



Access and excess problems in plant nutrition

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Abstract

As plant nutrition issues are redefined by society, new applications emerge for a basic understanding of nutrient use efficiency in soil-plant processes to avoid excess on rich soils as commonly found in the temperate zone and make the best of it under access-limited conditions common in the tropics. The main challenge of plant nutrition may be to increase the width of the domain between the access and excess frontiers, rather than to define a single 'economic optimum' point. Two approaches are discussed to widen this domain: the technical paradigm of precision farming and the ecological analogue approach based on filter functions and complementarity of components in mixed plant systems. Current understanding of plant nutrition, largely focused on monocultural situations, needs to be augmented by the interactions that occur in more complex systems, including agroforestry and intercropping as these may form part of the answer in both the excess and shortage type of situation. Simulations with the WaNuLCAS model to explore the concepts of a 'safety-net' for mobile nutrients by deep rooted plants suggested a limited but real opportunity to intercept nutrients on their way out of the system and thus increase nutrient use-efficiency at the system level. The impacts of rhizosphere modification to mobilize nutrients in mixed-species systems were shown to depend on the degree of synlocation of roots of the various plant components, as well as on the long-term replenishment of the nutrient resources accessed. In conclusion, the concepts and tools to help farmers navigate between the scylla of access and the charibdis of excess problems in plant nutrition certainly exist, but their use requires an appreciation of the site-specific interactions and various levels of internal regulation, rather than a reliance alone on genetic modification of plants aimed at transferring specific mechanisms out of context.

Introduction: threats to sustainability

Sustainability of farming and thus of agro-ecosystems depends on the ability of farmers to overcome current and future threats to a continuation of their enterprise in some form or other. These threats can derive from loss of on-site productivity, from 'angry neighbours' who no longer accept the lateral flows through air or water of elements and pesticides coming from the farm, from 'worried customers' who do not trust the quality of the products or don't agree with the production conditions, or from 'regulatory bureaucrats' in a policy frame that tries to control the activity of farmers. Plant nutrition research has traditionally focused on the first of these threats, and has helped to develop plant and soil management schemes that provide for

adequate nutrient supply to the current crop without unduly mining soil resources. A build-up of soil nutrient stocks, some not directly available to common crops, was seen as an unavoidable side-effect of improved crop nutrition and use efficiencies of 30–40% for fertilizer N characterize the main grain production systems of the world (Doberman and Cassman, 2001). The apparent success of this type of plant nutrition in the intensively used agricultural lands of the temperate zone, as well as in specific areas in the tropics, has given rise to increased fluxes into the environment and thus to the *angry neighbour*, *worried customer* and *regulatory bureaucrat* type of threat to sustainability of current farming styles. In the Netherlands, the country with the highest nitrogen surplus per ha (Smaling et al., 1999), new legislation requires farmers to keep

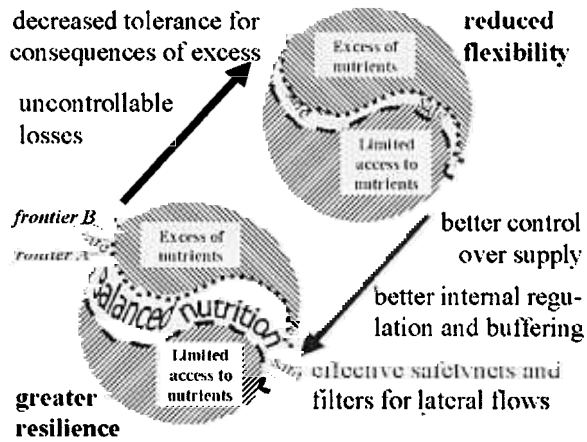


Figure 1. Domain for balanced nutrition ('OK') between frontier A that separates it from access limitations and frontier B that separates it from excess problems; various factors squeeze or increase the width of the OK domain.

track of a farm level nutrient budget and to pay for surpluses that exceed a permissible level; as payments are based on the net outcome at farm level it provides incentives for a more efficient use and recycling of nutrients in innovative ways (Neeteson, 2001).

To support the 'agility' of farmers to respond to these threats, efforts to increase nutrient use efficiency at field, farm and regional scale are needed. Where part of the initial success of growth-stimulating plant nutrition was based on a largely empirical approach, exploration of the upper limits and management of the excess situation need a more precise quantitative understanding of the soil-plant-environment relationship in heterogeneous fields (Cassman and Plant, 1992; Doberman and Cassman, 2001; Van Noordwijk, 1999).

In contrast to the problems of excess nutrition, in substantial parts of the tropics the lack of adequate supply of plant nutrients remains a major constraint to crop growth (Buresh et al., 1997). Lack of knowledge of plant nutrition, however, is not the major determinant of this situation. Fertiliser sources are generally used wherever they are financially feasible for the types of crops farmers grow, and relative prices of nutrient sources, labour and harvestable products explain most of the situations where soil fertility remains the main constraint to agricultural production for subsistence crops (Laegreid et al., 2001). Real impact on farmer's livelihood options in these circumstances is likely to come from economical and policy changes rather than from technical options for plant nutrition per se (Izac and Sanchez, 2001).

Threats to sustainable farming globally thus consist of on-farm concerns for the nutrient balance (Access problems), angry neighbours and worried or dissatisfied customers (Excess problems) and regulations and policies that are supposed to guide between the scylla and charibdis of access and excess problems, but that not necessarily give the right signals and incentives to farmers navigating their boats in between. Research can help to define and shift the two main frontiers, but should also focus on how to increase the width of the domain in between (Figure 1) not least to reduce economic and environmental risks. Research and development efforts on frontier A of restricted access may easily lead to overshoot across frontier B of unacceptable excess problems if there is only a narrow zone in between. Over-use of fertilizer in parts of Asia on horticultural crops and lowland rice (Dobermann and Cassman, 2001) exists, for a variety of reasons (Wang et al., 2001) close to upland systems where fertilizer access is still problematic. Similarly, regulation efforts aimed at frontier B and controlling the negative environmental effects of agriculture, can bring farms and the plants that form the basis of the production across frontier A, into serious access problems. Factors that determine the width of the 'SAFE' zone (balanced nutritional environment domain) may need further attention and instead of a single 'economically optimum fertilization rate', we may need to focus on the parameter domain where, given the variability of weather and other uncertainties, environmentally safe production is possible at acceptable returns to investment and labour. Global challenges in plant nutrition are thus formed by problems of limited access, problems of excess and the links between these two. In this paper we will explore the nature of the two frontiers and the domain in between the scales of a single root and society as a whole.

Excess and access problems in plant nutrition from root to societal scale

Plant nutrition research can focus on genes, cells, roots, whole plants, cropped fields, farms, the human food chain and/or society and land use. While at each level a type of *efficiency* (generally output per unit input, measured over specified system boundaries and for a given time frame) can be defined, these efficiencies are not directly linked. Efficiency is not a scale independent property - efficiency of a system can be obtained despite relative inefficiency of subsystems,

while efficiency of a system does not guarantee that it contributes to the efficiency of macro-systems. For example, cassava is a very effective and efficient nutrient scavenger that can acquire nutrients from poor soils and provide reasonable crop yields under low input and low-labour conditions, making it a crop of last resort on depleted soils in the (sub)humid tropics. The nutrient content of the tubers that are harvested is substantial, while the price per unit dry weight is low. So the 'added value' by the plant relative to the nutrients depleted from the soil is low, and if we calculate the 'nutrient replacement cost' we may find that up to 60% of the price a farmer gets for the tubers would have to be used for buying fertilizer to balance the budgets of N, P and K (ignoring the other nutrients exported with the harvest) (Van Noordwijk, 1999; Whitmore et al., 2000). So the plant-level nutrient uptake efficiency, the human labour use efficiency in the production process, and the short-term farm level nutrient use efficiency (allowing for output without external input) are not matched by a financial nutrient replacement efficiency and hence the longer term farm level nutrient budgets in cassava production areas show a clear negative trend (Hairiah et al., 2000). Part of cassava tubers are industrially processed and shipped around the world as tapioca for use as fodder in intensive animal production in the 'developed' world. This trade contributes to the nutrient excess problems in animal waste disposal, thus the problems of 'excess' are linked to those of 'access' by this crop (Bouwman and Booi, 1998). If our aim is balanced nutrition at all relevant scales, we need to pay specific attention to the connection points between scales, and at each system level increase the domain between frontiers A (access) and B (excess).

Although 'access' and 'excess' domains can be recognized from root to societal scale (Table 1), the definition of the frontiers, and therefore of the 'SAFE' range, differs and suggest, for example, that interventions aimed at the frontier of root access to nutrients will not necessarily contribute to improving access to food of adequate quality by all people of the world. Where current molecular biology and biotechnological approaches focus on the access frontier at (sub)cellular (Kochian, 2001) or plant (Cakmak, 2001; Graham and Welch, 2001) level, it may be an understatement to say that challenges remain to a holistic understanding of plant nutrition in its societal context. Determinants of the 'SAFE' range at root and plant level are primarily based on the quality of the plant as a regulator, preventing access-mechanisms to generate internal excess of any of the nutrients or other

solute in the rhizosphere, and selectively increasing access by a numerical or functional response of the root system (with its symbionts). Although demand-driven regulation of plant nutrition was recognized in the 1940's, explicit description of 'plant nutrient demand' rather than concentration-dependent mechanisms as driver of uptake remains an exception (De Willigen and Van Noordwijk, 1987). The responses of plants in heterogeneous environments may differ qualitatively (Hairiah et al., 1993; contrasted to: Collet and Horst, 2001) from that in homogeneous systems and thus important aspects of the response of whole plants to their complex environments tends to be missed in the homogenization that is generally perceived to be necessary for valid experiments.

At field scale the boundaries between excess and access problems are primarily determined by the variability of both nutrient supply and demand between the plants that are managed as a single unit (typically a field). Variability in inherent soil supply or demand within a field will tend to shift the yield-response-to-fertilization curve to the right and the nutrient-excess-response-to-fertilization curve to the left, decreasing the 'safe' range from both sides (e.g. increasing fertilizer demand and nutrient losses) and confirming the challenges of productive and environmentally friendly agriculture (Van Noordwijk and Wadman, 1992; Whitmore and Van Noordwijk, 1995). Precision farming (Robert, 2001; Pierce and Novak, 1999) can potentially increase the width of the 'safe' range, by reducing the size of the management unit. A challenge for 'precision farming' however remains where the variability is temporal rather than spatial, e.g. due to poor predictability of mineralization rates. Spatial variability within fields can lead to non-homogeneous fertilization practices as soon as zones that differ in nutrient supply or crop demand can be recognized on the basis of differences in elevation, landscape genesis, distance to drains (De Vos, 1997, El-Sadek and Feyen, 2001), erosion and sedimentation zones on slopes (Van Noordwijk et al., 1998), heterogeneity caused by slash-and-burn land clearing and subsequent erosion/deposition (Ketterings, 1999; Rodenburg, 1999), animal defecation (including birds perching on trees; Belsky, 1994) or shading by hedgerows and field boundary vegetation (Mette et al., 2001). Specific agronomic practices further increase spatial variability, e.g. by nutrient transfer from grass strips to tree lines in orchards, tropical hedgerow intercropping, or by injection of slurry or fertilizer into the soil (Laegreid et al., 2001). Where these practices

Table 1. Determinants of the frontiers between the access problem, balanced nutrition and excess problem domains at different scales in plant nutrition

Scale	Access sufficiency frontier	Safe range	Excess avoidance frontier
Root	Zero-sink diffusion delivery to root, despite all rhizosphere modifications, is less than demand	Effective demand-based regulation of uptake and rhizosphere modification	Incomplete tolerance to concentration build-up if mass flow delivery to root surface exceeds C_{upt}^a
	Compensatory root development unable to reduce demand per unit root to available supply conditions	Internal buffer and elastic response in root development and function can achieve adequate supply of all nutrients required at any phase of plant development	Internal storage of excess elements in harmless forms to reduce accumulation around roots
Field – crop season	Patches with smallest supply per unit demand cause unacceptable yield shortfalls	Spatial variability in supply matches that of demand within the management unit (field or part thereof)	Patches with highest supply per unit demand cause lateral flows exceeding tolerance of neighbours
Field - long term	Total input is less than use+unavoidable losses	Balancing the nutrient budget at field scale	Total input exceeds use+tolerable losses
	Nutrient export in farm produce and unavoidable losses occur at less than (risk-adjusted, discounted) replacement costs of nutrients	Internal waste recycling and efficient application strategies increases domain where marginal benefits exceed marginal costs of nutrient use for profitable crops	Uncontrollable inputs derived from lateral flows exceed use+tolerable losses; tolerable losses smaller than unavoidable ones
Human food chain	Food of adequate quality and nutrient ratios is not available to, or affordable by part of human population	Sufficient choice for balanced diets at affordable consumer prices	Contaminant levels and nutrient ratios in staple+additional food supply exceed safety limits
	Limited stocks of exploitable nutrients; lack of economic incentives for nutrient recapitalization and balancing nutrient budgets on farms	Adequate regulation and economic incentives for nutrient chain managers	Lack of economic incentives for recycling and use of nutrient rich waste products in whole nutrient (food) chain

^a C_{upt} = uptake concentration or nutrient uptake flux divided by water intake flux.

increase heterogeneity within reach of the root system of a single plant, they may improve the efficiency of nutrient uptake (as in classical fertilizer band placement practices) and thus widen the safe range. Where heterogeneity is created on scales beyond the reach (below the rooting zone or laterally beyond reach) of a single plant, this will narrow the 'safe' range (Van Noordwijk et al., 1993). Spatial variability can always lead to two types of response by the farmer: 1) compensate for the patterns and try to achieve a more homogeneous situation, or 2) accept the differences and adapt to them, by differentiating the crops (including multi-species approaches), abandoning part of the land and/or focus efforts on the parts with the highest returns to investment of labour or inputs (Van

Noordwijk et al., 1994, 1998). Technical precision agriculture is largely based on the first approach, while much of the management decisions by small farmers living in heterogeneous environments are based on the second approach. Improvements are likely to come from a better integration of temporal variability into the spatially explicit management practices (Alphen and Stoorvogel, 2000).

Human nutrition and societal concerns over access and excess problems in plant nutrition are controlled by social and economic processes, for which technical and ecological opportunities only form pre-conditions. The access and excess frontiers are thus often based on judgmental terms ('adequate', 'tolerable'), e.g. environmental risks and costs are often difficult to quantify

and food quality is not easily defined apart from limits on pesticides and heavy metals, and involve different stakeholders. Negotiations rather than an 'objective' cost-benefit analysis of the various options therefore drive the definition of the 'safe' range. Technical increases in the width of the 'safe' range, however, can improve the chances that the political negotiation process can lead to mutually acceptable solutions for plant nutrition, as is the case for other natural resource management issues (Van Noordwijk et al., 2001). Where the merits of technical solutions depend on climatic and soil conditions, research on extrapolation domains of 'success' and 'failures' can play an important role in informing the policy debate.

Technical control and ecological analogue approaches

Two paradigms are currently used to decrease the conflicts between access and excess problems: the *technical control* paradigm of precision farming and hydroponics, and the *ecological analogue* paradigm of increased buffering and resilience. The two paradigms are not mutually exclusive, but they suggest different interventions into the status quo. Precision farming (Robert, 2001) differentiates farm operations including fertilization within a field and thus creates smaller management units to get a better tuning of supply to demand. The terminology of precision farming originated in the large fields of the US, imposed on a landscape without respect for underlying soil variability and thus highly heterogeneous, and is based on new information processing opportunities in mechanized farming. There is growing recognition that the small scale tropical farmer, on fields developed organically in the landscape has in fact also been making such site-specific management decisions that characterize precision farming (Sinclair and Walker, 1998; Berkes et al., 2000). Unfortunately, plant nutrition research for the tropics has largely resulted in blanket fertilizer recommendation schemes for the tropics (Dobermann and Cassman, 2001) and ill-adapted innovations (Fujisaka, 1994) rather than supporting the decisions farmers have to make in the real, heterogeneous world, and this probably contributes to the low overall nutrient use efficiencies of farming. The efficiency of fertilizer and organic input use varies with method of application (Cassman et al., 1998; Laegreid et al., 2001), but farmer incentives to the use of techniques that increase

fertilizer use efficiency critically depend on fertilizer price (Van Noordwijk and Scholten, 1994).

Doberman and Cassman (2002) define site-specific nutrient management more broadly as the dynamic, location-specific management of nutrients in a particular cropping season to optimize the congruence of supply and demand of nutrients according to their differences in cycling through soil-plant systems. This definition accounts for (i) regional and seasonal differences in yield potential and crop nutrient demand, (ii) between- as well as within-field spatial variability in inherent nutrient supply, (iii) within-season dynamics of soil N supply and crop N demand, (iv) location-specific cropping systems and crop management practices and (v) location specific objectives (tolerance for leaching losses, prices for products and inputs). Precision farming as currently practiced in temperate agriculture is still far from reaching its full potential (Doberman and Cassman, 2002).

In hydroponics the low predictability of variable soils is replaced in a more radical way by a system that allows for better technical control of supply and monitoring of demand in systems with a low buffer capacity and rapid response to management interventions (Heinen and De Willigen, 1995; Silberbush and Ben-Asher, 2001; Van Os, 1999; Van Noordwijk, 1990). Both of these technical approaches (precision farming and hydroponics) aim to reduce variability in space and time and tend to minimize the use of organic inputs (e.g. manures, plant residues, compost, etc.) because of their lower predictability of composition and nutrient supply dynamics (although there have been recent advances in databases and decision support systems that facilitate the use of organic materials e.g. Palm et al., 2001).

The ecological analogue approach, in contrast, accepts variability of supply and demand and the absence of full synchrony between nutrient supply and plant demand as facts of life and tries to reduce their consequences (Ewel, 1999; Joffre et al., 1999; Ong and Leakey, 1999; Trenbath, 1999). Specifically for nutrients, this may involve the use of 'safetynets' and filter strips to mop up leftover nutrients leaving the system (Van Noordwijk and Garrity, 1995). The terms 'safetynets' and 'filter' are used here in a generic sense of anything that can intercept a vertical or lateral resource flow. These efforts may require an increase in (manageable) complexity by intercropping and agroforestry and an increase in the internal (organic) buffer and soil nutrient capital (Vandermeer et al., 1998; Van Noordwijk and Ong, 1999).

The use of a biological safety net in the form of filter strips at field boundaries has been suggested in the temperate zone as one of the options for combining environmental standards and economically feasible production, returning some complexity to landscapes dominated by monocultures. Some of the principles of more complex agro-ecosystems of the tropics may indeed be of value in the temperate, intensive agricultural world as well (Vandermeer et al., 1998; Sparovek et al., 2002), as they may offer options to filter excess nutrients before they reach the neighbours' water or air, and can provide the visual attractiveness that consumers appreciate. The possible functionality of riparian filter strips may, however, be easily overestimated, and requires specification for each type of filter function.

Current understanding of plant nutrition is dominated by experiments with and theories for monocultures and is more geared to the technical control than to the ecological analogue approach. Options for combining external (inorganic) nutrient use with local (organic) sources remain under-utilized because current knowledge is too crude (Vanlauwe et al., 2001). In multi-species systems the potential combinations and benefits of such a combined inorganic-organic approach are increased due to the variations in spatial and temporal availability of plant residues.

Although the basic equations governing nutrient uptake in monocultures have been in use for several decades at the level of roots and root systems (Nye and Tinker 1974; De Willigen et al., 2000), the specific effects of plant rhizosphere modification (as a way of shifting the 'access' domain) are still a focus of research (Kirk, 2001; Claassen, 2001). Applications to intraspecific competition or longer-term effects of such modification are still relatively scarce. Rhizosphere modification effects on P may carry over to a subsequent crop, depending on the binding to soil particles and the biological availability of the active compound (Hocking and Randall, 2001; Gransee, 2001; Lu et al., 2001).

In the remaining part of this review we will explore how complex systems can play a role in issues of 'access' and 'excess' by considering impacts of rhizosphere modification by components of the system, and safety nets for leaching nutrients.

Reducing nutrient access and excess problems in complex agro-ecosystems

Complexity and residence time

Complexity in agro-ecosystems can consist of multiple components interacting spatially (at the same time), temporally (at the same place) or both. Temporal interactions are, almost by definition, one-way effects where the earlier events influence the later ones, while spatial interactions are often mutual, although the interaction strength can differ. The lowest form of complexity is thus found in rotational or sequential systems, and these have persisted into the most intensive agricultural production systems of the world, if only for reasons of pest and disease control (Desaeger, pers. com.). Crop rotations are (also) common in the tropics and although agronomically they are relatively well researched, their impacts on nutrient access and excess cannot be easily separated from other soil-borne effects. Overall, legume-rich fallows can be expected to improve N supply to subsequent crops, but the rate at which this supply can be accessed depends on the rate of mineralization and hence on the 'quality' of the litter (Palm et al. 2001). As various organic and inorganic pools can be modified in parallel, opinions on the parameters that provide the best predictor of 'fallow effects' differ between authors and crucially depend on the specific objective to be achieved (Cadisch and Giller, 2000). For example a plant residue with a low C:N ratio, low lignin and polyphenol content may be considered 'high' quality in terms of a fast nitrogen release but will be considered of 'low' quality for the purpose of mulch for soil erosion protection.

A basic concept in nutrient access and excess issues is that of mean 'residence time' in the rooted soil layers, indicating the time nutrients remain available under given climate and soil conditions for uptake by plants, before they are lost to deep ground water, surface water or to the atmosphere. In most temperate zone agricultural systems the residence time of nitrogen will be close to one growing season, with most of the leaching occurring in winter. In the tropics, the residence time of nitrogen decreases rapidly with increasing rainfall rates. De Willigen and Van Noordwijk (1989) provided examples of how N use efficiency by a maize crop in the humid tropics depends on synlocation and synchrony, relative to rooting depth and leaching rate. For P residence times are generally more than one growing season and thus carry over ef-

fects from one crop to the next one are likely to be strong. Can we manage nutrient residence time in the system? Slow release fertilizers have been developed but are not yet frequently being used as multiple small fertilizer application can achieve similar results. The regulation of nutrient release with organic inputs is determined by their quality, e.g. high C:N and/or high lignin/polyphenol content will increase residence time, but such effects are more difficult to control to ensure at the same time sufficient nutrient availability for current demand (Cadisch and Giller, 2001). Increasing residence time of nutrients in systems can also be achieved by reductions of mobility of nutrients by reduced soil water content e.g. via an increased crop water use (Suproyogo et al., 2002).

Competition and complementarity in simultaneous systems

The correct interpretation of the balance of positive and negative interactions in simultaneous systems remains a major challenge. Positive effects of intercropping in wheat/maize and wheat/soybean can be attributed (Zhang et al., 2001) to better growth of the border rows, due to increased light levels (2/3 of the overall effect) and better soil exploration (1/3 of the overall effect).

Root distribution of the component species has often been interpreted as direct indication of competition and complementarity in mixed cropping systems, including agroforestry (Van Noordwijk et al., 1996; Huxley, 1999; Wahid, 2001). The term competition can refer to a process of acquisition of a shared resource, or to the consequences this has for the growth and productivity of the competing plants. For a farmer competition only matters if the competing plants differ in value (per unit resource acquired) and thus intraspecific competition in a densely packed monoculture is not a concern, but competition with a weed is. Similarly, competition is a grave concern (Sanchez, 1995) in agroforestry system where trees of low direct use value prove to be effectively competing with annual crops valued by the farmer, while the interactions in a complex homegarden where all plants have value, is not seen as a problem (Van Noordwijk and Ong, 1999). For the plants involved, however, these value judgements do not matter, and an investigation can focus on the process of resource acquisition.

While low root length densities may be sufficient for uptake of mobile nutrients such as nitrate in a situation without competition (or one with intraspe-

cific competition in a monoculture of identical plants), the relative competitive strength of plants in a situation with shared access to a soil layer is proportional to their respective root length densities, making high root length densities functional from the perspective of an individual plant (Van Noordwijk, 1983; Robinson, 2001). A functional interpretation of root length densities thus is essentially different for a mixed plant situation than it is for the monocultures on which most plant physiological and agronomic research is focussed.

In a quantitative description of the way acquisition is affected by the presence of competition, we can distinguish:

- resource depletion by the other plants reduces availability (in a way that can be directly off-set by externally increasing resource supply),
- reductions of potential uptake per unit root length by the presence of other roots or 'interference'; as potential uptake is a non-linear function of total root length density, caused by a reduction of soil cylinder depleted per average root with increasing total root length,
- reductions of mobility of nutrients by reduced soil water content.

The first and third of these effects can, in special circumstances, be off-set or made into positive effects, by plants that increase the availability of nutrients in their rhizosphere and or that increase soil water content in nutrient-rich soil layers through the process of 'hydraulic equilibration' (Smith et al., 1999; Burgess et al., 2001). Although the second aspect of competition ('interference') would still remain, it is possible that the overall effect is positive, depending on the degree of 'synlocation' of the various types of roots. A specific form of synlocation can be imposed if roots of more than one plant species follow a limited number of cracks or macropores derived from old tree root channels (Van Noordwijk et al., 1991, 1993). The impacts of rhizosphere modification by any component of a mixed-species system depend on the degree of 'synlocation' of the roots of the different species (Figure 2; Van Noordwijk et al., 1999).

We used a process-based model of agroforestry (WaNuLCAS) in a case study to address the following question: Can we predict where and when rhizosphere modification by one species can be beneficial for accompanying plants? The WaNuLCAS (water, nutrient and light capture in agroforestry systems) model (Van Noordwijk and Lusiana, 1999, 2000; <http://www.icraf.cgiar.org/sea/AgroModels>) de-

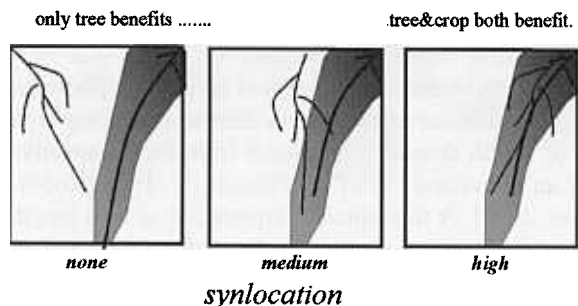


Figure 2. Conceptual scheme of different degrees of synlocation of roots of different plants and its consequences for the benefits of rhizosphere modification by one of them.

describes plant-plant interaction in above- and below-ground aspects. Competition and complementarity in use of nitrogen, phosphorus and water can be evaluated in the model for any combination of trees, crops, planting times, organic and inorganic input regimes, provided that basic properties of the root system and aboveground growth are known for the given soil and climate. The WaNuLCAS model incorporates key aspects of space (4 soil layers in 4 lateral zones), time (daily time steps, simulations up to 25 years or beyond), complexity (1–3 tree species can be grown simultaneously, crop calendar can be specified for each zone separately) and management (fertilization, organic inputs from outside or inside the system, aboveground tree management by pruning, manipulation of root distribution) of agroforestry. Interactions in P uptake in the model consist of a number of separate terms that can be studied in isolation or in combination in the model, in ways that are not easily reproduced in real world experiments (Table 2).

For the current exploration of rhizosphere modification and safetynet functions a default parametrization was used (Table 3) that reflects the BMSF site in Lampung (Sumatra, Indonesia) where WaNuLCAS validation tests were carried out focusing on deep N uptake (Rowe, 1999; Suprayogo, 2000).

The simulation results presented in Figure 3 applied to a setting where the default settings predicted approximately equal crop performance in three zones adjacent to the hedgerow trees, as positive (via improved N supply) and negative (via water supply) interaction effects where in balance. If rhizosphere modification by the trees is simulated as a 'medium' intensity (the technical details are specified in the caption to Figure 3), it would not affect crop growth in zones 3 and 4 (furthest away from tree), but could either increase or decrease crop growth in zone 2

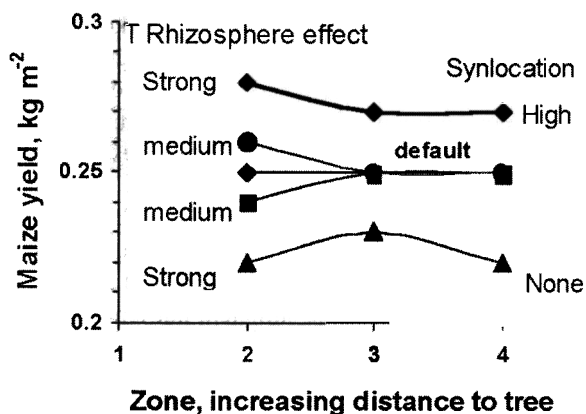


Figure 3. Predictions by the WaNuLCAS model of the impacts of rhizosphere P mobilization by hedgerows trees on the yields of adjacent maize in three zones with increasing distance to the hedgerow, in dependence of the degree of 'synlocation' of maize and hedgerow tree roots; the medium and strong $T_{Rhizosphere}$ effect refer to parameter values of 10 and 100 $\text{cm}^2 \text{day}^{-1}$, respectively, that determine the fraction of the immobile P pool in the soil that can be mobilized per day ($1 - 1/(1 + T_{NutMob} * \pi * T_{Lrv} * (T_{RootDiam} + T_{RhizosphereDiam})^2/4)$), with a root and rhizosphere diameter of 1 mm each and a tree root length density T_{Lrv} per zone as specified in Table 3).

(next to tree), depending on the degree of synlocation; for strong synlocation and a medium rhizosphere modification a slight positive effect would be expected in zone 2. If an (unrealistically) strong rhizosphere effect is simulated, the results show an expected increase of crop yields across all zones in case of strong synlocation, a neutral effect for partial synlocation and negative effects in all zones in the absence of synlocation.

Thus, we conclude that under high synlocation both species can benefit from the increased availability of nutrients in their root environment, but the net effect on the species modifying the rhizosphere may be positive, neutral or negative depending on the degree the companion crop was limited by the mobilised resource and is itself a more effective competitor for the resource limiting the mobiliser crop. The 'synlocation' parameter that appears to be crucial for the outcome of the interaction is potentially measurable (Van Noordwijk et al. 1993), but no data exist as yet. The problem of 'rhizosphere' modification and synlocation may partly be overcome by an effective mycorrhizal symbiosis that can scavenge in the rhizosphere of neighbouring roots or even directly connect them.

The impacts on the competing plants differ between the initial phase of near-exponential growth, where a setback in current growth affects future

Table 2. Interaction effects on P nutrition between plants A and B, either grown simultaneously (with partially overlapping root zones) or sequentially on the same site

Effect of plant A	Simultaneous		Sequential	
				Determinants of impact on B
Uptake interference				Relative root length densities of A and B
Reduce P concentration in soil solution by uptake			0/-	P demand A, root density A, P buffering soil
Increase P stocks by residue recycling	0		0	P harvest index A, effective decomposition rate residues A
(Potentially) increase P concentration by P mobilization	(0	++)	(0	+) Root synlocation, immobile soil P reserves, mobilization strength A
(Potentially) increase P concentration by mineralization of P _{org}	(0	++)	(0	+) Root synlocation, organic P reserves, phosphatase effectiveness plant A
Reduce P mobility by soil water uptake			0	Rainfall, soil type
(Potentially) increase P mobility by hydraulic lift	(+)		0	Deep roots A, rainfall, soil type
(Potentially) increase P mobility by reduced P sorption	(0	++)	(0	+) Root synlocation, rhizosphere effect A
Overall effect				Determinants of impact on B
				Recharge from less mobile P pools
				P harvest index A, effective decomposition rate residues A
				Half-life time mobilization effect, immobile soil P reserves, mobilization strength A
				Half-life time mineralization effect, organic P reserves, phosphatase effectiveness plant A

growth as well, and the closed-crop stage of linear growth, where only current growth rates are affected. This means that negative early effects of competition, e.g. before positive rhizosphere modification effects become operational, can normally not be compensated by positive effects later on in the growth period. The interaction of all these positive and negative effects acting at different spatial and temporal scales, may require the use of simulation models that can keep track of cumulative effects as shown above.

Safetynets in sequential and simultaneous systems

Concept

The concept of deep nutrient uptake by trees has been discussed for more than a century (Huxley, 1999),

but only applies to soils that have appreciable nutrient stocks derived from weathering or subsurface lateral flows. For nutrients of low mobility, long time frames apply and a low efficiency of uptake on a yearly time scale can still lead to appreciable depletion over the lifetime of a perennial crop or tree. For mobile nutrients, however, the residence time of nutrients in the subsoil is limited, and interception by trees or other deep-rooted vegetation has to occur while nutrients are on their way out of the reach of the root system or the soil system. For such situations the term 'safetynet' has been coined. Key questions on the way safetynets and filters function in natural resource management are:

- How effective are different types of filters for intercepting flows as can be expected in different rainfall regimes for nutrients differently sorbed and buffered by the soil?
- How does the filter or safety net efficiency depend on the ‘mesh size’ as determined by root length density and thickness of the soil layer involved?
- How quickly will filters saturate under high inflows?
- How fast can the filters regenerate between events?
- Do filters have a direct value and can they be treated as a separate ‘land use practice’?
- How effectively can intercepted nutrients be reused in the systems?

A first theoretical analysis of safetynets by Van Noordwijk (1989) showed that a limited window of opportunities exist in a sequential system for a deep-rooted fallow to intercept nutrients leached beyond the shallow crop root zone in cropping years. As argued by Sommer et al. (2001), nitrate sorption in subsoil can slow down nitrate movement to increase the chances of recapture by subsequent fallow vegetation. Subsoil nitrate sorption is common in acid tropical soils (Suprayogo et al., 2002, Wong et al. 1990) although its effectiveness in decreasing leaching is limited (Suprayogo et al., 2002).

For nutrients of higher mobility a more permanent presence of a safetynet is required. Cadisch et al. (1997) and Rowe et al. (1999) have explored how such a safetynet function may depend on tree root length density in the layer underneath the crop root zone and provided evidence from ^{15}N placement experiments that uptake from deeper layers can be substantial, provided aboveground ‘demand’ exists. Again, a simulation model that looks at the interactions between leaching rates, aboveground demand, N_2 fixation and the possibilities for uptake from various parts of the soil profile is needed to move beyond qualitative statements. Rowe et al. (1999) calculated for hedgerow intercropping experiments in Lampung (Indonesia) that the non- N_2 fixing tree *Peltophorum dasyrrachis* recycled 42 kg N ha $^{-1}$ year $^{-1}$ by uptake from below the crop root zone, while the N_2 -fixing *Gliricidia sepium* recycled only 21 kg N ha $^{-1}$ year $^{-1}$.

Safetynet efficiency: Effect of rainfall

In a series of WaNuLCAS simulations (Table 3) that excluded P limitations on crop or tree growth, a gradual shift from water to N limited growth conditions was obtained (Figure 4) by applying multipliers

on the daily rainfall records for Lampung. The predicted maize yields, with or without trees, was highest for an annual rainfall of two-thirds of the actual record (2318 mm year $^{-1}$), with a rapid reduction for lower rainfall values and a gradual decline for higher rainfall (Figure 4A). The presence of a hedgerow tree shifted the water limitation curve to the right (Figure 4B), showing that even at an annual rainfall of 2300 mm on 5-10% of the days in the cropping season water can be the growth limiting factor in the presence of hedgerows; it also shifted the nitrogen limitation curve to the left, indicating a positive effect on N supply of the (non- N_2 fixing) tree *Peltophorum dasyrrachis*. N leaching is predicted to be reduced by the presence of hedgerow trees at all rainfall rates above 1000 mm year $^{-1}$, and the total filter efficiency increases (Figures 4C and D). Filter effectiveness for the same tree and crop parameters decreases non-linearly with increasing rainfall, as the residence time of solutes in the deeper soil layers decreases non-linearly with a larger surplus of rainfall over evapotranspiration. Below an annual rainfall of 1000 mm year $^{-1}$ the amount of water and N leaching into and out of the subsoil layer 4 (the deepest soil layer considered, e.g. 0.5–1 m depth, see Table 3) becomes negligible and the calculation of the filter function loses its meaning. The absolute increase of filter efficiency due to the presence of trees increases with decreasing rainfall from 9% at 1.4 times the rainfall (3260 mm year $^{-1}$) to 19% at 50% of the default rainfall (1160 mm year $^{-1}$), for the default crop and tree root length densities.

Safetynet efficiency: Effect of root length density and distribution

A further WaNuLCAS model exploration of these effects at the default rainfall showed a strong dependence of filter functions in layer 4 (the deepest soil layer considered) on the tree root length density in this layer (Figure 5). Filter functions for situations with hedgerow trees start to increase below the crop-only situation (maize is supposed to have a few roots in layer 4) if tree root length density exceeds a value of 0.001 cm cm $^{-3}$, and reaches a maximum when tree root length density in this layer becomes 1 cm cm $^{-3}$ (Figure 5B, note logarithmic scale). Tree biomass benefits from more roots in layer 4, but saturates at a tree root length density in layer 4 of 0.03 cm cm $^{-3}$ (Figure 5C), as this apparently is sufficient to carry the tree through the dry season. In the predicted impacts of the hedgerow on the maize crop (Figure 5D) the

Table 3. WaNuLCAS parameter settings used as default for the simulations of Figures 3–6; detailed definitions and other default parameters are specified in van Noordwijk and Lusiana (1999).

Parameter	Value
AF_Zone(Zn1) – width of zone that includes tree	
AF_Zone(Zn2) – width of second zone	
AF_Zone(Zn3) – width of third zone	
AF_ZoneTot – total width of the simulated area	
AF_DepthLay1 .. 4 – depth of the four soil layers	0.05, 0.15, 0.3 and 0.5 m, respectively
Rt_CLrvm1 (Crop root length density layer1)	6.67 cm cm ⁻³
Rt_CLrvm2 (Crop root length density layer2)	3 cm cm ⁻³
Rt_CLrvm3 (Crop root length density layer3)	0.1284 cm cm ⁻³
Rt_CLrvm4 (Crop root length density layer4)	0.0064 cm cm ⁻³
Rt_TLrv1..4Zn1 (Tree root length density layer1, Zn 1...4)	2, 1, 0.5, 0.25 cm cm ⁻³ , respectively
Rt_TLrv1..4Zn2 (Tree root length density layer1, Zn 1...4)	1.5, 0.75, 0.4, 0.2
Rt_TLrv1..4Zn3 (Tree root length density layer1, Zn 1...4)	1.3, 0.45, 0.3, 0.15
Rt_TLrv1..4Zn4 (Tree root length density layer1, Zn 1...4)	1.2, 0.37, 0.15, 0.1
Cropping season	4 cropping seasons (2 per year), started on December 6 th , followed by next crop in 30 th March
Ca_PlantYear	0, 1, 1, 2, respectively
Ca_PlantDoY	340, 90, 340, 90, respectively
Tree planting	Trees were planted 5 months before planting 1 st crop
T_PlantY	0
T_PlantDoY	205
T_GroResInit, Initial growth reserves in tree	0.01 g m ⁻²
T_CanBiomInit, Initial tree canopy biomass	0.1 g m ⁻²
T_WoodBiomInit, Initial tree wood biomass	0.1 g m ⁻²
T_WoodHInit, Initial tree height	0 m
Pruning	Pruning prior to every crop planting
T_PrunPlant?	
Soil Texture:	
Percentage of clay	30
Percentage of silt	10
Percentage of sand	60
Slope	
AF_SlopeSoilHoriz	
Fertilizer	No fertilizer added
Ca_FertAppYear, first year if fertilizer application	100
Mc2_SomInitType:	3
Mc2_CorgInitMeh	1
Mc2_CrefMeth3	2

model predicts that a strong difference between crop zones exists for tree root length densities in layer 4 up to 0.1 cm cm⁻³, and that higher tree root length densities in layer 4 actually benefit the crop, despite a higher biomass and thus stronger direct competition.

The positive (safetynet functions) and negative (competition for water and N) impacts of simultaneous tree roots on maize yield was further analysed by separating relative tree root distribution from absolute root length density. Results for these calculations show (Figure 6) that negative overall effects of the tree can

be expected for trees that have all their roots in the topsoil, and for trees with only 0–10% of their roots in the subsoil, at low overall tree root length. These same relative tree root distributions at higher total root length (i.e. higher absolute root lengths in both top and subsoil) can have a moderate positive effect on maize yield, while tree root systems with 20% or more of their roots in the subsoil were consistently positive for the crop, the higher the total root length, the more positive the impact on maize.

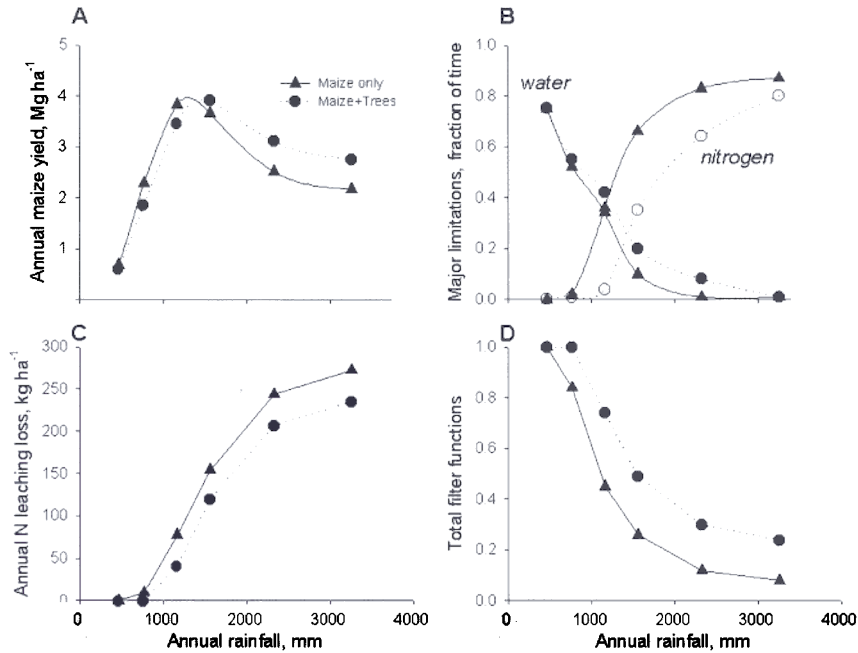


Figure 4. (A) Model predictions of maize yield (two crops per year; for a standard parametrization, see text) as a function of annual rainfall (obtained by using multipliers on the 1993 Lampung daily record - see arrow), with or without the presence of regularly pruned hedgerows of non-N-fixing trees; (B) The fraction of the growing periods that either N or water is the main limiting factor (causing at least 10% reduction in growth on a given day and being the strongest current limitation); (C) Annual loss of N by leaching and lateral sub-surface flow; (D) Overall filter efficiency for N, defined as uptake/(uptake+losses).

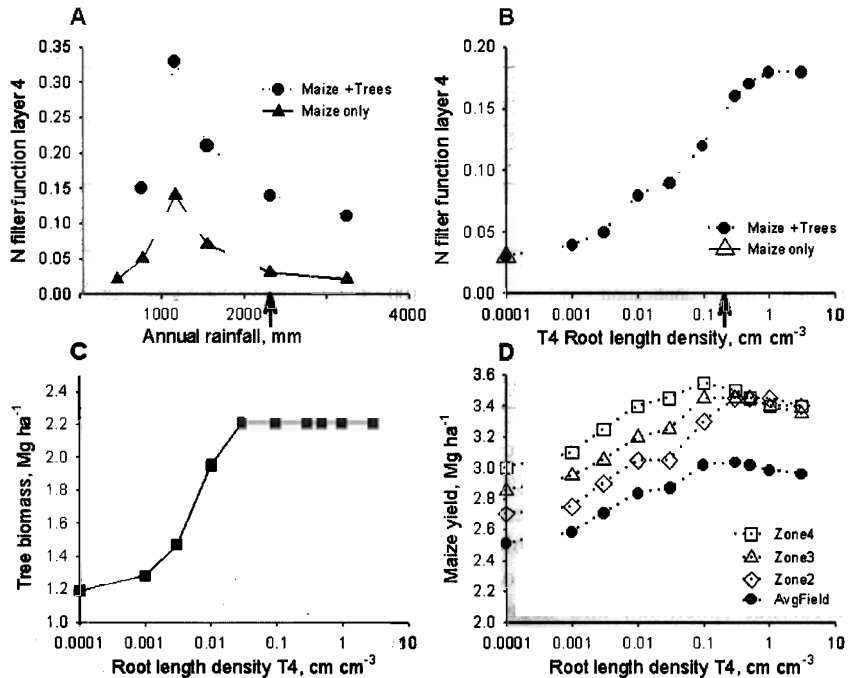


Figure 5. Filter function (=uptake/(uptake+leaching) for nitrogen of the fourth soil layer, (A) as a function of annual rainfall and (B) as function of tree root length density in layer 4 (N.B. logarithmic scale). (C) and (D) show tree biomass and maize yields in the same simulations. For input parameters see Table 3.

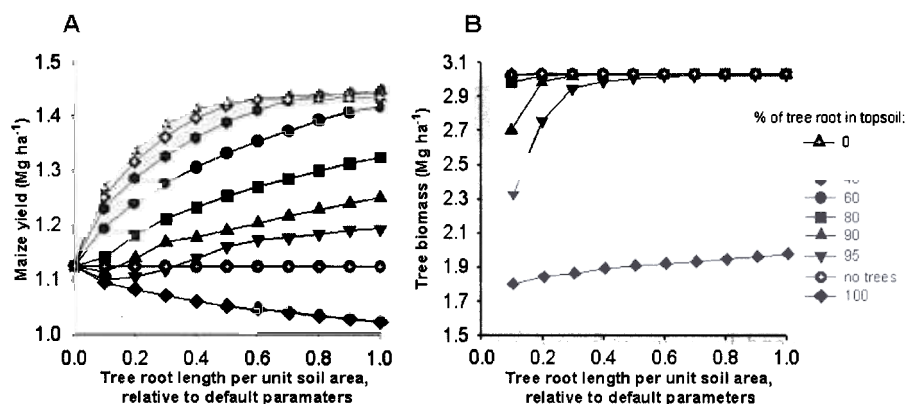


Figure 6. Predicted maize yield (A) and tree biomass (B) for the default rainfall situation of Figure 4 (2318 mm year⁻¹), when relative distribution of tree roots with depth as well as total amount of tree roots are varied independently. Whereas the 'default' tree root system had 21.5% of its roots in the top layer, a series of data was made that had 0–100% of its roots in the top layer and the remainder allocated to the deeper layers in proportion to the root length densities of the default case (the relative distribution over the four zones with increasing distance to the tree was not modified). For each of these root distributions, the total amount of roots was varied from 0.1–1 times the default, while maintaining the relative values.

A remarkable feature of these results is that at default values for total root length, the tree root systems with 60% of their roots below the topsoil led to (slightly) higher maize yields, than those with more (up to 100%) in the subsoil, while at lower total root system size the 100% in subsoil (0% in topsoil) was better for the maize. Although this effect is much too subtle to be recognized in any field data, it seems counter-intuitive. On detailed analysis the differences in crop N uptake between trees with 0 and 40% of their roots in the topsoil arise during dry spells in the cropping season when the sparse crop roots in the deeper soil layers have slightly more N available in situations where the trees forage partly in the topsoil.

Sensitivity analysis of the model thus shows that the tree root length density below the main crop root zone may have complex and partially unexpected effects on crop performance in situations where negative effects via competition for water and positive effects via improved N supply vary in intensity during the growing season. Positive effects of the trees via improved N supply would increase with time, and the current results averaged over 2 years (4 crops) are only a first indication of the overall impact of including hedgerow trees into the maize production system.

Apparently the tree root length density required for a safety-net function can be quite low, as it depends on the residence time of the mobile solute in the layer where the filter function is supposed to occur. For real trees the known root-length densities indicate that only a partial safety-net function can be expected to occur,

as root length densities in the subsoil are normally less than 1 cm cm⁻³, but above 0.001 cm cm⁻³.

Maximum efficiency attainable for a safety-net is less than 1 and depends on 'plant demand' and supply in other soil layers, residence time of the solutes and the relative extraction efficiency. For a different set of parameters Cadisch et al. (1997) obtained filter efficiencies up to 90% for a tree root length density of about 1 cm cm⁻³. If less N is available from other layers and tree demand is higher, higher safety-net efficiencies can be obtained in the model outcomes.

Overall, we conclude that filter functions for nitrogen on its way to leach out of the soil profile are related to rainfall, tree N demand and tree root length density in a strongly non-linear fashion. In formulating and using WaNuLCAS as a mechanistic model for interactions in more complex agro-ecosystems, we quickly realize that parameters that can greatly influence the model outcome are insufficiently known. These parameters refer to the longer term replenishment of the nutrient pools accessed by deep-rooted trees or by plants with specific rhizosphere effects, as well as to the spatial correlation of roots or mycorrhizal hyphae of interacting plant species. For the performance of the system as a whole, however, management of the aboveground biomass and its effect on nutrient demand dominates the opportunities to make use of more complex agro-ecosystems to achieve a higher overall nutrient-use efficiency. The simulation model provides a framework for combining knowledge on component behaviour to system-level assessment of plant nutrition.

Challenges to make it work

Complexity of agro-ecosystems is no guarantee for avoiding excess nutrition problems. The relicts of a previously functional complexity in the landscape in the form of the hedgerows of North Germany (Mette et al., 2001) can reduce nutrient use efficiency at system level if farmers ignore their role in recycling nutrients and fertilize the partially shaded parts of their fields as much as the rest. However, a better understanding of the nutrient stocks and flows in such systems may lead to a recognition of new functions of woody landscape elements as filter strips. Filters are only effective, however, if they remain undersaturated. If the biomass from filterstrips is not regularly removed by harvesting, filter functions can only be expected for N and only through denitrification (or ammonia volatilization). Safetynets only function if there is unfulfilled demand – they are thus not compatible with yield maximization of all system components, as supply is fluctuating with weather conditions, especially in systems with substantial organic reserves. The ecological analogue thus has clear limitations if close-to-maximum crop yields are expected. Where regular cutting or pruning of filter strips is needed to maintain their functionality, the biomass so obtained must have sufficient direct value to justify the labour use for the farmer. Overall, the technical control paradigm of reducing nutrient excess problems via unrecognized spatial availability in supply may offer a more direct approach to the parts of the world where nutrient excess problems are urgent, but filters may help in addition to that.

In conclusion, the concepts and tools to help farmers navigate between the scylla of access and the charibdis of excess problems in plant nutrition certainly exist, but their use requires an appreciation of the site-specific interactions and various levels of internal regulation, rather than a reliance on genetic modification of plants aimed at transferring specific mechanisms out of context.

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