table C2. For a hazelnut harvest of 2000 kg DM per ha per year, the lifespan until 50% of the initial soil nitrogen stock is extracted is displayed for different scenarios.

Scenario	Lifespan N low	Lifespan N high	lifespan N average
no inputs, harvest only	66.7	233.6	150.1
5% rock weathering, harvest only	69.5	266.1	167.8
10% rock weathering, harvest only	72.3	298.6	185.5
atm. dep. & bird dep. , harvest only	68.4	230.0	171.1
atm. dep. & bird. dep., harvest & leaching & gaseous emissions & erosion	68.4	275.4	164.7
atm. dep. & bird dep. & N-fix. (freel.) , all outputs	75.2	734.4	249.2