



Can the ecosystem mimic hypotheses be applied to farms in African savannahs?

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Abstract. The first ecosystem mimic hypothesis suggests clear advantages if man-made land use systems do not deviate greatly in their resource use patterns from natural ecosystems typical of a given climatic zone. The second hypothesis claims that additional advantages will accrue if agroecosystems also maintain a substantial part of the diversity of natural systems. We test these hypotheses for the savannah zone of sub-Saharan Africa, with its low soil fertility and variable rainfall. Where annual food crops replace the natural grass understorey of savannah systems, water use will decrease and stream and groundwater flow change, unless tree density increases relative to the natural situation. Increasing tree density, however, will decrease crop yields, unless the trees meet specific criteria. Food crop production in the parkland systems may benefit from lower temperatures under tree canopies, but water use by trees providing this shade will prevent crops from benefiting. In old parkland trees that farmers have traditionally retained when opening fields for crops, water use per unit shade is less than in most fast growing trees introduced for agroforestry trials. Strong competition between plants adapted to years with different rainfall patterns may stabilise total system productivity – but this will be appreciated by a farmer only if the components are of comparable value. The best precondition for farmers to maintain diversity in their agroecosystem hinges on the availability of a broad basket of choices, without clear winners or ‘best bets’.

1. Introduction

1.1. *Two mimicry hypotheses*

Only 8% of Africa’s land area comprises fertile soils and the remaining 92% can be defined as marginal lands, which are either too dry, too wet or too saline (Yaker, 1993). Inherent soil fertility is low as most of the continent is geologically old and highly eroded and recent volcanic activity strictly localised. Large areas of apparently ‘unsuitable’ marginal lands are cleared each year for agricultural production, leading to further land degradation. Yet recent studies of some of these natural ecosystems, especially tropical grasslands, have shown that they can be highly productive (Solbrig et al., 1996). If current agricultural interventions are indeed inappropriate, would it then not be better to mimic savannah ecosystems, seen today in the East African Serengeti, where large mammals harvest and convert the primary production of the vegetation whether grass or trees. Tropical savannahs have long

histories of human occupation and the strategies of plants, animals, and people in savannah areas can accordingly provide clues for designing and managing new strategies in line with present needs and circumstances. However, previous attempts to improve the management of savannahs have been disappointing (Hadley, 1985), and few have explicitly addressed the balance between trees and annual or perennial understorey vegetation, while attempting to ascribe value to both.

The first ‘mimicry hypothesis’ (Ewel, this volume) argues that agricultural systems should benefit from imitating the structure and function of natural ecosystems, since components of the latter result from natural selection towards sustainability and the ability to adjust to perturbations. As our second mimicry hypothesis, we will subscribe that, apart from structure and function, agroecosystems shall benefit from resembling the diversity of natural ecosystems as well.

These mimicry hypotheses, especially the second one, might well be viewed as rooted in the long standing ‘romantic’ perspective of imitating Mother Nature, but they have rejuvenated and been appreciably modified in the wake of environmental interests over the last three decades and are now much more open to a rigorously objective scientific analysis. The ‘benefits’ both hypotheses can refer to are:

- a larger total production if combinations of different plant life forms are used rather than a monoculture;
- a higher efficiency in terms of human operation since less effort will be needed to achieve the same results where one works ‘along with’ rather than ‘against’ nature;
- reduced downstream effects if total resource capture in an agroecosystem can be engineered to simulate that of the natural system which it replaces. For example, both additional and reduced water use can grossly affect groundwater flow patterns and have unexpected effects elsewhere;
- better maintenance of environmental service functions in the landscape.

The hypotheses refer to two potential classes of compatibility between agroecosystem and natural ecosystem: total resource use (in the context of this paper relating to either to water and nutrients) or diversity.

The diversity issue, as addressed in our second hypothesis, is clearly the more speculative and contentious. We will focus on the role of diversity in managing risk, i.e. essentially the old adage of ‘don’t put all your eggs in one basket’, and relate the relevance of diversity to stability and resilience of resource capture in a fluctuating environment.

1.2. Segregate or integrate agriculture and environmental service functions?

The mimicry hypotheses suggest that an ‘integrated’ approach to land use, in which ecological functions in the landscape are affected as little as possible, is superior to a ‘segregated’ approach in which parts of the landscape are

managed towards maximum productivity and other parts reserved for 'environmental services' (Van Noordwijk et al., 1997). These environmental services may include the reduction of disturbed patterns of 'lateral interactions' in the form of surface or groundwater flow of solutes and sediments, wind assisted gaseous exchange of water vapour, specific gasses and particles, or movement of organisms, whether linked to pests and diseases and their potential control, or to biodiversity of intrinsic value.

The above issues are not purely of academic interest. Per-capita food production continues to decline in sub-Saharan Africa. The question is not just to maintain the current productivity of agroecosystems but how to achieve a considerable increase without compromising agroecosystem resilience. To meet the human population expansion, the annual sustained growth of agricultural production in Africa will have to rise by 4% over the next 25 years, i.e. 1% above the population growth rate, rather than 1% below as is the current situation (Badiane and Delgado, 1995). Total production growth will have to come from increases in productivity per cultivated area if we are to cure 'land hunger' (Van Keulen and Breman, 1990). To achieve this it may be more economical to restrict production to the best land and pursue a 'segregated' pathway for development of land use, where negative externalities of land use or a lack of environmental services can be compensated for elsewhere.

The declining per capita food production of Sub-Saharan Africa is perceived to be largely due to the existing policy environment which does not sufficiently favour smallholder rural development, or provide sufficient financial incentives for farmers to intensify their land use (Sanchez and Leakey, 1997). Priority issues in this respect are past and ongoing depletion of soil fertility as a fundamental biophysical constraint to food security and the domestication of indigenous trees to produce high value products. One may then ask whether these priorities are compatible with the mimicry hypotheses.

The objective of attaining food security can be achieved in different ways, with increasing degrees of market integration, namely by:

- stable agronomic production of the main staple food by the vast majority of the population;
- production of staple food on a few specialised farms within a specific country/region, together with a stable source of income (derived in or outside of agricultural enterprises) for all inhabitants to allow them to buy their staple requirements;
- as above, but with a population earning sufficient income to import food on a sustained basis from specialized farms elsewhere in the world.

Trees can contribute specifically to food security in three ways:

- by providing the main staple or emergency foods in times of shortage (e.g. from planting desert date, *Balanites aegyptiaca*);

- by increasing the opportunities for growing staple food crops by enhancing soil fertility (e.g. planting of N₂ fixing woody species);
- by providing income from high value products ('money in farmers pockets').

The first and third ways are based on direct value of tree products, whereas the second one refers to an added value derived indirectly from trees in a support function role.

1.3. Soil fertility and tree domestication related to the mimicry hypotheses

If the nutrient resource base for agricultural production has to be increased, one may ask whether such replenishment can be accomplished in the context of systems mimicking nature, or within simple, specialized crop production systems? There are some indications of positive interactions or at least additive effects between soil organic matter (provided by trees) and inorganic fertilisers (Breman and Kessler, 1997; Palm et al., 1997), but it is not yet clear whether agroforestry has a major role to play in the soil replenishment initiatives which are currently underway (Sanchez et al., 1997). The analysis by Breman and Kessler (1995, 1997) of the added value of woody plants in the Sahel and other semi-arid regions, suggests that trees may indeed increase nutrient and water availability for annual food crops and pasture production, but only if trees:

- have the right properties (can generate stem flow of water, are deep rooted, are unpalatable and of low 'quality', and thus able to contribute more to long term accumulation of soil organic matter rather than rapid mineralisation, exhibit slow growth rate and have a long life span);
- are used at an appropriate tree density;
- are properly managed by pruning, lopping and controlled harvesting;
- are growing on appropriate sites and soil types in which the above goals can be realistically achieved.

Trees with the best set of properties, such as *Faidherbia albida*, may increase grain yield in the Sudano-savannah zone by 200–400 kg ha⁻¹, provided they have an average tree canopy cover of about 20%, can gain access to the water-table, and are not foliated during the crop growing season. A general 'grow more trees' approach is not likely to meet such conditions.

Tree domestication aims at converting wild species with proven direct or indirect value, currently collected from the wild or maintained in agroecosystems, into crops or service components of agroforestry systems of high potential value. It involves genetic selection and may involve vegetative propagation to capture and perpetuate the properties of superior individual members of tree populations. Guidelines have been developed for species prioritisation aimed at identifying what one might term 'cinderella trees', namely species overlooked by science but long appreciated by local people.

High-value trees can fit in specific niches on farms while leaving more open land to staple food crops or annual crops grown for markets (Sanchez and Leakey, 1997). The current approach used in this arena has some elements in common with the mimic hypothesis, but it is focused on domesticating the components, rather than domesticating the system. Indeed, Michon and de Foresta (1997a, 1997b) have contrasted domestication of agroforests to tree domestication, and argued that if the agroforest context is kept in mind during the tree selection process, tree improvement does not necessarily lead to germplasm which is only suitable for orchard-like tree monocultures. Elaborating on their argument, we suggest that a strategy for domesticating the system might start by asking which elements of the current system rank of lowest value and try to increase the performance of these or find ecological equivalents as replacements. However, for this to happen, it would require fundamental understanding of how both natural and partially domesticated agroecosystems function. The targets of tree domestication as currently formulated do not include traits to promote compatibility between the trees and other components of a particular agroforestry system. For example, faster growth, shorter stature and earlier fruit production are desirable for fruit trees, but these characteristics obviously make the same subjects less suitable for employment as 'parkland trees'.

1.4. *Competition, diversity and the second mimicry hypothesis*

Competition between trees and crops is often viewed as an inherently negative aspect of agroforestry systems, which one has to avoid or reduce by appropriate management protocols. Indeed, this view has led to the conclusion that one should shy away altogether from simultaneous agroforestry systems in drier climatic zones and rather focus on fallow rotations (Sanchez, 1995). As competition for water and nutrients is an inevitable feature of natural ecosystems, a purely negative view of competition couched in such terms appears inconsistent with the mimicry hypotheses, and is possibly an inappropriate basis for developing agroecosystems. But it remains debatable whether competition is so inherently negative that the above conclusion is warranted. No doubt it depends on one's perspective and on the way one evaluates the different components of the system. Cannell et al. (1996) related a biophysical advantage of agroforestry to at least some degree of complementarity of resource capture, as opposed purely to absence of competition between components. Van Noordwijk (1996) explored the degree of complementarity needed to provide a total value beyond that of the best separate monoculture performances of the system's components. If the value attached to the two competitors is equal (per unit resources captured), even a slight complementarity can be sufficient to make the combination worthwhile. If, however, one component has no discernible direct value, its presence in a system can only be justified if there is strong complementarity in resource capture and effec-

tive transfer of captured resources from it to other valuable components of the system. So competition need not be a disadvantage from the perspective of management of an agroecosystem, as long as the manager in question is a 'generalist', who places value on several, if not all, components of the system. In such a situation, the presence of strong competitors may contribute to the stability (reduced variance) of the combined system, as we will see below.

As an example of the above, farmers in semi-arid Kenya have developed a parkland agroforestry system which includes a highly competitive, fast growing native species, *Melia volkensii*, because it provides a wide range of products for household needs as well as generating income to cover the cost of children's school fees. It is a member of the mahogany family, valued principally because its high quality timber is termite resistant, coarse grained and easy to work. At the same time, its leaves and fruits provide a good fodder for goats, sheep and cattle, and the leaves can be used as a repellent for fleas and ticks. Typically, a farmer establishes five to ten trees, mainly from wildings, on a farm, and these trees can generate more income than crops from the rest of the farm over a period of five to eight years. Thus, this species is considered as 'compatible' with the agroecosystem even though it is highly competitive with crops.

1.5. *Outline of this chapter*

In the pages which follow, we will focus our discussion of the application of mimicry hypotheses to the savannah zone, as there are considerable differences of opinion about feasible and desirable pathways for development of agroecosystems in this zone (Jones et al., 1998). The parklands of the savannah zone can be compared to the Spanish 'Dehesa' system (Joffre et al., this volume), and the forest-derived landscape in NE Thailand (Sae-Lee et al., 1992). The vegetation in all these areas consists partly of trees deliberately retained after natural or fallow vegetation has been cleared, or of trees deliberately planted. The proportions of such spontaneous and planted trees can vary noticeably between regions but, in all cases, trees spared during land clearing are maintained essentially because of their potential useful products or functions, and/or compatibility with crops. In such cases, tree species diversity can be considerable and intra-specific variation may still resemble that of a natural tree population (Boyle, pers. comm.). Furthermore, if these trees are propagated by seeds, they may still be effectively part of the natural tree population. If domestication and selection proceed, genetic diversity can be expected to decrease.

In this chapter we explore how current understanding on the structure and function of African savannah might be used to design or improve agroforestry systems for sub-Saharan Africa (Tothill and Mott, 1985; Walker, 1987; Belsky and Amundson, 1998). Ong and Leakey (this volume) compare the resource capture and influence of trees on crops in agroforestry systems using evidence from the savannah. In this chapter we address:

- the abiotic and biotic environment of savannah systems;
- constraints on total resource usage within such systems;
- the possibility of risk reduction through increased diversity;

and conclude by discussing the value of the mimicry hypotheses as a basis on which new or existing savannah systems might be improved.

2. Structure and function of African savannahs

2.1. *Vegetation and climate*

There is nothing particularly new in the recognition of ecological zones in Africa and the need to take into account information of soils, vegetation, climate and locally developed farming systems when planning agriculture and forestry (De Vos, 1975; Van Noordwijk, 1984). Separate terminologies persist for west, east and southern Africa for similar vegetation types and ecological zones. Within the main savannah zone spanning from Africa's west coast to the Ethiopian highlands, one commonly distinguishes a Sahel, Sudano- and Guinean savannah zone, with additional man-made derived savannah in the wetter forest zone. In eastern and southern Africa the term miombo woodland is used for a vegetation similar to the Guinea savannah (Campbell et al., 1998). Rainfall as fraction of potential evapotranspiration for the various savannah types in western Africa is < 0.21 for the Sahel, $0.21-0.40$ for Sudan savannah, $0.40-0.66$ for Northern Guinea savannah, $0.65-0.88$ for Southern Guinea savannah, and $0.75-1.0$ for derived savannah (Sanford and Isichei, 1986). The major rivers flowing through the savannah zones (Niger, Nile, Zambezi) derive their water from rainfall on mountains in the forest zone and, thereby provide additional resources of water and nutrients on that small fraction of the land, on which a considerable proportion of the total human population subsists.

The standard deviation of annual rainfall is remarkably constant across climatic zones of the savannah, so that the coefficient of variation (standard deviation divided by the mean) increases almost inversely proportional to a decreasing mean. Thus, El-Tom (1975) calculated that zones of the Sudan, with mean annual rainfall values of 1300, 900, 600, 400, 150 and 50 mm had coefficients of variation of 11, 15, 25, 30, 60 and 100%, respectively. Although water resources in the savannah zone are considerable in magnitude, they fluctuate widely in time and can be equally variable in space. This selects for a balance between two opposed strategies within indigenous floristic components, namely an opportunistic strategy of rapid expansion when resources are present and surviving in seed or other dormant forms in less favourable periods, and a complementary strategy of slow, steady growth, with ample internal storage and survival mechanisms.

Walker (1987) defined savannahs as those tropical (or sub-tropical) ecosystems characterised by strong seasonality (wet summer/dry winter) related to

water stress, dominated by a continuous herbaceous vegetation consisting principally of grasses (usually C_4 type species) and sedges, and a few scattered trees and shrubs. For the purpose of this chapter we will describe the structure and function of savannah ecosystems in terms of the flow of water and energy through the system rather than dwell in detail on the botanical composition and behaviour of plant species. Figure 1 is the model proposed by Solbrig et al. (1996) to predict the function of tropical savannahs in terms of water, nutrients, fire and herbivory. According to this model, mesic woody species would be expected to dominate when water is relatively abundant, but give way to moist forest at the extreme wet and to dry desert regions at the ends of the biome. Nutrient supply can modify the vegetation expected for a given rainfall zone, so that, for example, a combination of low rainfall and high nutrients (e.g. Serengeti in Kenya) can support a savannah grassland rather than desert, whereas a decrease in nutrient supply would be expected to induce desertification without change in rainfall. Local effects of soil types and topography compounded with effects of fire and herbivory modify the density of the tree layer, and productivity and rates of water and nutrient flow through each system.

Judging from the relatively sparse data available, belowground productivity of savannah, ignored in many earlier studies, can exceed the aboveground part. For example, total productivity of grassland of the Nairobi National Park

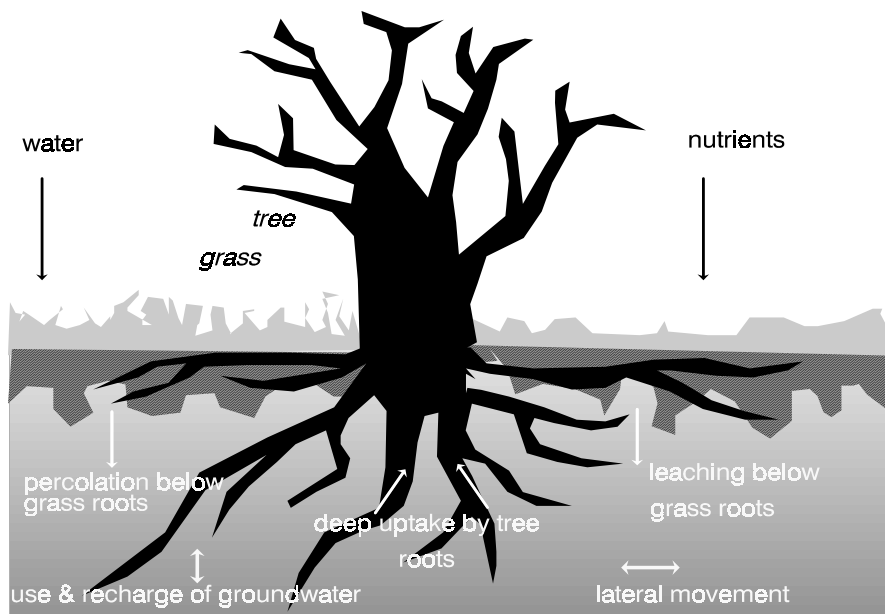


Figure 1. Water and nutrient cycling in savannah. Deep tree roots obtain water and nutrients from lower layers of the soil. Tree leaf and litter fall decompose on the upper layers where they are utilised by the grass layer. Source: Adapted from Solbrig et al. (1996).

(annual rainfall of 800 mm) was estimated to be $18.8 \text{ t ha}^{-1} \text{ y}^{-1}$ of which only $8 \text{ t ha}^{-1} \text{ y}^{-1}$ was above ground (Long et al., 1992). In Rwenzori National Park (rainfall of 900 mm), Uganda, total productivity of savannah grasses proved to be greater at $23 \text{ t ha}^{-1} \text{ y}^{-1}$, with two-thirds as below ground biomass (Strugnell and Piggot, 1978). The values indicate that the efficiency of production of the perennial C_4 type grass vegetation can be much higher than previously estimated. Recent studies indicate that a large number of grasses and tree species allocate a high proportion of their photosynthate and nutrient reserves to roots and underground organs, largely as an adaptation to herbivory and fire. In general, the biomass contribution from shrubs and trees tends to be very low comprising only 1 to 5% of the total biomass of grasses.

2.2. *Water use*

The herbaceous layer comprises the dominant component of all savannah and is accordingly likely to have greatest impact on the flow of water through the soil-plant-atmosphere continuum and on the net primary productivity and mineral cycling of the system in relation to fire and herbivory. Grass production is tightly linked to seasonal rainfall since grasses are generally shallow-rooted. For instance, as shown in Figure 2a, leaf area index matches rainfall distribution at the Nairobi National Park. During the short rains (October–January) both above and below ground biomass was quite similar but below ground biomass was highest during November. Then, in the long rains (February–June) shoot growth was greatest. Virtually all the grass root biomass (Figure 2b) was present in the top 15 cm of the soil. Trees are deciduous at this site, as both trees and crops depend on the same soil water supply from seasonal rainfall for their growth. Only in riverine habitats where trees access deeper water can such species afford to be evergreen. This situation is similar to the sandy savannahs of southern Africa where trees and grasses compete strongly for soil water, and do not have distinct rooting zones as previously assumed (Knoop and Walker, 1985; Walker, 1987). Thus, at sites like Nairobi National Park, where a high proportion of rainfall never penetrates beyond the root zone of grasses, the community is grass dominated. In South Africa, Adcock (1983) demonstrated a negative correlation between the proportion of trees and water holding capacity of the topsoil. In contrast, (some) neotropical savannahs of South America show two distinct patterns of soil drying and root distribution, where trees maintaining high transpiration rates throughout the year but grass roots are confined to the topsoil and desiccate in the dry season (Goldstein and Sarmiento, 1987).

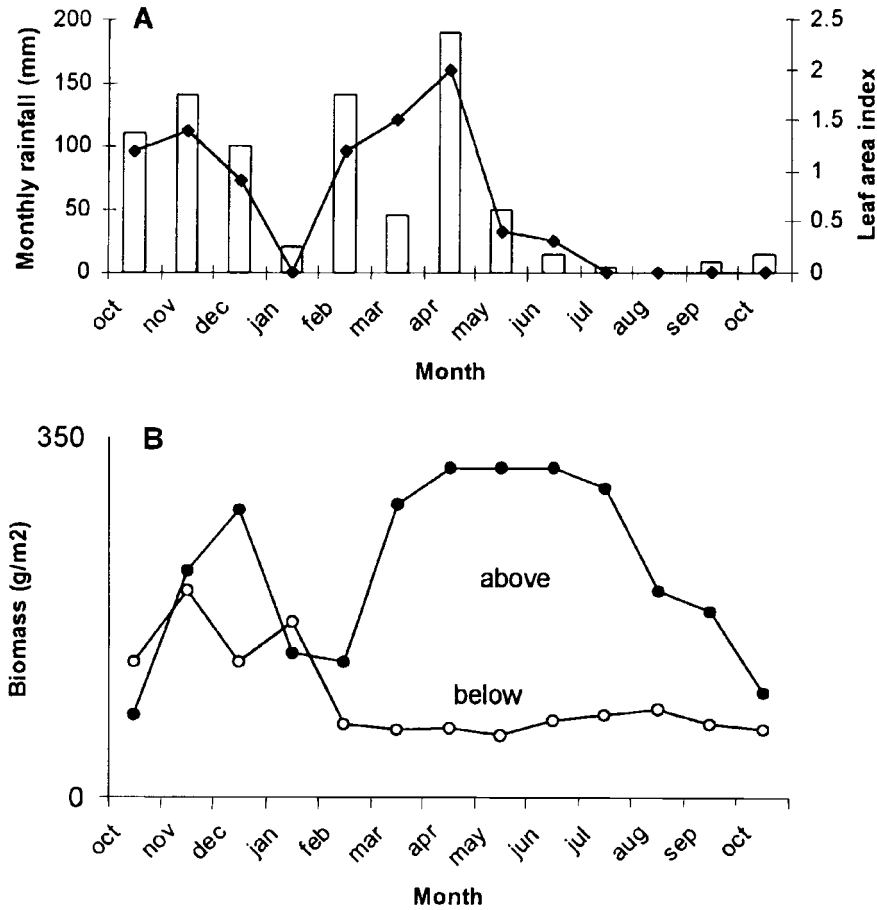


Figure 2. Monthly rainfall and leaf area index (a) and above- and below-ground biomass production (b) of grassland at Nairobi National Park, Kenya. Source: Adapted from Kinyamario and Imbamba (1992).

3. Structure and function of agroecosystems in the savannah zone

3.1. Human livelihood strategies in the savannah

Human hunter/gatherer strategies in savannah have traditionally depended on roots and tubers as main staple, enriched by fruits and grass seeds in season and supplemented opportunistically by the highly variable outcomes of hunting fauna. Thus, the hunter/gatherer is both a generalist and an opportunist. By contrast, keeping livestock in migratory herds (or in a semi-sedentary transhumance system) can develop progressively into a recognisable specialisation, as it exploits a resource which itself is of generalist nature, exploiting grazing resources when and where they exist and not depending, therefore,

on any single location throughout the year. Traditional crop production in the savannah zone relies heavily on risk-prone grain crops rather than tubers and has typically utilised a much lesser diversity of species than is utilised in the forest zone, where it became the dominant livelihood strategy rather than a complement to livestock keeping. Introduction in colonial times of cassava has provided an attractive root crop for the wetter parts of the savannah zone and facilitated highly specialised production of this species. Part of the tree resources of the savannah have been maintained in what developed into parkland systems, and may have actually benefited from increased water availability wherever grass was replaced by food crops.

People have modified the biotic environment of the savannah zone by:

- removing predators and competitors to allow *Homo sapiens* to emerge as prime carnivore;
 - reducing the population density of grazers competing with domesticated livestock;
 - removing trees from the landscape which supply nesting sites for granivorous (weaver) bird pests;
 - removing game animals acting as a host to *Trypanosoma* and trees ('bush') which provide cover for the tse-tse fly which act as vector for this disease.
- These two strategies at managing trypanomiasis partly counter this major constraint to keeping livestock in wetter parts of Africa (Delaney and Happold, 1979).

When conservation of wildlife became an issue of global interest, a segregated pathway of development emerged as the obvious choice in which the richness of animal populations was maintained in national parks (generally on agriculturally marginal lands) while agricultural development was focused elsewhere. Well-defined and articulated boundaries were thus established between the two. There has, however, also been some interest in pursuing an integrated pathway of development and conservation where game ranching is managed as a semi-domesticated ecosystem. But this closest of approaches to mimicry has failed to provide for more than a small niche market. The current approach to conservation accepts segregation of activities as an implicit element, encouraging at the same time social integration through wider participation by local communities in wildlife protection and thereby sharing benefits from tourism.

3.2. Agroforestry as derived agroecosystems or mimics?

Parkland savannah systems are agroecosystems which have selectively maintained a considerable share of the mature trees of the natural savannah, but have replaced most of the original understorey with food crops, often alternating with fallow periods when the regenerating grass and shrub vegetation are grazed. These parkland systems extend into the dry Sudano-savannah zone. Model predictions of agroforestry systems with fast growing trees in such

water limited environment indicate that trees have a strong negative impact on crop production (Mobbs et al., 1998; Cannell et al., 1998). Cannell et al. (1998) concluded from their model that although total resource capture will nearly always be higher if trees are added, simultaneous agroforestry systems are inappropriate in regions with less than 800 mm rainfall due to:

- a) the low water use efficiency (dry matter production per unit transpiration) of C₃ trees at dry sites, and
- b) the sensitivity of C₄ crop yield to shading.

Food security in this zone may be seriously jeopardised by (re)introducing trees unless tree roots have access to the water table, and at the same time, improve soil fertility and/or produce biomass of high value (fuel, gum, fodder, fruits).

The main agroforestry system of the parklands has elements of sequential (fallow-crop rotations, Torquebiau and Kwesiga, 1996) as well as simultaneous systems, as low tree density is maintained throughout the cropping period, while shrub and tree biomass increases during the fallow phase. Traditional systems of this type, such as the gum arabic (*Acacia senegal*) fallow rotation of the Sudan, are generally in decline but embrace an interesting balance by deriving value across and within fallow and crop stages. Tree species in the parklands vary with rainfall, from the desert date (*Balanites aegyptica*) in the drier parts to shea-butter nut (*Vitellaria paradoxa*, *Butyrospermum* sp.) and néré (*Parkia biglobosa*) in wetter zones. Aboveground tree density in parklands may be low, but all land area between trees is normally exploited by tree roots, which may extend up to 40 m from the tree trunk (Van Noordwijk et al., 1996).

Results from five-year-old *Grevillea robusta*/maize agroforestry trials at Machakos, Kenya, a site with similar rainfall to Nairobi National Park, showed that 90% of the biomass from tree and maize was produced during rainy seasons (Lott, 1998). Utilisation of deep water by the trees was small but gradually depleted the shallow soil profile (1.5 m). Indeed, production of biomass during the long dry season, July–October, accounted for only 10% of the total annual biomass produced by the tree. This low productivity was due to the small amount of residual water after the harvest of the crop, low tree root density below 1 m depth and a daily tree growth rate of about one-third of the value attained during the rainy season. A major difference between the savannah and the agroforestry systems was the lower biomass of the maize (usually about half that reported for savannah grassland) and strong negative competition effect of trees in the relatively young agroforestry systems on crops, reducing yields by 30–70% compared to a no-tree control.

3.3. Leaf area fraction as an indicator of water use per unit shade

Ong and Leakey (this volume) conclude that the positive influence of trees on grass productivity in African savannah requires considerable time to

become apparent because of its association with slow growing trees. In the absence of convincing indirect benefits for crop production, trees must be proven to provide direct benefits to farmers if adopted in widespread fashion. However, agroforestry literature on tree-crop interactions is largely based on studies with *young* trees, with the exception of some studies of parkland systems, while literature on tree-grass interactions in savannah mainly considers *mature* trees. There is considerable evidence that mature scattered trees in such environments are associated with improved soil nutrient supply in both savannah and parkland systems, but it is uncertain whether trees actually increase the total pool of nutrients in the system or simply re-distribute existing soil nutrients more effectively across the landscape (Belsky and Amundson, 1998). If higher nutrients under trees are due to redistribution, no net gain in production at the landscape scale should result. It might still be worthwhile to the farmer, however, if it would allow the same family food requirements to be met by either farming a smaller area of land or using less labour. Unfortunately, few studies have sampled soil nutrients randomly over sufficiently large areas to test these suggestions. For example, Chivaura-Mususa and Campbell (1998) reported increased soil fertility under mature scattered trees in both the savannah and arable lands in Zimbabwe but their study only compared understorey soil to open soil 15 m away from the tree trunk. In such environments, tree roots are known to spread laterally well beyond their canopies (e.g. up to seven times the canopy dimensions of *Burkea africana* as reported by Rutherford, 1982) so it would remain uncertain as to whether the contrast in soil fertility resulted from redistribution or truly from addition of nutrients.

Van Noordwijk (1996) presented an algebraically-solvable model of tree-soil-crop interactions for situations where shade (light capture) and mulch (nutrient supply) are the dominant interactions and water availability is not limiting. This 'shade and mulch' model pointed to the ratio of light captured per unit nutrient recycled as the main criterion for testing effectiveness of fast growing trees for early succession in agroecosystems such as hedgerow intercropping. Apart from reducing light availability, tree canopies may also reduce temperature and increase humidity at crop level, a vital property in view of the fact that savannah temperatures during the growing season can become elevated well above the optimum for crops. This potentially additional advantage of trees will, of course, be (partly) offset by water use by the tree. In similar fashion to the 'mulch per unit shade ratio' concept, we may use the 'shade per unit water use ratio' as an indicator of suitability of trees for situations where microclimatic effects and water use dominate a tree-soil-crop interaction.

Mobbs et al. (1998) in their agroforestry model did not include a direct effect of tree canopies on the temperature in the crop zone, but their crop model did suggest that a decrease in crop temperature by 1 °C and a parallel increase of air humidity for the understorey vegetation increased crop grain yield by 15% at all three sites tested. Whereas crop production in parkland

systems may benefit from lower temperatures under tree canopies, water use by trees providing this shade may often prevent crops from benefiting. In older trees, however, a considerable part of the total shade can be provided by branches rather than leaves, and thus not be directly linked counter-productively to transpiration.

To further explore this relationship, we extended earlier descriptions of above- and belowground tree architecture based on self-repeating (fractal) branching (Van Noordwijk and Purnomosidhi, 1995), with leaves (or fine roots) conceived as end structures of the system. This functional branch analysis scheme is based on the following entities:

- a parameter for the change (or conservation) of cross-sectional area in each branching point;
- a parameter for the allocation of cross sectional area over the branches (links) produced as offspring at each branching point;
- the average number of offspring and the minimum diameter of branch links;
- two parameters to describe the relation between link diameter and link length; the average distance between leaves and the area per leaf; and
- two parameters indicating leaf turn-over (by describing the link diameter at which leaf density starts to decline by leaf fall and the diameter at which it reaches zero).

All parameters can be measured non-destructively. This functional branch analysis scheme was used to evaluate the fraction of total surface area which is comprised of leaves. Results (Figure 3) show that the leaf area fraction decreases with tree stem diameter (age), especially in the 0–10 cm stem diameter range. As might be expected, leaf area fraction also decreases with wider spacings between leaves, smaller area per leaf and more rapid leaf turnover. For older trees, the leaf area fraction may fall below 50% for some of the parameter combinations tested. Preliminary measurements in Machakos (Kenya) (Table 1) suggest that for *Balanites aegyptiaca*, the leaf area fraction can be less than 60%, compared with more than 90% for *Melia volkensii* and *Gliricidia sepium*. Fast growing trees introduced for agroforestry trials differ in leaf area fraction for similar tree diameters to those of trees which farmers have traditionally spared when establishing field crops. Maintaining well-established trees may thus convey advantages which are not easily replicated by planting new trees.

3.4. *A model for predicting agroforestry water use across a rainfall gradient*

The WaNuLCAS (Water, Nutrient and Light Capture in Agroforestry Systems) model, developed by Van Noordwijk et al. (1998) and Van Noordwijk and Lusiana (1998, 1999) incorporates predicted interactions and effects of a four-layer soil profile, with four spatial zones, a water and nitrogen balance, and uptake by a crop and a tree. The model can be applied to simultaneous as well

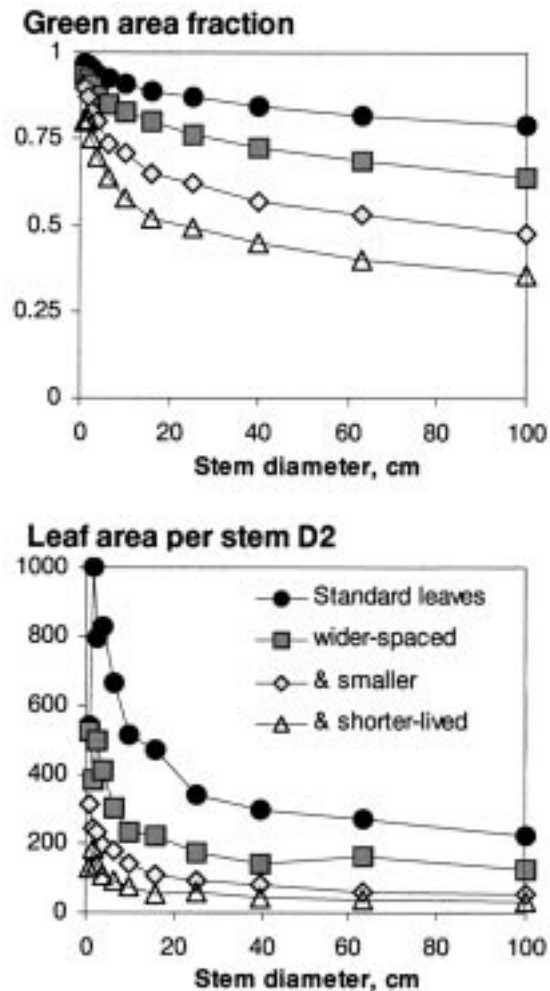


Figure 3. Calculations with a fractal branching model of the relationship between tree diameter and (a) the part of the total leaf + branch projection area formed by leaves; and (b) the relationship between leaf area and stem diameter². The various simulation runs were based on a stepwise change from a 'standard' parameter set, by doubling the distance between leaves, halving the area per leaf and halving the life span of leaves.

as sequential agroforestry systems and may accordingly help towards evaluating the continuum of options ranging from 'improved fallow' to relay planting of tree fallows to rotational and simultaneous forms of hedgerow intercropping through to isolated trees in parklands. It also explicitly incorporates management options such as tree spacing, pruning regime and choice of species or provenance and reflects various functional tree characteristics such as root distribution, canopy shape, litter quality, maximum growth rate and speed of recovery after pruning.

Table 1. Tree stem diameter (D_o), minimum branch diameter (D_{min}) and leaf area per unit branch length for four isolated trees at ICRAF's research station in Machakos (Kenya), and calculated values for the green area fraction, using the functional branch analysis scheme.

Species	Age (yrs)	D_o (cm)	D_{min} (cm)	Leaf size (cm^2)	Inter-leaf distance (cm)	Leaf area/ branch length ($cm^2 cm^{-1}$)	Green area fraction
<i>Balanites aegyptiaca</i>	16	15.6	0.17	2	1.9	1.04	0.46
<i>Acacia tortilis</i>	15	13.2	0.13	1	0.72	1.38	0.60
<i>Melia volkensii</i>	4	19.9	0.80	305	8.2	37.3	0.92
<i>Gliricidia sepium</i>	11	15.4	0.32	160	1.6	102	0.98

Source: Van Noordwijk (in prep.).

The first step, in the case of parklands, would be to analyse the spatial pattern of trees in the landscape and derive from this a set of 'equivalent circle' representations, which represent the cumulative distribution of distances of random points to the nearest tree. Whether tree distribution is clustered, random or regular, it is always possible to find a combination of circles which effectively embraces this specification. The system as a whole can then be represented by a weighted average of the results from different radii of a model of circular geometry. As a first order approach, we can then explore the interactions of such circular zones, using an amount of detail in the interactions within each cell of the model which would not be possible for discretization of the field as a whole. Limitations to this approach are that we essentially have to assume that every part of the soil is influenced by the nearest neighbour tree and not by others, and that tree size and age are independent of spatial position within the field. If the latter assumption does not hold, lateral interactions between neighbouring trees can not be treated on the basis of a symmetry rule. While accepting these shortcomings, we can still use the model to explore effectively the density of trees compatible with zones of different rainfall pattern (Figure 4). An advantage in total biomass production for agroforestry is associated with a larger water uptake and less drainage or groundwater recharge, especially at low-to-intermediate rainfall.

The WaNuLCAS model can also explore the consequences of differences in root distribution (both horizontally and vertically), rainfall pattern and soil physical parameters on the water balance of a system at patch scale. The effects of water redistribution on the soil surface by run-off/run-on can be simulated with the model, and by appropriate combinations of model runs, run-off/run-on relations between patches can be investigated. We have included options to consider hydraulic lift and the reverse flow from wet topsoils to dry subsoils, when trees are 'harvesting water' after the first rains (Ong and Leakey, Pate and Dawson, Pate and Bell, this volume). The total quantity of water involved in this reverse flow appears to be relatively small for reasonable parameter values (results not shown here) suggesting that the main function as far as the tree component is concerned is that this process

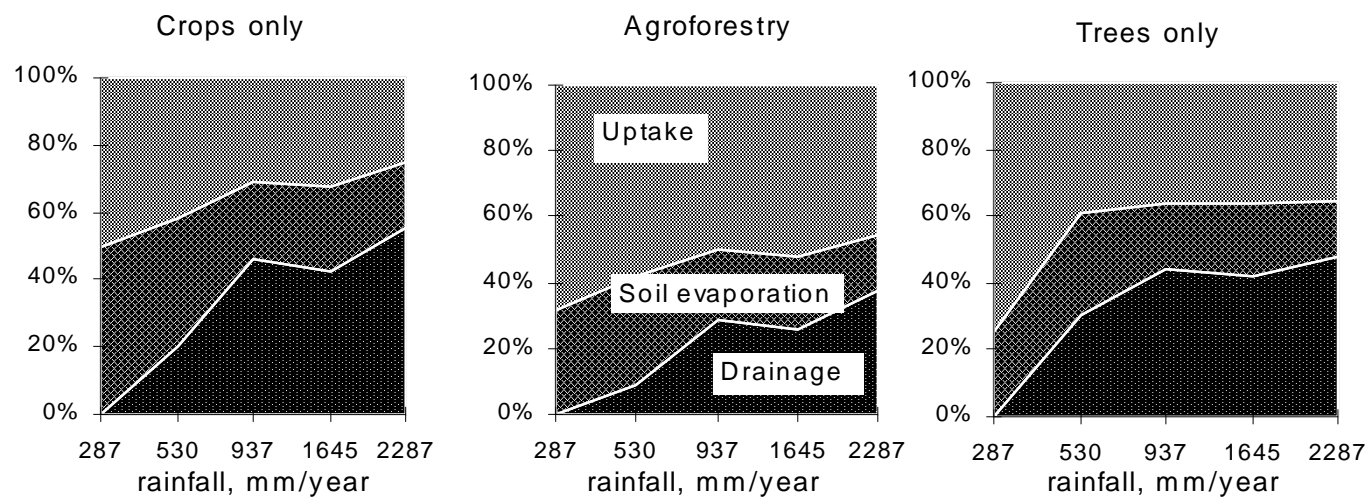


Figure 4. Water balance for WaNuLCAS calculations for a parkland system, or a separate crop or tree system, across a rainfall gradient. Source: Van Noordwijk and Lusiana (1998).

allows its roots to expand into dry soil layers while on their way to the groundwater table.

The main strength of the model appears to be its ability to explore longer time scales than available in any experimental data set, and thereby predict responses to stochastic variations in rainfall. Experimental evidence in Machakos indicates that in years with less-than-average rainfall, trees survive by gradually depleting belowground stores of water, whereas in years with more-than-average rainfall these water stocks would be replenished. Without trees, extra rainfall would, of course, translate to extra flow of rivers. A major challenge ahead of us is to explore the landscape scale consequences of what we now know at tree and plot level. Landscape mosaics at intermediate scale may radically differ from the weighted sum of their components, because lateral resource flows (above or below the soil surface) and lateral resource capture (e.g. scavenging tree roots) cause neighbourhood effects (Van Noordwijk and Ong, 1996). Subsurface water flows allow specific strips in a catena to use additional resources. Such effects probably underly the success of line plantings of *Gliricidia* in Mali (ICRAF Annual Report, 1994), and this success must not be mistaken as indication that the technologies concerned can be increased successfully to operations at larger scale. Trees can buffer some of the inter-annual fluctuations in agroecosystems, just as they do in natural savannah systems, but the value of this to the farmer depends on the products which are obtained from the tree.

4. Reducing production risk through diversity

4.1. Diversity and stability

Knoop and Walker (1985) attributed the remarkable functional stability and resilience (ability to recover from change) of savannahs to unique properties of species and their interaction at system level. Special attributes include seed dormancy through seed bank recovery, vegetative reproduction, the presence of underground reserves and related coppicing ability, phenology of different species in relation to rainfall distribution and adaptations to drought and grazing. Parallel attributes of systems include the slow release of inorganic nitrogen, conservation of nutrients by vegetation, reduction of anaerobic conditions by trees and the trophic complementarity between species in system concerned. However, recent reviews suggest that some savannah systems have become degraded below a biotic threshold which prevents them from recovering to their initial 'climax' once the disturbance is eliminated. This then leads towards a different 'stable' vegetation state after disturbance (Belsky and Amundson, 1998). They cited several processes such as loss of topsoil, losses of dominant or keystone species (including mycorrhizal partners), invasion by weedy species, loss of soil microorganisms and severe soil compaction as possible causes for such thresholds.

A principal reason why the debate on stability and complexity of natural and agroecosystems is so confused is that insufficient recognition has been given to the hierarchy of systems considered. Stability at higher system levels does not imply stability of its constituent populations, at lower levels or *vice versa*. The implicit assumption is often made that stability at lower hierarchical levels is necessary before stability will accrue at higher level. In fact, the reverse may be true when the higher level is a 'generalist' for whom different resources are interchangeable. A number of examples may illustrate this type of stabilisation for generalists at different system levels:

- a) A plant which roots in superficial as well as deep layers of soil may maintain near constant rates of transpiration despite wild fluctuations in the soil water content of the topsoil and usually more damped fluctuations in the subsoil.
- b) The genetic diversity in a plant or animal population can be maintained despite substantial selective pressures and resulting shifts in gene frequencies, so long as the selection pressures involved fluctuate and favour different genes under different circumstances.
- c) A mixed plant community may maintain resource flows at a stable level, while its component species may be fluctuating widely, for example in an internally generated cyclical succession or in response to external disturbances.
- d) From the perspective of a grazer interacting with a mixed plant community, a stable feed supply can be achieved with highly variable components, e.g. in a grass – legume (e.g. clover) mixture maintained in a competitive balance in terms of soil N level; the 'meadow' as a whole may be stable while patches within it are fluctuating in a cyclical manner, yet the grazing cow consumes all.
- e) At field level, farmers can achieve stable yields by intercropping different cultivars or crops, especially when the relative performance of the crops depends on external factors which can not be predicted with any degree of certainty at the time of sowing. This unpredictability may be due to subtle unrecognised spatial heterogeneity within the system, as shown for barley-oat mixtures on soils with patches of low pH (De Wit, 1960), or to events happening after a crop is established, as in the case of maize-sorghum mixtures of the floodplain of the Nile in S. Sudan (Struif Bontkes, 1986). In these examples the various food crops may be of comparable value to the farmer for maintaining subsistence diets and/or for sale on the market.
- f) At farm level, a farmer can try to balance different field-level enterprises which are attractive but risky, by maintaining a portfolio of complementary activities, e.g. a combination of market- and subsistence-oriented activities.
- g) A successful 'human livelihood' farm-urban system can achieve stable food supplies simply by linking very diverse and potentially risky specialized

farming enterprises, leading to the paradox that the food choice in the ‘developed’ part of the world is more diverse than at any time in human history while all of this is produced on farms which are less diverse than at any time before. The more specialized farms are exposed to substantial risks, but pay for protection by insurance schemes and social networks.

The above examples spanning a wide range of systems have a common theme: a ‘generalist system’ can switch between resources and achieve stability on the basis of a diverse set of relatively unstable components. In many earlier versions of the ‘diversity-stability’ hypothesis no distinction was made between the various ways of evaluating a system – from its component parts or from an overall ‘generalist’ perspective, by integrating its various components.

A common feature of the above examples is that specialisation on less resources may increase the efficiency of using these resources and acquiring them in competition with other factors, and thus increase average yield or success. Nevertheless, it increases risks which can then be partly avoided by focusing (specialising) on stable resources, or subverted by using ‘several baskets to carry eggs to the market’. In human societies, the scale at which risks can be managed has been generally shown with increased sophistication in economic development from subsistence to market integration. Market forces drive farmers in the direction of more specialised and risky farms, but also provide opportunity to externalise the risk from a strict farm-based system to broader social-financial systems (Vandermeer et al., 1998). Economic portfolio theory is well developed in financial markets to reduce risks while benefiting from the specialist advantage in taking risks.

4.2. *How much diversity is needed?*

Risk reduction in diverse systems is based on effects of mixtures on the expected yield (mean) and its variance. If the sum of all components reflects the ‘generalist’ perspective of the success of the system, the variance of this sum follows a simple rule for normally distributed variates: it equals the sum of variances of all components (weighted for their share in the total system), plus a term reflecting the covariance, or the degree to which success of components tends to coincide with successes or failures of other components. This rule for the variance of multi-component systems is essentially more favourable than the rules for deriving averages. Average total yield for a mixture can be higher, equal to, or less than the proportionate sum yields of the components (Figure 5a). However, the variance can only be equal to or less than this proportionate variance. There are thus many opportunities for variance reduction contributing to risk reduction (Figure 5c). For example, for a two-component system with a correlation coefficient of -1 , one can construct a system which has zero variance (Schweigman, 1985). Under such conditions risk reduction is hardly a valid argument for maintaining diversity, as

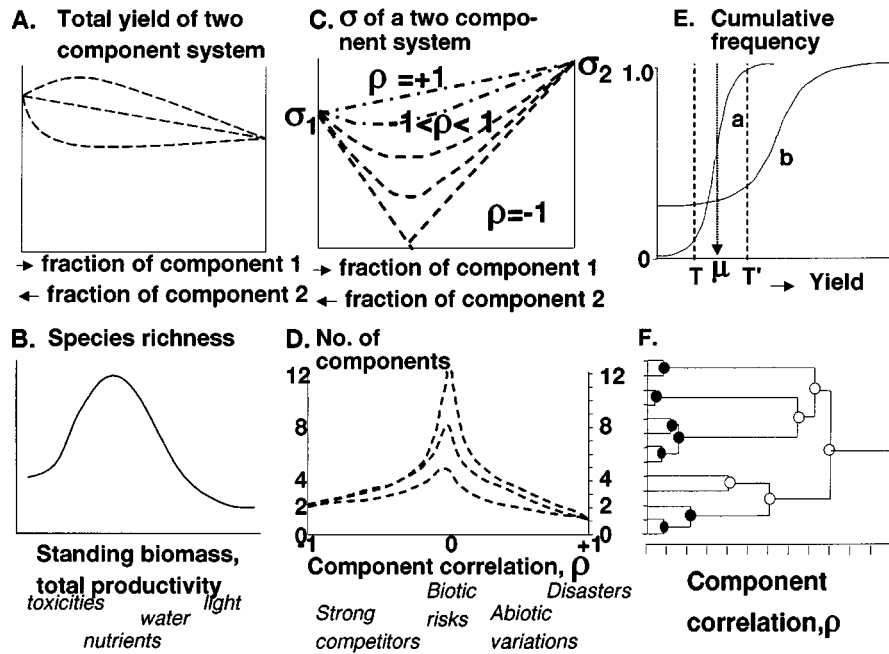


Figure 5. Replacement series (Yin-Yang figures) for average and variance of total production (a and c) and the possible species richness in relation to total production and dominant growth limiting factors (b) and to the covariance between components and the nature of the external source of variation (d); risk can be defined as the probability of not meeting a target T and the choice between component a and b can depend on the target as well as on the probability of yields (e); by classifying production options by their similarity, a rigorous procedure for selecting components of a risk-minimising portfolio of activities can be constructed (e).

a well-designed two-component system can reduce the variance to zero. However, if the covariance between the various components is zero, and all components fluctuate independently of each other, the variance of the sum will decrease with $1/N$, where N is the number of components (compare with Trenbath, this volume). Once N has reached a value of four or eight, variance will have been reduced to 25 or 12.5% of the variance for a single component system, respectively, and further increases in number of components beyond such a value might not be worthwhile.

The diversity of plants in temperate grasslands has been linked to the total standing biomass or productivity, as envisaged by the 'Grime corridor' depicted in Figure 5b. Tentatively, this can be understood as indicating that there are more opportunities for niche differentiation and complementarity in the lower middle part of the range. Here nutrient shortage, rather than extreme conditions (lowest part), water shortage (upper middle), or light (higher part of the range), are the main limits to plant production (Figure 5b). Speculating in the same mode, we can interpret the X-axis of the graph linking optimum

system diversity to correlation between components (Figure 5d) as referring to a range of sources of external variation, *viz*:

- disasters, affecting all components to a similar degree leading to a high correlation of components and giving little opportunities for risk reduction by diversity;
- weather related abiotic risks, allowing differences in response and adaptations and leading to partial, but generally positive correlations in performance;
- biotic risks based on outbreaks of specific pests and diseases, leading to virtual independence in response and maximum scope for reducing risk by increasing diversity;
- risks specifically affecting strong competitors in the system, leading to negative correlations in performance and compensatory production of the component least affected by the external agent. The situation carrying a correlation of -1 may arise as an extreme case of this type of relation.

In this view, risk reduction by diversity is least effective against ‘disasters’ and most effective (leading to the lowest system variance) when a small number of strong competitors are present, which fluctuate primarily in relation to specific biotic variables.

4.3. *The combination of options most reductive of risk*

The theory discussed so far gives a first indication of what advantages can be expected from maintaining component diversity (‘how many baskets’) – but it does not tell which ones to select (nor ‘how to allocate the eggs’). Van Noordwijk et al. (1994) used a model to apply these concepts for water-limited sorghum production in the Sudan savannah zone. For a large number of production options (combinations of soil position in the catena, crop duration and N fertilisation) yield predictions were made on the basis of 30-year rainfall records. Through a cluster analysis technique, a dendrogram was constructed (Figure 5f) indicating functional groupings of production options at each level of similarity (covariance). By testing whether the reduction in variance possible at each level in this dendrogram is worthwhile and choosing the representative of each group showing highest average production, an objective routine can be derived for choosing both the number and type of options to be used. However, this is possible only if the source of external variation is known and the response of each possible component to this variation is predictable.

This procedure is in marked contrast, however, with most current practices aimed at yield stabilisation by testing crop genotypes across a large number of sites and years, and selecting the one with the best average and lowest variance as the most stable producer. This latter procedure presupposes that the best system will have a single component – as soon as one accepts that the optimum number may be one rather than two, the procedure misses

out on opportunities provided by two components of high variance but performing well in contrasting years. For example, late and early maturing varieties are likely to fail in a stability test at component level, but may form a very stable pair, performing reasonably well on average over a number of seasons regardless of variations in rainfall. It may be better in such a case to keep the differently performing cultivars in separate fields, rather than as intercrops, as they might interact negatively at plot level, even though their use separately in an ecosystem might reduce overall risks at farm level.

Spatial heterogeneity of soils is normally seen as a negative attribute, especially if one aims at a homogenous crop producing close to the theoretical maximum without nutrient and water limitations. Heterogeneity of the soil, however, may contribute to yield stability if the different patches engender different response of crops to variation in rainfall. Brouwer et al. (1993) has made an interesting analysis of effects of soil variability from this perspective in Niger.

4.4. Risk transmission in specialist – generalist chains

The examples given above, where a generalist can be relatively stable while depending on fluctuating components, span a wide range of systems. We can now turn to consider what happens when we arrange these systems in a hierarchy.

If we simplify the choice to a G (generalist) and S (specialist) strategy, and assign a higher efficiency (production under suitable conditions) to S and a smaller variance to G, we can consider four basic sequences: S-S, G-G, S-G and G-S, with the G component always based on at least two resources. The S-S sequence may be too risky for the upper level, while the G-G sequence may be sub-optimal in efficiency, so the S-G and especially G-S sequence may achieve the best outcome from the perspective of the upper level. If we extend the analysis to chains of three or more levels, we find that S-G-S or G-S-G sequences provide attractive opportunities for combining efficiency and stability.

If we apply this concept to farmers in a subsistence economy, we find analogy with the G-S link in specialised animal husbandry, where grazers have choice of a wide range of food resources, and a S-G link in crop fields where farmers grow a large number of crops in a mixture, embodying a large degree of exchangeability between food sources in the human diet.

Finally, if the G-S-G sequence proves superior, it is interesting to note what happens if a new level with sufficient influence on the underlying levels is added on top of the hierarchy. One possible result is that it may induce all of the components to reorganise (flip over) from a G to an S strategy (or *vice versa*), thus bringing the whole system in a confused state of transition for a while as it undergoes structural readjustment. Economic development and market integration essentially add hierarchical levels of this type to a given chain, with farmers no longer comprising the main driving force of the system,

but becoming dependent on policies and market forces generated in towns. The influence of the town market place is to have a generalist tendency and implicitly or explicitly induce farms to specialise (Vandermeer et al., 1998). This specialisation reduces farm-level diversity and, therefore, increases risk to farmers, unless an institutional framework develops to provide a buffer and safety-net to protect specialist farmers. Here we come right back at the existing policy environment, which does not sufficiently favour smallholder rural development and does not provide sufficient financial incentives for farmers to intensify their land use (Sanchez and Leakey, 1997).

4.5. *Diversity and priority setting*

The value of agro-diversity for risk reduction is most obvious where the constraints involved act independently across a number of possible systems. Clearly, the value of diversity as insurance against risk increases with the lifespan of the components, and with the time needed to replace them were they to be wiped out by pests or diseases. The arguments for tree diversity on farms are clearly stronger than those for diversity in annual crops since the latter can be replaced relatively easily and quickly should adverse conditions prevail. However, the cost of maintaining diversity remains, wherever components are being maintained which do not live up to their expected utility value.

If all components had equal value per unit resource use, competition would not be harmful and might contribute to stability of overall yields. The whole issue of weeds and competition thus starts with differences in value per unit resource use, between desirable and less desirable components of the system. Efforts to increase the value of 'desirables' inevitably increases the contrast in the above values, and therefore increases the real and perceived problems involved. Efforts at domesticating trees can help to maintain agroecosystem diversity, but may equally induce a specialisation on a few tree species. If domestication were to aim at the agroforest rather than at the tree, priority might have to be given to adding value to trees which grow well but have little value, instead of concentrating on tree species which are already rated as most valuable components. This perspective may stimulate us to re-think priority-setting exercises within a given system. Conventionally, for example, priority rating starts by listing options and ranking them in terms of utility value. Entities at the top of this list of values would then be normally considered to be priority choices for further research or action. However, when we wish to stimulate conditions favouring diversity, we may well have to focus on the middle part of our value listing to find priorities for action. If the overall aim is to be able to grow plants that have value, we may as well adopt a policy of adding value to plants which grow well, rather than ascertaining how and where to grow plants which attain a high value. There is no consensus as to how returns from effort in domestication relate to current value. Possibly an S-shaped curve is involved, with a difficult start for low-value products,

followed by a phase of near-constant returns to investment before diminishing returns set in. Initial gains in performance by selection are often supposed to be larger than can be obtained in subsequent steps in selection. Product values and markets are conservative, however, and it is much easier to benefit incrementally from existing success of products than to create new types of use and markets for those products. The scope for focusing efforts on middle-value options remains to be tested.

5. Concluding remarks

We have focused in this chapter on two mimicry hypotheses, one relating to resource use and the other to diversity. Clear indications exist for the first hypothesis to be relevant in that there are clear advantages in productivity and less downstream effects if man-made land use systems do not deviate far from the resource use patterns exhibited by natural ecosystems within the same climatic zone. However, with complete technical control of resources, additional input supply and removal of excess outputs a measure of flexibility becomes possible. At a field or plot scale there may be considerable scope for utilising more resources, but only for a limited period of time, and so long as the environmental buffer stocks last. Alternatively, improvements may accrue from capture of resources from neighbouring plots and fields, and this may indeed be part of the reason why border plantings of trees are so common in the savannah zone (Van Noordwijk and Ong, 1996).

The value of diversity (second hypothesis) strongly depends on our perspective and in particular on the ability of farmers to derive value from a large number of components. The currently prevailing negative perception of competition in mixed systems remains valid if one component dominates the total value the farmer expects to derive from a system.

The question remains as to whether these mimicry hypotheses are of value as such. Agroecosystems can either gradually evolve locally by increasing the intensity of managing natural systems (as happened with the parklands), or be designed and synthesised *de novo*. In the first scenario the boundaries of what is possible are likely to be heavily constrained but can be explored on a trial and error basis. However, old, slow growing trees cannot easily be reconstituted in a system once they have been removed, so prospective analysis of likely constraints may help in avoiding calamities. In the case of *de novo* synthesis, the mimicry hypotheses can not only provide inspiration, but also indicate the overall constraints for a particular mimic solution to remain sustainable. However, prescriptions for agroecosystems derived from comparisons with natural systems and their diversity should not be accepted as anything more than useful hypotheses for action. Higher level stability at landscape or regional scale may well be achieved by allowing a degree of specialisation, limiting farm-level diversity. The best precondition for farmers to maintain diversity in their agroecosystem is probably the availability of a

broad basket of choices, with deliberate avoidance of prescribing clear winners or 'best bets'.

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7. Note added in proof

The discussion of variance in Figure 5 and Section 4.2 assumes the absence of interaction effects on the means.

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