
Agroforestry Abstracts

Ecological interactions in agroforestry systems

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Abstract

Agroforestry encompasses a set of land use practices which aim to realize the benefits from growing woody and herbaceous species together, commonly by the addition of trees to land already being used for pasture or for growing annual crops. It thus concerns the ways in which the presence of a plant can change the environment of its neighbours, generating a favourable balance between negative and positive plant interactions, and thereby increasing total yield, reducing yield variance and conserving resources. These ecological issues include a time dimension, and are akin to socioeconomic concepts regarding productivity, stability and sustainability in marginal land use systems. In this review, theories regarding interspecific and intraspecific interactions, and the mechanisms concerned, have been used as a basis for interpreting the results of experimental studies in agroforestry, in order to gain an understanding of the processes that determine productivity and its maintenance in these systems. The review is presented in three main sections. The first considers agroforestry in the context of ecological principles concerning interactions between species and the ways in which the presence of a plant can change the environment of its neighbours. The second section uses the conceptual framework developed to appraise concisely published research findings, under the headings competition, predation, mutualism and commensalism. The third section elaborates three key issues connected with the objectives of agroforestry: overyielding; the reduction of yield variance; and maintenance of resources.

I. Introduction

1. Preface

The British Government's Overseas Development Administration (ODA) has been funding studies of agroforestry systems, as part of a strategy for research on renewable natural resources (ODA 1990), through its strategic research programme in forestry and agroforestry. The selection of projects for funding has tended to be reactive in approach, and funded research has inclined towards site specific studies. In keeping with ODA policy, there is a wish to pursue research which has regional or global significance, and which permits integration with other strategy areas, particularly plant sciences, and agronomy and cropping systems.

The need to design a viable, long-term plan for support of agroforestry research, which encompasses pre-determined initiatives of wider relevance and allows financial assistance to evolve in a systematic way, has thus been recognized. Such a structured approach can be achieved by focusing on the fundamental processes operating within agroforestry systems and developing models of the processes involved, with the eventual aim of using models as tools in agroforestry management and practice (Jarvis & Sinclair 1990).

As an initial step towards the formulation of a coordinated research programme on the development of models for agroforestry systems, it has been necessary to assess the current state of knowledge regarding ecological interactions in such systems. The findings of this aspect of the review are reported here, with the objective of identifying areas of weakness in our understanding of the interactions and processes involved in agroforestry systems, and hence, where future research funding should be directed. Modelling aspects will be covered in a second review (Muetzelfeldt, R.I.; Sinclair, F.L.).

2. Background

The term 'agroforestry' encompasses a diverse set of integrated land use practices employed for a variety of purposes. Definitions which describe the components or concepts involved (Lundgren 1987; Young 1989a; Nair 1991) are useful for identification (Figure 1), but do not impart information regarding the mechanisms common to such practices which are essential to their functioning.

Agroforestry also takes an interdisciplinary approach to land use, requiring the combination of social, ecological and economic factors (Sinclair 1992). As such, and perhaps as befits a relatively new research area and new way of thinking, a plethora of reviews and bibliographies have been published concerning the subject, and particularly the benefits to be gained by adoption of such practices. A great deal of this literature concerns speculation rather than evidence, and has not led to a cohesive theoretical framework for considering the fundamental processes involved.

It is easy for theorizing to run ahead of the evidence. The aim of this paper is not to repeat the descriptive review process from a new angle, but rather to use developed theories concerning ecological interactions and processes as a basis for interpreting the results of experimental studies in agroforestry research, and thus to gain an insight into the common processes that determine productivity and its maintenance in these systems. This approach should also help to highlight those areas where information is still required.

Although agroforestry systems are modified or disturbed environments and cannot be described as natural, they do represent a move away from the markedly artificial systems of monocultural production towards mimicking aspects of natural ecosystems, with an emphasis on species diversity and resource conservation. Further, there is currently a shift in approach, away from zoned agroforestry arrangements

AGROFORESTRY

Agroforestry is a collective name for land-use systems in which woody perennials (trees, shrubs, etc.) are grown in association with herbaceous plants (crops, pastures) and/or livestock in a spatial arrangement, a rotation, or both, and in which there are both ecological and economic interactions between the tree and non-tree components of the system.

Figure 1. A description of agroforestry.
Source: Young 1989a.

using exotic woody perennials, towards more intimately mixed combinations involving dispersed indigenous trees (Ong *et al.* 1991a; Sinclair 1992). The use of theory from population and community ecology is thus not inappropriate, although it must be applied cautiously in relation to agroecosystems.

The research literature in agroforestry, and progress made towards a full understanding of this system of land use, is reviewed below in three distinct sections. The first considers agroforestry in the context of ecological principles concerning interactions between species and the ways in which the presence of a plant can change the environment of its neighbours. The second section uses the conceptual framework developed to appraise concisely published research findings, whilst the third elaborates three key issues connected with the objectives of agroforestry.

II. Section 1: Interactions between species

Agroforestry encompasses a set of land use practices which aim to realize the benefits from growing woody and herbaceous species together, commonly by the addition of trees to land already being used for pasture or for growing annual crops. In this section those benefits or objectives, as perceived by the farmer adopting agroforestry, are considered from a socioeconomic and ecological perspective, and the key issues involved are raised. However, first an examination is made of what agroforestry entails in terms of the interactions between species which are components of the system.

Interactions between species are mediated by the environment through the 'response and effect' principle (Goldberg & Werner 1983), which states that the plant and its environment modify one another (Figure 2) so that the environment causes a response in plant function and growth, and the plant then has an effect upon the environment by changing one or more of its factors (Clements 1928; Goldberg & Werner 1983). Thus plant morphology and life history are governed by the environment, but at the same time the plant can change its environment. The nature of the interactions within and between species therefore concern the ways in which a plant can influence its neighbours by changing their environment, either directly, by addition or subtraction (e.g. of nutrients), or indirectly (e.g. by encouraging insectivores) (Harper 1977).

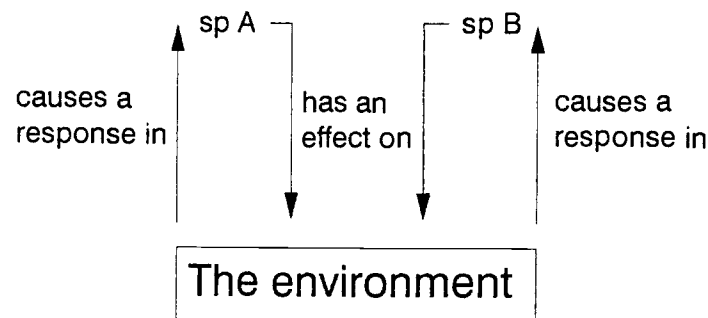


Figure 2. The response and effect principle.
Source: Goldberg & Werner 1983; redrawn from Vandermeer 1989.

1. Ecological interactions in agroforestry

When trees are added to cultivated land there are a number of possible outcomes of the interactions between tree (species A) and crop (species B). Species A may affect the environment in a negative way

with respect to species B, or in a positive way, and hence an individual of species A may cause an increase (+), decrease (-), or have no effect (0) on the fitness of an individual of species B (Williamson 1972). The five resultant interactions, (-,-), (-,0), (+,+), (+,0), (+,-), have been defined in various ways in the ecological literature (e.g. Schoener 1988), with considerable semantic argument particularly between British and American authors. Rather than reviewing the position, the more common definitions will be used.

Competition is defined as an interaction between two individual plants that reduces fitness of one or both of them. It is taken to cover both mutually deleterious interactions (-,-) and asymmetric interactions (-,0), because a great many interactions between plants are asymmetric, and the fitness implications are often not known in advance (Crawley 1986). This definition of competition has the advantage of making no assumptions about the mechanisms involved but describes competition by its net result, i.e. a negative effect on one or both species, and thus has flexible criteria which can be measured.

Concerning mechanism, competition can be divided into exploitation and interference, the former occurring when plants compete by reducing the availability of shared, limiting resources such as light, water, and soil nutrients. Interference occurs when fitness is reduced by 'behavioural' mechanisms which do not directly involve limiting, shared resources (Schoener 1983; Crawley 1986), i.e. the production of toxic substances. Interference is usually strongly asymmetric, whilst exploitation may or may not be.

It should be noted that the term 'interference' can have a more general sense (Harper 1977), where 'the presence of a plant changes the environment of its neighbours ... such changes ... brought about by the proximity of individuals, may be called 'interference', a blanket term which does not define in any way the manner in which the alterations in environment are produced'.

Interactions between two individual plants that increase the fitness of one or both of them, i.e. positive interactions, are separated on the basis of reciprocation. Mutualism is defined as a symmetric interaction, in which there is reciprocal enhancement of fitness (+,+), whilst commensalism describes asymmetric interactions (+,0) in which only one individual benefits from the association (May 1976; Pierce 1989). Examples of mutualism in agroforestry include mycorrhizas and nitrogen fixing microbes, and examples of commensalism include microclimatic and soil amelioration by trees.

Returning to the tree-crop situation, if species A affects the environment in a negative way with respect to species B, competition between plant species occurs, whereas if species A affects the environment in a positive way with respect to species B, and species A itself is either positively affected or not affected, mutualism or commensalism occurs. 'Facilitation' has been used as a single term to describe interactions between plants with a positive result (Vandermeer 1989).

Asymmetric competition (0,-) and asymmetric facilitation (+,0) may occur concurrently, and will be observed as an interaction between plants with a (+,-) net effect, using the above notation. In this context it should be emphasized that the result of interaction between plants is very dependent on density. For example, if species A and B are grown in monoculture and in mixture but with overall plant density kept constant, then most experiments have shown that in mixture one of the species grows less than in monoculture, and the other is unaffected or grows more. If, however, the density of each species is the same in the mixture as in the monocultures, then quite commonly the growth of both is reduced (Rutter, personal communication). The mechanism by which the plants affect one another is probably the same in both cases, but the result may be either (+,-) or (-,-).

Interactions between plants with a (+,-) result have not been specifically defined, though perhaps the term 'counteraction' could be used to describe a balance between competition and facilitation. On the other hand, (+,-) interactions between two individual animals, or between an animal and a plant, are termed predation, which is defined as an interaction that results in enhanced fitness of the predator at the expense of the other individual, either animal or plant. Plant-herbivore interactions thus also have the result (+,-), though it should be noted that through various mechanisms the effect of grazing animals on many plant communities is to reduce the quantity of some species and increase others.

It is also worth noting that apparent competition (Holt 1977; Lawton 1989) may occur in agroforestry systems. This term refers to a three way interaction on two trophic levels, for example a resource-limited, generalist herbivore, or a pathogen, and two plant species. The two plant species A and B appear to compete because an increase in the biomass of species A leads to an increase in the herbivore or pathogen population, which in turn leads to a decrease in species B biomass. In other words the species A-herbivore and species B-herbivore interactions are both (-,+), leading to an apparent (-,-) interaction between species A and B.

Using these ecological concepts concerning interactions, a classification can be created for the research literature and the immediate aim of agroforestry defined. Published studies can be simply separated in terms of the observed net result or effect of the interactions occurring, i.e. competition (-,-), (-,0), predation (-,+), mutualism (+,+) and commensalism (+,0), and considered as evidence to support the advantage of agroforestry, which aims to create a favourable balance between the different types of ecological interaction occurring, minimizing negative interactions (competition and predation) and maximizing positive interactions (mutualism and commensalism).

2. The objectives of agroforestry

Adoption of agroforestry is, as noted above, commonly by the addition of trees to land already being used for cultivation, and the immediate question is simply 'what is the advantage, if any, of growing crops in an agroforestry practice as compared to other types of land use practice?' The farmers' aims, in adoption, are (i) to increase total yield from the land, (ii) to widen the range of produce and thus spread risks, and (iii) to preserve their livelihood and survival by conserving resources (Nair 1991). Development agencies hold strategic long-term interests in the conservation and environmental gains that may be achieved, and believe that agroforestry will be readily adopted by farmers if they, the farmers, perceive a real benefit (Wood 1989).

The objectives of the farmer (Table 1) can be stated in socioeconomic terms (Conway 1987) as: (i) productivity (the output of valued product per unit of resource input); (ii) stability (constancy of productivity in the face of small disturbing forces arising from the normal fluctuations and cycles in the surrounding environment); and (iii) sustainability (ability of the system to maintain productivity when subject to a major disturbing force, i.e. stress or shock). The concept of vulnerability of the land use system may also be used, where diversity of produce reduces the degree to which the system is vulnerable to stresses, shocks or trends (its 'sensitivity'), and increases its ability to recover ('resilience').

From the ecological perspective, a change in farming custom of this kind concerns the ways in which an individual plant (the tree species) can affect its neighbours (the crop species) by modifying their environment (Harper 1977). The modifications that can result may have a positive consequence for the neighbouring plants, due to amelioration of the environment, or a negative consequence, due to deleterious effects on the environment. Clearly the aim in moving to an agroforestry practice is to maximize the positive consequences, thus enhancing productivity and conserving resources. Interpreting the socioeconomic concepts in ecological terms, the key issues are (i) overyielding, (ii) reduction in yield variance, and (iii) maintenance of resources, all of which may result from increasing species diversity either in space or time.

Table 1. The land users' objectives in adopting agroforestry

Objective	Socioeconomic concept	Ecological concept
Increase total yield	Productivity	Overyielding
Multiple products	Stability (reduced vulnerability)	Reduced yield variance
Preserve livelihood	Sustainability	Maintenance of resources

3. The key issues

Overyielding, or yield advantage, has been examined in relation to intercropping, and occurs where a greater amount of land would be needed, by monocultures, to produce the same quantity of yield that could be produced on one hectare of polyculture (Willey 1979; Vandermeer 1989). Is there good evidence of overyielding in agroforestry systems, and if so, what are the enabling mechanisms in terms of the balance between positive and negative interactions?

Land use practices such as agroforestry, which increase species diversity by polyculture, are equated with spreading or avoiding risks, because they are more stable in the face of short-term environmental or economic fluctuations as a result of the increased potential for compensation by one component when another fails (Rao & Willey 1980). Again, what evidence is there for yield variance being reduced (i.e. increased stability) by the move from monoculture to polyculture due to interspecific interactions with an environmental source of variation?

Reduction in yield variance, or increased stability, is linked to the concept of sustainability. However, whereas 'stability' concerns short-term fluctuations in productivity, 'sustainability' concerns the long-term fluctuations (Conway 1987). If resource losses from agroecosystems through cropping are not balanced by inputs, such systems will deteriorate, and thus sustainability can be equated with maintenance, or protection, of the resource base. How can equilibrium, where the rate of resource consumption equals the rate of resource supply (Tilman 1988), be achieved in a plant community whose dynamics never reach a state of equilibrium?

Consideration of the temporal aspects is important in these three issues. Almost all the controlled competition experimentation has used annuals (especially crops and weeds) or herbaceous perennials (especially grassland species), and experiments have lasted one or very few years. Agroforestry, however,

involves long-lived plants; if there is overyielding then there is an implication of greater, perhaps more efficient, exploitation of the environment, which is only beneficial if it can be sustained. Overyielding and protection of the resource base are thus inter-related, because overyielding is only desirable if it can be sustained, and that requires continued resource supply over time.

4. Spatial factors

Interactions between neighbouring plants such as exploitation and interference competition, or neighbours influencing each other by suppressing the activities of predators, are dependent on the proximity of neighbours, i.e. are density dependent, and the spatial relations of individuals are, consequently, critical within plant populations. Immediate neighbours which may interfere with the growth of a plant in the field can be divided into three categories, intracolonial, intergenotypic and interspecific (Harper 1977). Intracolonial neighbours are parts of the same genet, for example the shoots on a tree that can differ phenotypically in age or size, and make different demands on environmental resources. Intergenotypic neighbours are genets derived from different seeds and therefore usually of different genotypes, whilst interspecific neighbours are genets of different taxa.

Most experimental studies of the reactions of plants to density have been made on stands of single species. Experimental studies of the growth of species in mixtures entail varying density of the mixture and proportional composition. Additive experiments, where the density of species A is maintained constant and the density of species B is varied (Clatworthy 1960), are difficult to analyse because density and proportions are confounded. Substitutive experiments, where the two species A and B are sown in varying proportions while maintaining overall density constant, i.e. a 'replacement series' (Wit 1960), overcome these problems, and such designs are suitable for studying plant-plant interactions. The results of replacement series experiments can take one of four forms, based on the contribution of each species to the total yield of the mixture, in the context of the proportional composition.

A measure of the 'aggressiveness' of one species towards the other can be determined from substitutive experiments, and is termed the 'relative crowding coefficient' (Wit 1960). The concept of 'relative yield' is, however, preferred when the combined yields of species A and B in mixture cannot be predicted from the pure stand yields. The 'relative yield' of species A is the yield in a mixture of species A and B compared with its yield in a pure stand of A. The sum of the relative yields for A and B is called the 'relative yield total' (RYT), and is directly comparable to the 'land equivalent ratio' in intercropping and agroforestry where values >1.0 indicate overyielding by the system. Values of $RYT=1.0$ indicate that both species have similar requirements for limiting resources in the environment, whilst values <1.0 indicate mutual antagonism by depletion of the environment for the other species, and values >1.0 imply either that the species have different resource requirements, or avoid competition with each other (Figure 3), or have a symbiotic relationship.

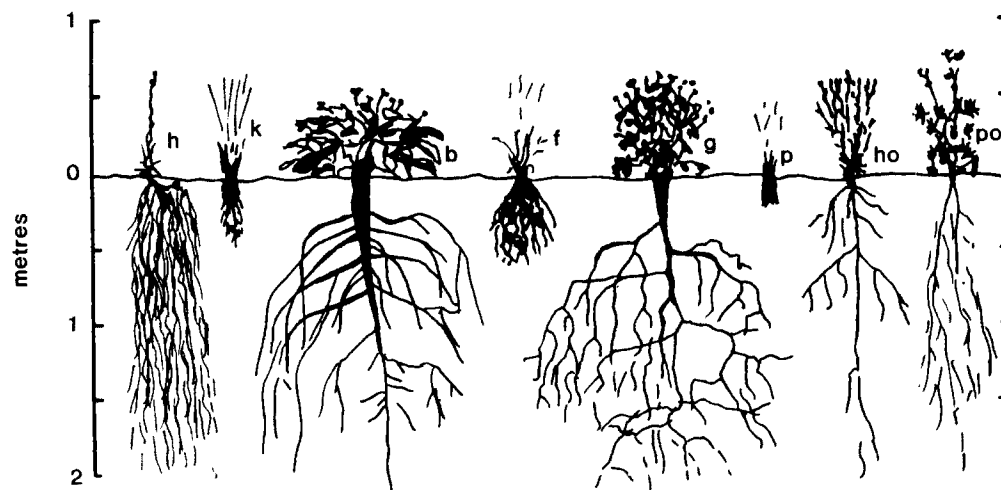


Figure 3. Avoidance of competition by below ground niche differentiation.

Schematic bisect showing the root and stem relations of important prairie plants, drawn from photographs and data obtained by the excavation and examination of 325 root systems of 8 species: (h) *Hieracium scouleri*; (k) *Koeleria cristata*; (b) *Balsamorhiza sagittata*; (f) *Festuca ovina ingrata*; (g) *Geranium viscosissimum*; (p) *Poa sandbergii*; (ho) *Hoorebekia racemosa*; (po) *Potentilla blaschkeana*.

Source: Weaver 1991; redrawn from Harper 1977.

Thus, for example, a cereal crop in monoculture may yield 4 tons/ha, dropping to 3 tons/ha when grown amongst trees, but the trees may additionally yield 2.5 tons/ha fuelwood and a similar amount of fodder, resulting in a total of 8 tons/ha, double the original yield of the land (Dixon 1992). Competition between the two species for limiting resources in this example leads to a reduction in the growth of both

species, and the aim of good agroforestry practice is to weaken competition by planting combinations of species which allow niche differentiation to occur, i.e. root systems exploiting different soil depths and hence different parts of the resource base. Such a practice, which avoids competition, results in greater productivity per unit of land from mixtures of species than from pure stands.

The concept of selecting 'good combinations' of species is an important component in the use of indigenous knowledge, which aims to capitalize on the experience of the farmer (Walker *et al.* 1991). The term 'ecological combining ability' has been used (Harper 1967) to describe the characteristics of species that have a greater degree of niche separation as a result of breeding or natural evolution. The ability of such species combinations to coexist and utilize different parts of the same niche may be amenable to the type of approach used by Grime (1979) and Grime *et al.* (1988), where species are classified with respect to their 'primary ecological strategy' in a three-strategy model: competition (competitor), stress (stress-tolerator), and disturbance (ruderal). Perhaps the species used by local farmers are clearly separated in a model of this kind (Figure 4), or a similar phase plane diagram using, say, water use efficiency, nutrient use efficiency and/or other parameters as axes.

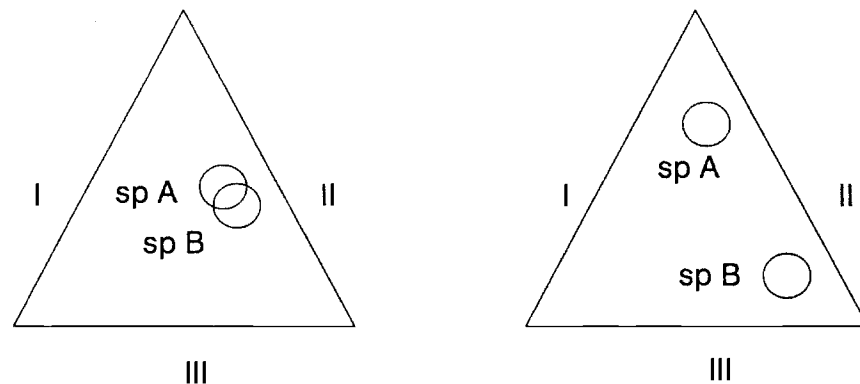


Figure 4. Representation of a three strategy model for a conceivably 'bad' (LHS) and 'good' (RHS) combination of two species, A and B, separated in a three axes (I, II, III) phase plane diagram. (After an approach used by Grime *et al.* 1988).

5. Interactions and limiting resources

So far species interactions have been described by their result, i.e. in a phenomenological way, and any statement of the actual mechanisms involved has been avoided. If, however, focus is to be made on the fundamental processes operating in agroforestry systems (see preface), a different approach which explicitly states the processes whereby individuals of one species influence individuals of that and other species is required (Tilman 1988). A major advantage of the mechanistic approach is that it can initially be narrowly focused, but then broadened to include other mechanisms and a wider view of the ecosystem. Hence, generality is achievable by determining the mechanisms of interaction, as is the potential to make explicit predictions.

The two most likely mechanisms of plant competition are exploitation (resource competition) and interference (allelopathic competition), as detailed above. Plant-plant interactions are not direct effects of one plant on another, but effects on the environment acting as an intermediate, i.e. via the response and effect axiom (Goldberg & Werner 1983). So for interspecific resource competition, changes in the density, or biomass, of a plant species are likely to affect the availabilities of various resources in the environment, such as nitrogen, water, phosphorus and light, and thus influence the growth of other species indirectly. As the population density or biomass of a species increases there is an increased rate of consumption of the resources and the availability of the resources is lowered.

In order to predict the outcome of competition information is required on the dependence of the rates of growth of each species on resource availability (Tilman 1986); in other words the resource consumption rate of each species (amount of each resource per unit biomass per unit time), determined by the growth rate, and the dynamics of resource supply. For mineral nutrients, resource 'levels' or 'availability' can be defined as the measurable concentration of a usable form or forms of the resource in the soil, whilst the supply rate of a resource is the rate at which usable forms of the resource are released into the soil (Tilman 1988).

Tilman takes an equilibrium approach to plant competition for limiting resources where, at equilibrium, the reproductive rate of a species is equal to its death rate and resource concentrations are constant, i.e. the rate of consumption of each resource balances the rate of supply. Limiting resources are ones which cause an increase in plant growth rate when their availability is raised. The equilibrium point for a given species in a particular habitat will thus depend on the dynamics of resource availability, and the species with the lowest requirement for a given, limiting resource will outcompete other species with higher requirements (Figure 5). This is not applicable in an agroforestry system, where the 'plant community' is managed and equilibrium is never achieved. The concepts still apply, however, and the

extent to which species in an agroforestry system compete will depend on the size of the resource pools in the system, and in turn on the flows of resources through the system.

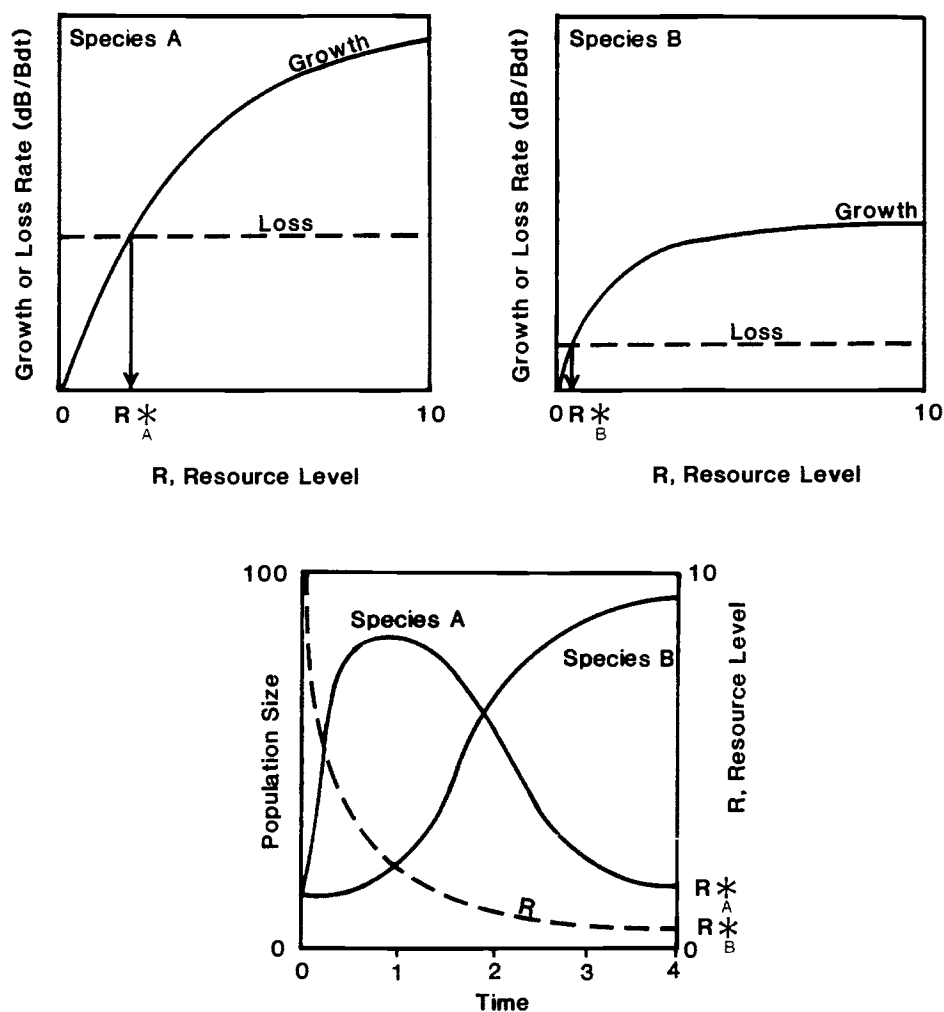


Figure 5. Resource dependent growth curves for two species, A and B. (A) Resource-dependent growth (solid curve) and loss (broken line) for species A. R_A^* is the amount of the resource species A requires to survive in this habitat. (B) Similar curves for species B. (C) When two species compete for a single limiting resource (R), species B, which has the lower equilibrium resource requirement (R^*), should completely displace species A once equilibrium is reached.

Source: redrawn from Tilman 1988.

To predict the consequence of plant competition for more than one resource it is necessary to know the dependence of the growth of each species on the availability of all limiting resources. The growth rate of a plant is then determined by the availability of the resource in lowest supply relative to the plant's need, and at equilibrium, species can coexist in habitats where the growth of each is limited by a different resource. It should be noted that the mechanisms of intraspecific and interspecific resource competition are complicated by size and age dependent processes in plants, and by virtue of plants being morphologically and physiologically plastic (Tilman 1988).

Mechanistic, or process based, studies which view agroforestry in terms of flows of resources such as light, water and nutrients through the system, and distribution of these resources between the various components of the system, are thus integral to understanding the mechanisms of plant-plant interactions. The resource levels in the environment at the tree-crop interface will determine the responses of the component species, and be affected by them.

6. Resources and growth

In natural ecosystems resource supply through the environment governs plant growth and form. It has been proposed (Tilman 1982; Tilman 1988) that the physical separation of essential resources required by plants into an above-ground resource (light) and below-ground resources (water and nutrients), results in plants facing an inescapable trade-off in dealing with such a constraint. For a light limited plant to obtain

more light, it must allocate more of its photosynthate to shoot growth (Figure 6), and thus a smaller proportion of its photosynthate to root growth. Similarly a nutrient limited plant must allocate more photosynthate to root growth and hence proportionately less to the growth of stems and leaves if it is to obtain more nutrients. The pattern of plant allocation to above- versus below-ground structures should thus influence the competitive ability of a plant in a given habitat, and also the relative competitive abilities of the different component species in an agroforestry system.

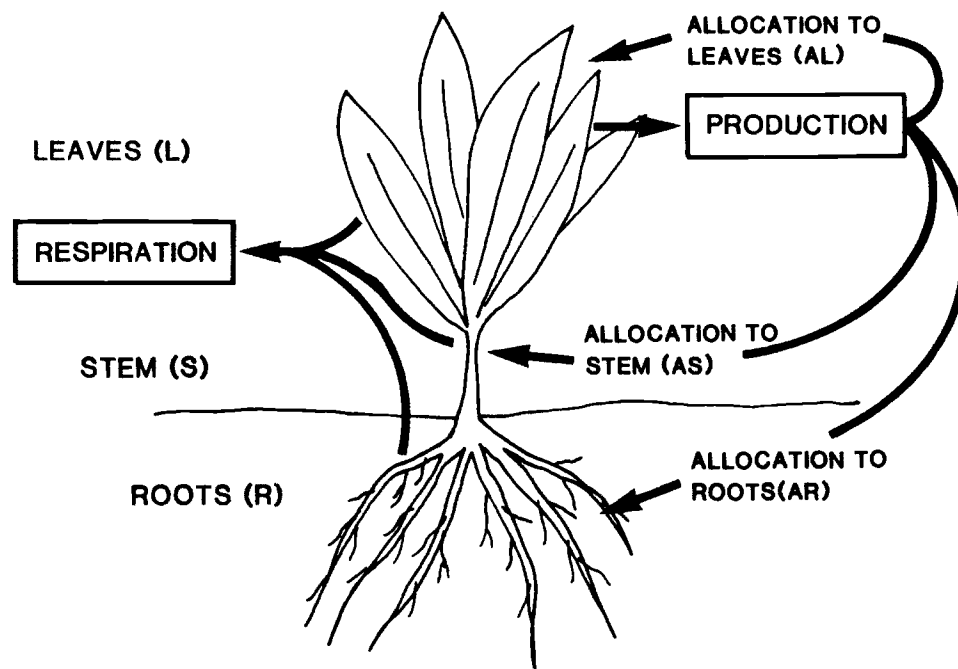


Figure 6. A model for the allocation of carbon during growth.

A diagrammatic representation of growth in a plant that can allocate its production to additional leaf, stem, or root biomass.

Source: redrawn from Tilman 1988.

A model of nutrient and light competition amongst continuously growing size-structured plant populations has been developed using the above concept (Tilman 1988). Modelling will be discussed in detail elsewhere, but here conceptual aspects of models will be considered as a means of structuring ideas and thinking about the mechanisms involved.

7. Temporal factors

Agroforestry involves long-lived plants and the ability to sustain increased productivity. The time dimension is therefore important, particularly concerning the long-term dynamics of resource availability. Overyielding involves an increased rate of resource consumption (i.e. nutrient removal) and thus an increased rate of decline in soil fertility will occur unless the rate of resource supply is also increased (i.e. the replacement of nutrients). Production can only be sustained at higher levels if consumption and supply are balanced, and this will probably involve management intervention.

Relations between the components in a mixture of two species have been followed through time and the changes in proportions recorded and analysed, using a parameter called the 'relative replacement rate' (Wit 1960; Bergh 1968). The results of such experiments show that some species combinations are frequency dependent and others are not. For example, many combinations of grass species show frequency-dependent interactions whilst for mixtures of grass and legume frequency dependence can be removed by the presence of *Rhizobium*. Frequency-dependent situations arise when each species is affected more by its own density than by that of its neighbours, and imply some form of ecological differentiation in which the two species make different demands, compete for different resources, or compete at different times, i.e. have a different seasonal pattern of growth (Harper 1977).

Trees raised from seed have to pass through growth stages comparable to, first, the ground layer of vegetation, then the field layer and the shrub layer, before emerging in a canopy. Thus, the nature of tree-crop interactions in an agroforestry system will change with the life stage of the tree component. Selection of trees with seasonal growth patterns that avoid competition for resources with the crop will be important in enhancing crop yields. Additionally, for legume trees in agroforestry the interaction between tree and crop changes with time from reduced competition to facilitation. In a given year any benefit from nitrogen fixation by the legume tree is conferred on the companion crop by the avoidance of competition for

nitrogen, whilst in subsequent years the tree facilitates fitness of the crop by the release of nitrogen fixed in previous years through litter decomposition.

The stages of development in an agroforestry system are in some respects analogous to the stages of succession in ecosystems (Giller, personal communication). Succession is the process whereby one plant community changes into another. It represents community dynamics occurring on a time scale of the order of the life-spans of the dominant plants, and occurs because the probability of establishment changes through time for each species, as both the abiotic environment (e.g. the soil conditions) and the biotic environment (e.g. the nature and competitive ability of neighbouring plants) are altered (Crawley 1986).

Most primary successions are associated with the accumulation of nitrogen in the soil. Many of the early vascular plant colonists are legumes and other nitrogen fixing species which add substantially to the soil pool. Studies of plant colonization of waste heaps following china clay mining (Bradshaw & Chadwick 1980) suggest that the shortage of major plant nutrients, especially nitrogen, retards the succession, so that the appearance of legumes which can tolerate the acid nutrient-poor conditions is a critical step in the development of vegetation cover. These legumes are able to fix 30-50 kg N/ha annually, whilst experiments on virgin substrates have shown that woody plants cannot invade successional communities until 400-1200 kg N/ha have built up in the soil (Post *et al.* 1985). Prior to the appearance of legumes nitrogen accumulation is very slow, but after they have invaded a well-established stand of leguminous shrubs will take 20 years to accumulate enough nitrogen to form an ecosystem capable of supporting a large biomass.

Secondary succession begins with a more or less mature soil containing a sizeable bank of seeds and vegetative propagules. The observed 'succession' of species simply comprises the replacement of small, short-lived plants by large long-lived ones (Crawley 1986), each invading species altering the environmental conditions for the next.

The development of an agroforestry system embraces a number of these 'successional' elements. Crops can be supported by the land due to alteration of environmental conditions by nitrogen fixing species, which improve the organic matter status of the soil and increase the nitrogen pool in the soil. In the later stages of development, management practice will determine how 'mature' the agroecosystem becomes, influencing the final outcome of the succession.

III. Section 2: Summary of research progress

1. Classification of interactions in agroforestry systems

Table 2 presents a framework constructed in order to examine published research findings in a systematic way, using existing concepts from population and community ecology regarding ecological interactions. A description of the classification follows.

Ecological interactions can be separated into (i) physical and (ii) biological (intraspecific and interspecific) processes (Schoener 1988); these are analogous to the abiotic and biotic components of an ecosystem. The biological component encompasses the principal types of interactions that occur between species, namely (i) competition (-,-),(-,0), (ii) predation (+,-), (iii) mutualism (+,+), and (iv) commensalism (+,0), where the net result for each of two species is given in parentheses (Watkinson 1986; Schoener 1988).

Various taxonomies for competition exist within the American literature, distinguishing exploitative and interference competition (Park 1962) or consumptive, pre-emptive and interference competition (Schoener 1983). Here, it is unnecessary to sub-divide the term, which is taken to be a negative interaction, either symmetric or asymmetric. Similarly, predation can be divided into (i) predation proper, (ii) herbivory, and (iii) parasitism (Toft 1986). Here, a restricted sense of the word is used by considering only plant-herbivore interactions, where predation is again a negative interaction for the plant species.

Two kinds of mutualism occur, (i) facultative, and (ii) obligatory, depending on whether other species are necessary for persistence or not (Schoener 1988). Mutualism is thus a positive interaction, though in agroforestry perhaps the only genuine mutualisms are those involving nitrogen-fixing microbes or mycorrhizas and their hosts. A general term used to describe the process in which two individuals or populations of plants interact so that at least one exerts a positive effect on the fitness of the other, is facilitation (Vandermeer 1989). Thus, commensalism is equivalent to single facilitation, and mutualism is equivalent to reciprocal, or double, facilitation.

For intercropping systems a dichotomous classification has been proposed (Vandermeer 1989), based on (i) reduced competition and (ii) facilitation. Interactions between the crop (biological) and environment (physical) components of the system occur through the response and effect axiom (Goldberg & Werner 1983) and are thus embraced by this dichotomous classification. Such a taxonomy does not, however, allow for monospecific effects on the environment, i.e. temporal amelioration.

The classification used in this review takes a different approach, parallel to separation on the basis of processes and types of interaction (Schoener 1988), by splitting the ecosystem into (A) components, and (B) relationships. In this taxonomy, the components of the system are considered by separation into (A1) the physical environment, divided into above- and below-ground components, and (A2) the biological

Table 2. A system for the classification of ecological interactions in agroforestry systems

A. Components	
1. Physical environment	
i. above ground	
ii. below ground	
2. Biological environment	
i. plant	
ii. animal	
iii. microbe	
B. Relationships	
1. Abiotic-biotic interactions	
a. physical environment affecting biological environment	
b. biological environment affecting physical environment	
2. Biological interactions (intraspecific & interspecific)	
a. competition	consumptive pre-emptive interference
b. predation	predation proper herbivory parasitism
c. mutualism	facultative obligatory
d. commensalism	

environment, divided into plant, animal and microbe components. The physical environment concerns resources (light, water, nutrients), and includes landscape factors such as topography and climate, whilst the biological environment is defined by the agroforestry arrangement, or ecosystem architecture, and incorporates resource capture. 'Relationships' cover interactions both (B1) between the physical and biotic components, and (B2) amongst biotic components (intraspecific and interspecific). The first subdivision includes the control of resource fluxes, in terms of the effects of limited resources on plant growth and development (B1a), and mechanisms related to the consumption of resources by plants (B1b). Thus biological interactions (B2) represent the net result of plant-environment processes (B1).

Using this type of categorization, agroforestry constitutes a set of land use practices which aims to encourage a favourable combination of the ecological interactions, competition, predation, commensalism and mutualism, thus enhancing productivity of the land, and conserving resources. The results of research studies in agroforestry are surveyed against the background of this theoretical framework.

2. The literature review

(a) Introduction

Although it has been used before as a starting point for discussion (Tilman 1988), the following quote is provocative: 'there is an extensive literature in which it is demonstrated repeatedly that the [competitive] balance between a pair of species in mixture is changed by the addition of a particular nutrient, alteration of the pH, change in the level of the water table, [and] application of water stress or of shading. These experiments had a significant historical importance in emphasizing that the interaction between a pair of species was a function of the environment in which the interaction occurred, and an anecdotal value in defining, for a specialized condition of environment and species, the effects of a particular change. It is

very doubtful whether such experiments have contributed significantly either to understanding the mechanism of 'competition' or to generalizing about its effects' (Harper 1977).

Undoubtedly, in order to arrive at some general conclusions, study is needed on the mechanisms of interactions between species. Harper (1977) lists the following as some of the ways in which the presence of one plant will affect the growth of another:

- reducing light intensity
- changing light quality
- transpiring limited water
- changing the humidity profile
- absorbing limiting nutrients
- providing limited nitrogen
- sheltering or excluding predators (or sheltering the predators of predators)
- favouring or reducing pathogenic activity
- encouraging defecation or urination in the neighbourhood
- providing rubbing posts and so encouraging local trampling
- raising the soil level (accumulation of organic matter)
- liberating selective toxins
- changing soil reaction

As discussed above, a plant can thus influence its neighbours by changing their environment, either directly (e.g. by effects on resource levels or by toxins) or indirectly (e.g. by affecting microclimatic conditions and attracting animals). However, as Harper (1977) noted, 'the analysis of which particular factor acts in any one effect of neighbour on neighbour is bound to be extremely difficult and has rarely been achieved in experimental populations; it is infinitely harder in nature'. In practice the researcher has to accept correlations because establishing causation is most often not possible, for example in the task of separating interactions above and below ground (e.g. Donald 1958; Aspinall 1960; Snaydon 1971). Such problems should be borne in mind when critically examining published studies in agroforestry research.

A brief review of research findings and observed relationships within agroforestry systems follows, within the classification framework already described. Those studies which do not, *per se*, concern interactions between species (e.g. examination of processes within the ecosystem) have been grouped under the most relevant biotic interaction heading.

(b) Competition

Competition has been reviewed in general terms (e.g. Franco & Harper 1988; Schoener 1988; Tilman 1988), and in relation to intercropping (Vandermeer 1989) and agroforestry (Ong *et al.* 1991a; Monteith *et al.* 1991; VanDenBeldt *et al.* 1990; Ong & Black, in press). Recent research on competitive interactions in agroforestry systems has tended to concentrate on establishing the relative importance of above-ground and below-ground competition for resources (Snaydon & Harris 1981; Corlett *et al.*, 1992a,b), and on reduced competition, also described by the terms 'complementarity' and 'resource sharing' (Ong & Black, in press).

Above-ground competition for light

Many field experiments have been carried out to examine how one species, by reducing light intensity, can affect the productivity of another. For example, in studies examining the resource sharing ability of multipurpose trees in an intercropping system, crop yield was found to be depressed by competition with the trees for light (Srinivasan *et al.* 1990), a finding previously observed in studies on canopy effects (Kira & Kumura 1983). Studies in Nigeria (Kang *et al.* 1981) using *Leucaena leucocephala* intercropped with maize similarly indicated that above-ground competition for light was more important than below-ground competition, whilst an investigation in Sierra Leone to assess the effects of *Leucaena leucocephala* on the productivity of maize, cowpea and sweet potato (Karim *et al.* 1991) revealed reduced yields of maize and sweet potato in the rows immediately adjacent to the trees, more notably in those plots where nitrogen fertilizer was added to remove possible nutrient limitation.

Alley cropping experiments at ICRISAT, India, and ICRAF, Kenya, in which annual crops were grown between woody hedges of *Leucaena leucocephala*, have produced contrary findings. Although marked decreases in crop yield were observed when alley width was reduced below 5 m (Singh *et al.* 1989; Rao *et al.* 1990), the results suggested that changes in crop growth were predominantly due to below-ground competition between trees and crop for water, nutrients or both (Ong *et al.* 1991b). These authors concluded that in both semiarid and subhumid zones the presence of trees in a crop of maize or sorghum did not have either a detrimental or beneficial effect through above-ground interaction. However, the results of such studies must depend to a large extent on geographical factors which dictate the main limiting resource, i.e. light in the subhumid tropics and water in the semiarid tropics.

Above-ground versus below-ground competition

Determining the relative importance of above-ground and below-ground interactions is, as noted above, difficult (Donald 1958). Methods have included root separation and alteration in the levels of limiting resources. For example, vertical polythene barriers and trenches have been used to separate the roots of pearl millet and groundnut in an intercropping system (Marshall & Willey 1983), though little effect on the productivity of either crop was observed. Similar experiments involving *Leucaena leucocephala* hedgerows and annual crops resulted in yields of cowpea and sorghum close to the woody species being unaffected by the presence of root barriers (Singh *et al.* 1989).

Further experiments at ICRISAT, India, using *Leucaena leucocephala* and pearl millet grown in an alley cropping arrangement with different alley widths and the presence or absence of root barriers have been carried out (Corlett *et al.* 1992a,b). The proximity of millet to the *Leucaena* hedge, hedge shape, and the relative size of the two species were all found to modify the microclimate surrounding the millet, in terms of wind speed, incident radiation level, and soil temperature. Reductions in millet yield, comparing the species combination with millet monoculture, resulted primarily from shading of the crop. When root competition was reduced by the presence of a barrier, the millet grew taller and eventually attained the same height as the *Leucaena* hedge, thus partially avoiding shading. Increase in competition intensity with the development of size asymmetry (Goldberg & Werner 1983) between tree and crop components in agroforestry systems has been little studied.

A model of competition between trees and grass for radiation, water and nutrients has been constructed (McMurtrie & Wolf 1983), but, as noted by the authors, this model does not take into account spatial patchiness of the resources. When investigating the effects of more than one resource, the now abandoned concept of multiple limiting factors (Blackman 1905) — that plants respond proportionally to increased inputs of only the most limiting factors until another factor becomes limiting — could still be worth considering. In arid environments the availability of water may set an upper limit for productivity, even though co-limitation by several factors at the same time has been reported (Caemmerer & Farquhar 1984).

Root competition for water and nutrients

Nutrient uptake by plants is proportional to soil solution nutrient concentrations at the root surface, and is determined by the soil supply which in turn is determined for each nutrient by interactions between the nutrients and the soil properties. The mobility of an ion in soil has thus been noted as performing an important role in governing the magnitude of solution depletion adjacent to the root (Barber 1984). Detailed models of nutrient transport in the immediate root environment suggest that effective transport rates of nutrients are dominated by the 'apparent adsorption constant' and that for N, P and K different aspects of the root system are the most important (Willigen & Noordwijk 1987).

A model for calculating the rooting depth of a crop or crop combination required to intercept leaching nutrients for different conditions of soil and climate has been constructed (Noordwijk 1989). In shifting cultivation systems a deep-rooted fallow vegetation can recover nutrients leached to the subsoil during the cropping phase. The model can indicate the combinations of climatic zone and apparent adsorption constant for which such interception is possible. Using this approach, rooting depths for various leguminous cover crops have been described (Hairiah & Noordwijk 1989).

Clearly, the adaptation of plants depends on complex optimizations; the depth of root system that would be adaptive depends on the benefits gained in terms of water and nutrient acquisition, and their influence on plant function and the costs to the plant for developing and maintaining the root system (Passioura 1982).

Root interactions between species have received less attention until recently, partly due to the predominance of laboratory experiments involving pot grown, resource saturated plants, and partly as a result of the technical difficulties of studying root growth. Recent advances in technology, such as the miniaturization of video cameras to enable image analysis, and the use of nuclear magnetic resonance (NMR) imaging (Brown *et al.* 1991) are helpful aids which overcome some of the limitations of rhizotrons, but do not remove the need for destructive root excavation and coring.

Nevertheless, root interactions have been studied (e.g. Campbell 1989), and nutrient flux and interspecific root competition have been investigated using mechanistic modelling (Gillespie 1989), with the aim of manipulating below-ground competition for nutrients and water by spacing and the selection of trees and crops with different rooting depths. The latter work concluded that higher rooting densities promoted competition for nutrients due to decreasing inter-root distances.

Competition, spatial factors and resource capture

Intraspecific competition and density dependent effects have been little studied in the context of productivity in agroforestry practices. Systematic designs for quantifying the relations between yield and plant population density in crops have been suggested (Bleasdale 1967; Nelder 1962; Huxley & Maingu 1978; Willey & Rao 1981), and population densities have been studied (Natarajan & Willey 1980; Upadhyay *et al.* 1990), particularly the effects of planting density on water use efficiency (Eastham *et al.* 1990) and on soil organic matter and nutrient pools (Sparling *et al.* 1989). Pearl millet at low population density has

been demonstrated to compensate by tillering, so that productivity and light interception are unaltered by increases in density (Azam-Ali *et al.* 1984).

The capture of resources by trees in relation to density dependence has been the subject of extensive research work. Much of the work and modelling effort to examine light and rainfall interception, windflow, mass transfer etc. has treated populations of trees as a single entity, the forest stand, with a horizontally homogenous distribution. The studies of Rutter *et al.* on rainfall interception by tree canopies demonstrated that evaporation of intercepted water was a major cause of the differences in the water yield of afforested catchments (Rutter *et al.* 1971; Rutter *et al.* 1975). A model of rainfall interception loss was constructed (Rutter & Morton 1977; Gash & Morton 1978), which has recently been re-evaluated with respect to the effect of tree spacing (Teklehaimanot & Jarvis 1991a; Teklehaimanot *et al.* 1991). Evaporation of intercepted water from forest canopies comprising widely spaced stands of trees, as applied in agroforestry systems (Teklehaimanot & Jarvis 1991b) has been studied, with the conclusion that interception loss per unit leaf area changes as tree spacing increases, and thus extrapolation from forest stands is inappropriate since tree crowns must be considered as individuals. It is presumably also necessary to assess the root systems of individual trees to understand below-ground processes.

The separation of incident precipitation into throughfall, stemflow and interception loss in relation to canopy structure for a temperate conifer plantation has been estimated (Ford & Deans 1978). A positive correlation between the spatial pattern of throughfall and fine root distribution was observed (Ford & Deans 1977). The environmental impact of plantation forestry using fast-growing tree species in India has been examined (Calder *et al.* 1986; Harding & Rosier 1989; Newson & Calder 1989; Calder 1991; Calder *et al.* 1991) in connection with the relations between water use and growth, based on measurements of daily transpiration rate and cross-sectional area (Calder *et al.* 1992). A model for calculating transpiration and growth of *Eucalyptus* plantations in water-limited conditions has been developed (Calder 1992) based on these studies.

Light interception by forest canopies has also been examined in detail, particularly for temperate stands, though light transmission through widely spaced trees has received less attention. Studies on tropical plants include the effect of shading (Murray & Nichols 1966; Huxley 1967; Mathai & Chandy 1988), herbaceous understorey responses to changes in canopy cover (Anderson *et al.* 1969; Lee 1989), the relations between leaf area and light transmission (Ewel *et al.* 1982), and the effects of light and temperature on pearl millet productivity (Ong & Monteith 1985).

Measurement and modelling of light interception in discontinuous canopies in relation to productivity has been carried out, notably for row crops (Allen 1974; Mann *et al.* 1980), orchards (Jackson & Palmer 1979; Charles-Edwards & Thorpe 1976) and forests (Norman & Jarvis 1975). The distribution of leaf area in space between and within individual tree crowns primarily determines the fraction of incident light intercepted by trees (Wang & Jarvis 1990) and hence tree productivity (Russell *et al.* 1989). Three dimensional models have been constructed for isolated trees (Charles-Edwards & Thornley 1973; Mann *et al.* 1979), and for regular, widely spaced tree stands (Jackson & Middleton 1988), and have included analyses of the spatial heterogeneity of transmission to the understorey (Anderson 1991). Whilst such models could predict the seasonal light interception and carbon gain of a given configuration of canopies in an agroforestry system, in order to predict performance over time a greater understanding of carbon partitioning and canopy development for widely spaced trees is required.

Regarding intercropping systems, leaf area index and dry matter production have been studied for cassava-cowpea and cassava-peanut crop combinations in Colombia (Mason *et al.* 1986). It should be noted that the estimation of leaf area for crops, canopies and individual trees has been difficult, and measurements subject to considerable error. Recent development of techniques for non-destructive measurements of leaf area (Lang *et al.* 1985; Lang & Xiang 1986) that can be used for individual tree crowns (Lang & McMurtrie 1991) could enable seasonal development of leaf area for different components of agroforestry systems to be monitored.

Alteration in light quality has been little studied in relation to agroforestry, though it is known that depression of the red to far red ratio of light penetrating a canopy and linked to leaf area index, is detected by phytochrome in understorey plants and affects their growth and development, notably the initiation of lateral buds, leaf and internode extension rates and tillering (Morgan & Smith 1981; Grace 1983a,b,c; Kronenberg & Kendrick 1986). The detection of close neighbours by plants via changes in the ratio of red to far red light may also occur (Ballare *et al.* 1987; Casal & Smith 1988), and it is conceivable that light quality affects root architecture, reducing below ground competition.

Competition with a third species

Weed control should be considered, as it can be viewed as an example of three species competition (Levine 1976) in which a secondary species controls the weeds and releases the main crop from strong competition with the weed (Vandermeer 1989). Weed control can alternatively be regarded as pre-emptive competition by our classification, in which a second, cover crop is used between rows of the principle crop to exclude weeds (Liebman 1986).

In Nigeria it was found that a maize-cowpea combination failed to suppress weeds early in the growing season but had a significant effect later on (Ayeni *et al.* 1984), whilst a cassava-maize combination failed to control weeds at any stage of growth (Unamma & Ene 1984). In Costa Rica, however, the

cassava-maize combination was found to suppress invasion and growth of weeds successfully (Soria *et al.* 1975). Weed suppression is often achieved by the use of tree prunings as a mulch on the soil surface.

Reducing competition through niche differentiation

Productivity may be enhanced through the mechanism of reduced competition, sometimes termed the 'competitive production principle' (Vandermeer 1989). The mechanism refers to situations where two species can more efficiently utilize necessary resources when in combination than in monoculture, despite one species having an effect on the environment that results in a negative response in the other species. The term 'complementarity' has been used to describe spatial or temporal sharing of resources (Monteith *et al.* 1991), but does not differentiate between reduced competition and the net result of competition and facilitation occurring together. More recently complementarity has been defined as 'the efficiency with which mixtures of species capture and utilize limiting growth resources' (Ong & Black, in press).

Resource sharing can occur both spatially and temporally. Regarding spatial sharing, radiation interception by intercrops has been measured at different points in the crop and expressed as the quantity intercepted per row of each crop relative to that for a monoculture of each crop, and called the resource capture ratio (Marshall & Willey 1983; Stirling *et al.* 1990; Ong *et al.* 1991c). This is analogous to the land equivalent ratio used for determining yield advantage (Mead & Willey 1980). Temporal resource sharing concerns phenological mechanisms, and leads to enhanced productivity due to the capture of more resources rather than changes in the efficiency of resource utilization (Willey *et al.* 1986; Ong & Black, in press). Examples include increased light interception and water use by growing combinations of fast and slow growing crops, e.g. sorghum and pigeonpea (Willey *et al.* 1986), and maize and pigeonpea (Sivakumar & Virmani 1980), and the timing of canopy development for combinations of tree and crop, e.g. *Faidherbia* [*Acacia*] *albida* and pearl millet (Brenner 1991).

Niche differentiation on the basis of root architecture has been considered for alley cropping (Noordwijk 1989), by the selection of trees such as *Leucaena leucocephala*, *Gliricidia sepium* and *Acacia barteri*. Optimal spatial distribution was conceived as requiring deep root development for 'nutrient pumping' and limited horizontal development in order to reduce competition with crop roots (Hairiah & Noordwijk 1986; Noordwijk 1989).

Studies of fine root distribution have also been carried out to examine whether certain trees (*Cassia siamea*, *Eucalyptus camaldulensis*, *E. tereticornis*, *Leucaena leucocephala* and *Prosopis chilensis*) would compete with crops for nutrients and water (Jonsson *et al.* 1988). It was observed that the vertical root distribution of these species was similar to that of *Zea mays*, implying strong competition between crop and tree. It was also suggested that such findings tended to contradict the idea of deep-rooting trees acting as nutrient pumps in agroforestry systems. In temperate silvopastoral systems, allocation of biomass to roots in *Prunus avium* has been shown to increase, and the vertical distribution of roots in *Fraxinus excelsior* to be downwardly displaced, through competition with aggressive swards (Tomlinson & Eason 1990; Campbell & Dawson 1991). Such changes in tree rooting pattern indicate a response to reduced water and nutrient availability in the upper soil layers as a result of resource consumption by the sward. Mixtures of trees and crops may therefore exhibit more extensive niche differentiation than would be expected from observation of root architecture in monoculture.

(c) Predation

Although interactions involving animals are outside the remit of this review, it is worth noting that most studies concerning plant-herbivore interactions appear to have considered cases where the herbivore is a designed part of the system, e.g. sheep, goats, cattle (Grace 1983b; Goto *et al.* 1986; Gill & Wood 1992; Toit *et al.* 1990; Maxwell 1990; Hawke, 1991). Losses due to pest predation may account for one third of crop yields in Africa, but there seems to be little information on plant-herbivore interactions in terms of reduced pest losses and changes in pest populations in agroforestry systems. Enclosure experiments would allow the importance of vertebrate pests (herbivores and granivores) to be determined, for example, what happens to competition and yields when an enclosure is placed round an agroforestry system? Similarly, what is the difference in yield when pesticides are applied to (for example) a crop of millet in monoculture as compared to a crop of millet grown in an agroforestry system; what is the relative importance of pests in these two land use practices, and are fewer or more pests present in the latter case?

Crop pests have been described in the context of agroforestry systems (Epila 1988), and the potential of insect pests of intercrops to infest an oil palm agroforestry system examined (Dhileepan 1991). However, the ability of these systems to attract predators, e.g. birds, and whether such predators are insectivores (and of benefit) or granivores (and of detriment) has been little studied. The importance of agroforestry for controlling insect predators of livestock is also unclear.

By contrast, reductions in pest losses for intercropping systems are well documented, and a number of reviews exist (e.g. Perrin 1977; Kass 1978; Risch *et al.* 1983) from which it is clear that diversified agroecosystems frequently show reduced herbivore attack compared with monocultures. Hypotheses for the observed protection from pests have been presented (Aiyer 1949; Root 1973), and incorporated into three categories by Vandermeer (1989): (i) the disruptive-crop hypothesis (a second plant species disrupts the ability of a specialist pest to efficiently attack its proper host), (ii) the trap-crop hypothesis (a second plant species attracts a generalist pest that would normally be detrimental to the principal crop species),

and (iii) the enemies hypothesis (the intercrop system attracts more predators and parasites than the monocultures, thus reducing the pests through predation or parasitism).

(d) Mutualism

Despite the small number of mutualistic interactions occurring in agroforestry systems, the importance of the two considered here, nitrogen fixing microbes and mycorrhizas, is immense, and considerable research effort is presently being devoted to gaining a better understanding of the processes involved. Both are mutualistic because they operate on the basis of transfer of resources (Fitter 1986), with the plant trading carbon in return for nitrogen in the case of root nodules containing N-fixing microbes (Sprent 1979), and phosphate plus other ions and water in the case of mycorrhizas (Harley & Smith 1983). The carbon costs of nitrogen fixation may be high (Minchin & Pate 1974), but the ubiquitous occurrence of mycorrhizas suggests that carbon is less limiting than phosphate in many situations (Fitter 1986).

Mycorrhizas

Dealing first with mycorrhizas, most fall into two major morphological types, the vesicular-arbuscular mycorrhizas (VAM), and the ectomycorrhizas (ECM). VAM infect most herbaceous species and some woody species, whilst ECM are largely confined to woody species (Eason *et al.* 1991). The hyphae of the mycorrhizas act as a kind of secondary root system, facilitating uptake of nutrients by the host, phosphate in particular.

Mycorrhizas tend not to exhibit a high degree of host specificity, and their hyphal links can unite plants of the same and different species (Newman 1988). Such direct hyphal links thus offer possible routes for the partially closed cycling of nutrients and assimilates between plants (Finlay & Read 1986; Eason *et al.* 1991), with attendant implications for ecosystem functioning. For example, VAM infection has been shown to markedly increase the transfer of ³²P from dying roots of *Lolium perenne* to living plants of *Plantago lanceolata* (Ritz & Newman 1985), and from *Lolium perenne* to *Acer pseudoplatanus* and *Fraxinus excelsior* (Eason *et al.* 1991). There is also evidence of direct uptake of phosphorus from litter via mycorrhizal hyphae such that the soil pathway is bypassed and an entirely closed cycle exists (Herrera *et al.* 1978).

Nitrogen fixation

As noted above, nitrogen fixation by the prokaryotic cyanobacteria and bacteria has major economic consequences (Hamilton 1988). The taxonomy of N-fixing organisms is difficult, and continually being updated, with symbiotic N-fixing micro-organisms being divided into several groups which include the leaf associations and root nodules of the *Alnus*, *Cycas*, *Parasponia* and leguminous type (Bezdicsek & Kennedy 1988). Global estimates of inputs for nitrogen fixation and for losses through leaching and denitrification are difficult to obtain (although figures have been produced, see Hardy 1975), as are estimates for crops and individuals. Serological methods such as agglutination, immunodiffusion, ELISA, immunofluorescence and monoclonal antibodies are used to identify N-fixing organisms (Vincent 1970; Dudman 1977), with differentiation of strains involving the use of DNA probes and antibiotic resistance.

Various factors such as soil type, pH, temperature and water content affect the survival and functioning of N-fixing organisms (Marshall 1964; Weber & Miller 1972; Rice *et al.* 1977), and other organisms including actinomycetes, bacteria and fungi are antagonists of some rhizobia (Pugashetti *et al.* 1982). In soil where roots are absent rhizobia grow poorly unless supplemented with carbon (Bezdicsek & Kennedy 1988). Competition, in the form of interaction between similar rhizobial strains, is important because it determines the proportion of nodules occupied by a given strain; inoculation is thus carried out at high levels in order to saturate the system (Weaver & Frederick 1974).

Reviews concerning soil nitrogen budgets (Legg & Meisinger 1982) and the transfer of nitrogen between legumes and other crops (Henzell & Vallis 1977; Whitney 1977) have been published. In Asia, grain legume crops such as *Arachis hypogaea* (groundnut) and *Glycine max* (soyabean) are grown in rotation with rice, maize and cassava, the legumes providing a substantial nitrogen input through biological fixation of atmospheric nitrogen (Cadisch *et al.* 1989; Giller & Wilson 1991). The nitrogen contribution of *Sesbania sesban* and *Leucaena diversifolia* to maize in alley cropping systems in the highlands of Rwanda has also been examined, using ¹⁵N techniques (Rubaduka & Giller, personal communication).

The possible benefits of N₂-fixation by grain legumes for intercropped cereals have been examined to determine whether the legume, by fixing N₂ purely for its own use, is thus only weakly in competition with the cereal for soil nitrogen, or if the legume contributes nitrogen directly to the intercropped cereal (Morris 1986; Giller *et al.* 1991). Prior studies of the transfer of nitrogen between legumes and cereals in an intercropping system have produced conflicting results, with some finding no evidence for transfer (Wahua & Miller 1978; Ofori *et al.* 1987; Kessel & Roskowski 1988), and others the contrary (Eaglesham *et al.* 1981; Heichel & Barnes 1984). Giller *et al.* (1991) observed less than 5% of the ¹⁵N label in a legume (*Phaseolus*) being transferred to maize in a pot experiment.

(e) Commensalism

Research work which directly or indirectly refers to commensalism as a positive interaction in intercropping and agroforestry systems has been reviewed (Young 1989a; Monteith *et al.* 1991; VanDenBeldt *et al.* 1991; Ong & Black, in press). Increased productivity due to positive interactions between species has been called the 'facilitative production principle' (Vandermeer 1989), where the environment of one species is modified positively by another species so that the first species benefits from the presence of the second.

Competition and facilitation most often occur together, however. For example trees may compete with a crop for light, leading to reduced crop yield through shading, whilst at the same time increasing soil organic matter and hence soil moisture content, and the availability of nutrients for the crop through leaf litter. It is the sum of negative and positive interactions, or net effect, that is observed, and detailed study is required to separate the two.

Within the research literature there have been two main areas of investigation under the heading of commensalism, (i) amelioration of the microclimate by the use of trees as shelterbelts, and (ii) soil amelioration and nutrient cycling. Most work in the latter area has thus concerned the ameliorative effects of trees on the soil component of agroecosystems (Sanchez 1987; Anderson 1987; Lal 1989; Young 1989a), and specifically the importance of litter production, quality, decomposition and nutrient release (Ingestad 1987; Harrison *et al.* 1990; Szott *et al.* 1991;), and organic matter accumulation (Goh 1980; Paul 1984; Fassbender *et al.* 1991). Interactions between microclimate and vegetation have been reviewed (Grace 1977; Monteith 1981; Jarvis 1989; and Monteith 1990).

Shelter and shelterbelts

The use of trees as shelterbelts is an old practice which has been well documented and examined (Zohar & Brandle 1978; Mozheiko & Semyakin 1984). Studies concerning shelterbelts primarily used as wind-breaks have been carried out, particularly in the context of effects on plant water use efficiency (Greb & Black 1961; Eimern *et al.* 1964; Kort 1988; Davis & Norman 1988). Overhead shelter from spaced trees as opposed to shelterbelts has been examined (Green *et al.* 1991) by considering plant canopy aerodynamics and windflow through a plot of widely spaced trees using a fluid dynamics model. Investigation with this model suggests that the results of shelterbelt research cannot be applied to agroforestry designs involving dispersed trees.

Beneficial microclimatic modifications have been reported for crops of millet and groundnut grown as intercrops with *Leucaena* hedges (Corlett *et al.* 1989), especially where the latter provide protection from the wind. The positive interaction due to microclimate amelioration was, however, balanced by the negative effect of competition for water. Stimulation of crop growth by shading has also been observed (Wilson *et al.* 1986), and shading in relation to pollarding discussed (Russo & Budowski 1986).

Nutrient cycling

Research work in this area has included studies on litter nutrient composition (Rout & Gupta 1987; Sharma & Pande 1989; Cameron & Spencer 1989) and nutrient release from tree leaf litter (Carlisle *et al.* 1967; Glover & Beer 1984; Beer 1988; Dunham 1989; Eason 1991; Okeke & Omaliko 1991). Organic matter accumulation through root turnover has received some attention (Kummerow 1981; Shparik 1988; Fahey *et al.* 1988) though quantification, particularly of fine root turnover, has been problematic. Build-up of soil organic matter is important for the improvement of water holding capacity and soil tilth.

The influence of soil fauna, particularly earthworms, termites and ants on the physical, chemical and biological properties of soil has been noted (Lal 1988; Neelam Saharan & Singh 1988). Soil and crop management techniques employed in agroforestry are considered to favour and enhance the activity of soil fauna (Lal *et al.* 1978; Kang *et al.* 1985), which affect the rates of soil turnover (Nye 1955; Lal 1987), mineralization and humification of soil organic matter, soil texture and consistency, porosity (Wilkinson 1975), infiltration rate and soil-water retention characteristics (Lal 1987). The contribution of defecation by birds and livestock to nutrient cycling has also been investigated (Gill & Wood 1992).

Anderson (1987) notes that 'the selection of particular tree species adapted to local soil conditions can be used to (i) change the balance of cations returned to the soil surface in litter, (ii) build up soil organic matter, (iii) provide for fast or slow decomposing mulches to control nutrient release to crops, and (iv) enhance soil fauna activities'. Considerable research has been carried out on the selection and improvement of trees for environmental conservation (Leahey & Last 1980; Burley *et al.* 1986; Leahey 1987; Leahey & Ladipo 1987).

Nutrient cycling and synchronization

Linked to litter decomposition, nutrient cycling and productivity are the constraints of synchronization (Anderson 1987; Swift 1977; Anderson & Spencer 1991). Litter decomposition leads with time to the release of nutrients in a form available to plants; the rate of decomposition, and thus nutrient release, is controlled by climate and resource quality so that the efficiency of nutrient transfer will depend on the timing of release in relation to the maximal crop growth rate and plant nutrient demand (Swift 1987). Experimental work is being carried out under the TSBF programme to determine the relations between

climate, litter quality and plant demand, and to study the role of soil organic matter, acting as a plant nutrient sink and a source, in regulating the temporal and spatial patterns of nutrient availability.

Nutrient cycling and management practice

Cultivation practices such as mechanical tillage cause a decline in soil humus content as a result of changes in the soil thermal regime, disruption of soil aggregates and changes in the quality and quantity of plant residues returned to the soil (Swift & Sanchez 1984). The net effect of these disturbances on the the integrated components of the forest ecosystem is a sudden and rapid change from a system with high nutrient efficiency to one with low efficiency and a massive loss of nutrient assets.

Forest fallow has a restorative value, linked to the regrowth of deep rooted trees and shrubs which recycle plant nutrients from considerable depth in the soil profile, and build up soil organic matter (Anderson 1987). The management of tree prunings as mulches has been practised extensively, with the aim of obtaining nutrients for crop growth (Kass & Jimenez 1986; Budelman 1989).

Evidence of positive interactions

Many studies concerning the beneficial effects of nutrient cycling have been reported (e.g. Gurbachan Singh *et al.* 1988; Cuevas & Medina 1986), including changes in soil chemical properties associated with litter production and improved productivity (Singh *et al.* 1989), the transfer of nutrients from *Eucalyptus* to wheat via leaf litter (Sidhu & Hans 1988), effects of tree litter on sward production in a temperate climate (Eason 1988), and the involvement of soil organic matter (Fassbender & Alpizar 1987).

It has been reported that sustained crop yields can be obtained by incorporating the prunings from hedges of perennials (Kang *et al.* 1985), and that maize yields without fertilizer application may be doubled by using leaf mulches from nitrogen-fixing trees, with maintenance of yields during droughts (Anderson 1987).

The presence of litter at the soil surface improves water infiltration and reduces runoff and evaporation, so that surface litter and soil organic matter influence soil water fluxes and moisture regimes (Swift 1987). Positive interaction between trees and crops due to improvement of the soil water status by trees via interception, stemflow and increased water infiltration has been considered (Lal 1989; Jimenez Otarola 1989), as has the conservation of soil moisture by reduced evaporation due to vegetation cover (Penman 1948; Calder 1977; Eastham & Rose 1988; Grewal & Abrol 1986; Calder *et al.* 1991).

IV. Section 3: Key issues in agroforestry

Agroforestry is described as having the 'potential to increase productivity and provide multiple products while conserving resources' (Corlett *et al.* 1992b). The key issues explored further in this last section of the paper are precisely these three potential advantages, namely (i) overyielding, (ii) reduction in yield variance, and (iii) maintenance of resources.

1. Overyielding

The resolution of overyielding involves comparison of crop production in the land use system of interest against a standard, taken to be the performance in monoculture. If production is greater than can be obtained in monoculture, overyielding is said to occur, and if it is less then underyielding occurs (Figure 7). Overyielding can also be described as the 'yield advantage'.

In intercropping, the 'land equivalent ratio' (LER) is frequently used as a measure of the effectiveness of an intercrop (Mead & Willey 1980), and is identical to the 'relative yield total' (RYT) since it is based on the relative land requirements for intercrops versus monocultures. LER can be defined as the amount of land needed to produce as much in monocultures as can be produced on one hectare of polyculture (Vandermeer 1989):

$$\text{LER} = (\text{species A yield per hectare in polycrop} / \text{species A yield per hectare in monocrop}) + (\text{species B yield per hectare in polycrop} / \text{species B yield per hectare in monocrop}),$$

where values >1.0 indicate overyielding (i.e. the polycrop is more productive).

There are two general ways in which growing species in combination can result in a yield advantage: by diminishing the negative interactions that occur when species are grown in monoculture; and by enhancing the positive interactions that can occur when species are grown together. Negative interactions encompass predation (herbivory) as well as competition, and a yield advantage would be gained if the polyculture approach led to reduced pest losses.

The competitive plant interaction in a monoculture is wholly intraspecific, where individuals of the given species will occupy the same portion of the niche space available, and will have similar demands on the resource base. One species cannot occupy all parts of the space available, and thus other species can be introduced if they can occupy a different part of the same niche (i.e. niche differentiation can occur). Thus a mixture of species will lead to a reduction in intraspecific competition, by decrease in population

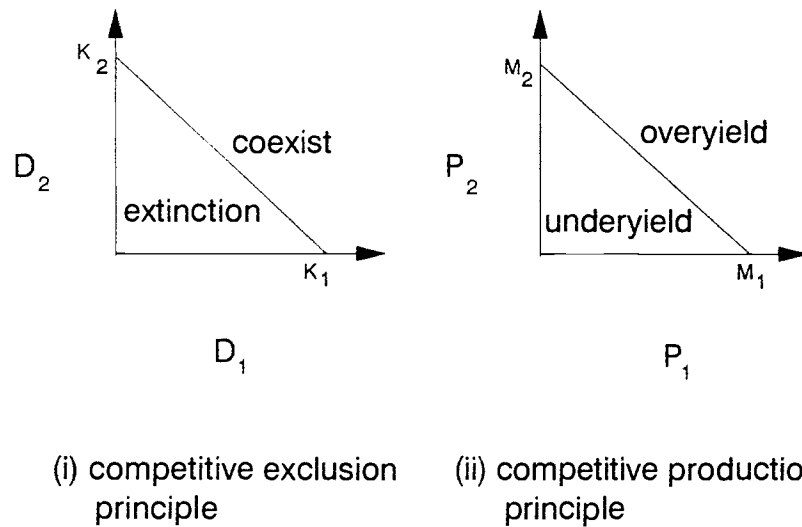


Figure 7. Diagrammatic representations of competitive exclusion and production principles.

In (i) D is the population density for species 1 and 2, and K is the carrying capacity; in (ii) P is the productivity for species 1 and 2, and M is the monocultural yield.

Source: redrawn from Vandermeer 1989.

density, and the introduction of interspecific competition. The success of the mixed species system will then depend on the intensity of interspecific competition; by maximizing niche differentiation (i.e. the ability to share resources in the niche), the intensity of interspecific competition will be minimized and the different species will be able to coexist with least decline in productivity. Overyielding will therefore be correlated with weakening competition.

Optimization of yield advantage can also be obtained from combinations of species by additionally exploiting the positive interspecific interactions that may occur (Figure 8), where one species provides some kind of benefit for another species by altering its environment in a positive way. Review of the literature has revealed many instances where a species, usually the tree component in agroforestry systems, ameliorates the environment for another species, usually an herbaceous crop, by increasing the amount of a limiting resource (water, nitrogen and other nutrients) or modifying the microclimate. It has been noted already that positive and negative interactions often occur together in species mixtures, and the term 'counteraction' has been used to describe a (+,-) net effect of concurrent asymmetric competition and asymmetric facilitation. Relative yield values <1 would suggest strong competition with weak facilitation, and values >1 weak competition with stronger facilitation.

A plot of land can be laid out in many different configurations for an agroforestry system (Young 1989b), and an elementary experiment would be to determine the differences in yield of the component species for each configuration (Figure 9), where the net effect of competition and facilitation will vary. Alternatively, target experiments can be carried out (Mead 1979; Goldberg & Werner 1983), in which the target is an individual, with other individuals placed systematically or at random around it at varying distances. The yield of the target is thus reduced as a function of the distance to the competitors, and a 'competition coefficient' can be calculated that describes the yield loss of the target per unit biomass of the surrounding competitors. The competition coefficient can then be plotted against the interplant distance and the occurrence of net facilitation detected (Vandermeer 1989).

As a final note regarding the ability of different species to coexist, for a two-species combination the biomass or productivity of one species can be plotted against that of the other (Figure 7). The carrying capacity (K) of each species is then the biomass that can be attained in the absence of the other species, and interspecific competition causes a reduction from the carrying capacities. If the point representing the biomass of each species in competition lies below an imaginary line connecting the carrying capacity of each species, then the two species cannot coexist (MacArthur 1972; Colwell & Fuentes 1975; Harper 1977)

2. Reduction in yield variance

The supposition on which reduced yield variability (termed 'yield stability' in agronomic literature) is based, as mentioned earlier, is that a more species diverse system has a greater capacity to deal with environmental variation, akin to the avoidance or spreading of risks through diversification, and consequently that diverse systems will be inherently more stable, i.e. less variable (Vandermeer 1989). This premise is not held universally, and it has been claimed that a more diverse system should be less stable (May 1974). Yield variability has been examined in relation to intercropping, where the change in variability in moving from monoculture to intercrop has been treated as a product of negative or positive interspecific interactions (Rao & Willey 1980; Rao *et al.* 1981; Faris *et al.* 1983). In agroforestry systems

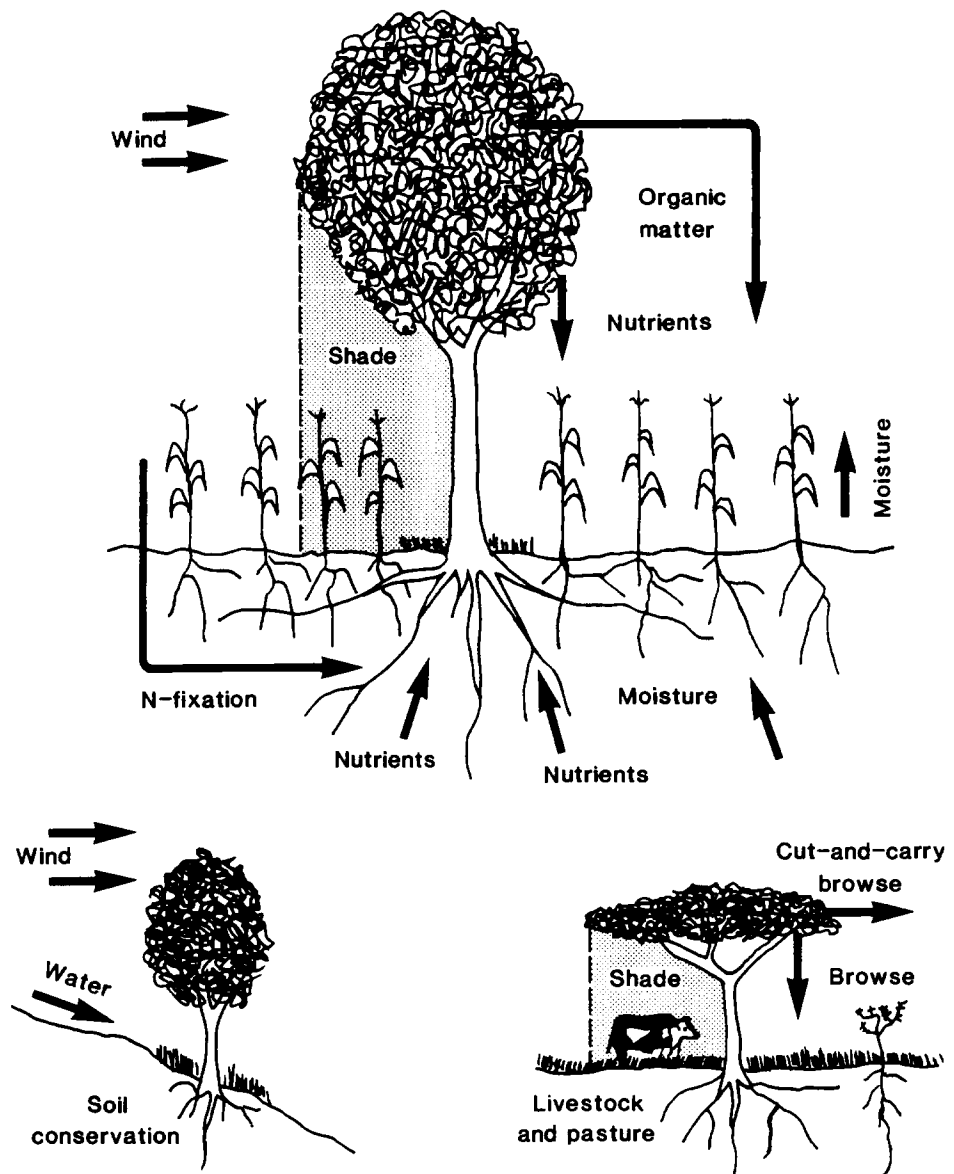


Figure 8. Positive interactions in agroforestry systems, mediated through amelioration of the environment.

Source: redrawn from Young 1989b.

a greater diversity of species often exists than in a simple intercropping system, but the numbers of species involved may still be very low and thus stretching use of the concept of stability.

Nevertheless, variability in intercropping can be determined using five variables: the monoculture yield of species A and B, the intercrop yield for species A and B, and the combined intercrop yield. The variance associated with each variable can then be used to compare variability for each species in an intercropping system with that in monoculture, and to estimate system variability by comparing the species combination in intercropping with that for both monocultures (Vandermeer 1989). The coefficient of variation has been used as the accepted measurement of variability, though alternative measures have been suggested (Rao & Willey 1980).

Thus, the variance of the sum of intercrop yields has been compared with the variance of the sum of monoculture yields for sorghum and pigeonpea, where the proportion of total yield attributed to sorghum was equal in the intercrop and monoculture (Rao & Willey 1980). It was found that the intercrop was less variable (i.e. more stable) than the monoculture. However, in a theoretical treatment based on the work of Schultz (1984), Vandermeer (1989) concluded 'that intercrops will tend to be more variable than monocultures if competition is operative, that they may be either more or less variable when facilitation is operative, and that they will tend to be less variable in cases where mutualism operates'.

The farmer may thus face a choice when considering land use options: whether to avoid risk or to maximize yield. Such a choice can be considered as an optimization problem in which yield is maximized and risk minimized, and the probability of remaining above a threshold yield value computed. Again this has been examined theoretically, with the conclusion that a secondary crop which is highly competitive

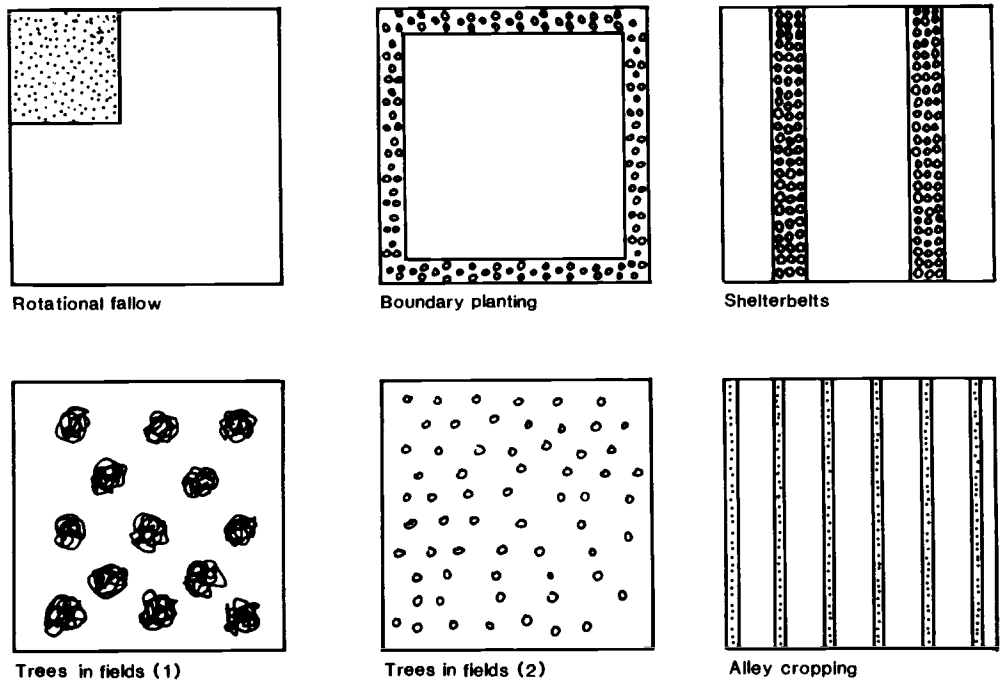


Figure 9. Possible agroforestry designs with a 25% tree cover. Six ways of arranging a 25% tree cover on one hectare. Within-field lines are tree/crop interfaces. Based on the concept developed by Huxley (1985). Source: redrawn from Young 1989b.

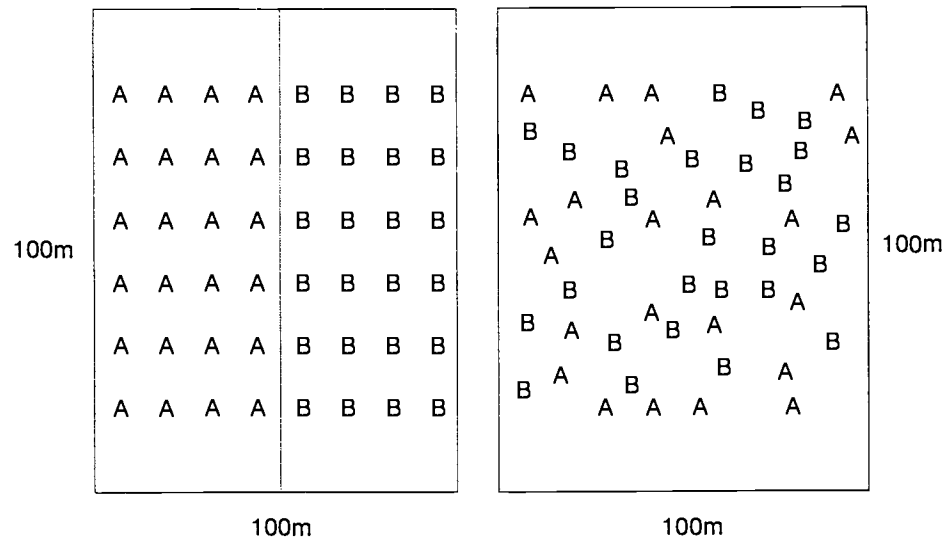


Figure 10. Alternative arrangements for a two species mixture (A and B) in 1 hectare, minimizing (LHS) or maximizing (RHS) interspecific interactions.

should only be combined with the principal crop if it can provide a strongly facilitative environment (Vandermeer 1989).

'Agroforestry' is a diffuse term covering a number of land use designs, from arrangements analogous to a gardener's allotment through to arrangements where species are distributed amongst each other. Both ends of this spectrum can have equal species diversity and thus, from the supposition above, such systems will be equally stable, but the marked difference in ecosystem architecture between them must have effects because of changes in the degree to which different interactions occur.

A relatively simple experiment could be designed (Figure 10) to examine the advantages and disadvantages of growing different species in discrete units or mixed together in one large unit. For instance two species can occupy a one hectare plot in two blocks, divided down the middle with one species on the left hand side and one on the right. Interspecific competition will be restricted to the boundary line between the two, with intraspecific competition being the predominant species interaction.

Rearranging this configuration so that both species are dispersed throughout the one hectare plot, intraspecific competition will be reduced because density is reduced (i.e. from 10 000 individuals in 0.5 ha to 10 000 in 1.0 ha), whilst interspecific competition will be markedly increased by mixing of the species. A similar design has been employed in the study of interference between two annual grasses, *Bromus rigidus* and *B.madritensis* (Harper 1961). The species were sown at a constant density and in equal proportions but the arrangements of individuals were such as to maximize contacts either within or between species. At the end of the growing season the yield of the two species was markedly different between the arrangements.

Since two individuals of the same species will have similar resource requirements, whereas two individuals of different species may not due to niche differentiation ('resource sharing'), the interaction shift from intraspecific to interspecific could result in a net weakening of competition. Such a rearrangement would be more advantageous when the resource base is patchy at the fine scale. Where the arrangement is for two monocultures side-by-side, and as stated, individuals of a given species have similar requirements for resources, the resource base will need to be uniform within each side of the plot if maximum productivity of all individuals is to be ensured.

Indeed it could be said that this is precisely what modern agriculture strives to achieve by use of agrochemicals; growing crops as monocultures requires that the farmer makes the resource base as uniform as possible, so that variability in yield throughout the crop is kept to a minimum. The application of agrochemicals can be thought of as creating homogeneity in the resource base. Where agrochemicals are not available, either because they are not produced or are costly, the farmer must make use of land with a resource base which is patchy. Monocultures grown on such land will show considerable variability in growth across the crop, and thus increase in species diversity by intimate combinations of crops, with the potential for greater utilization of a patchy environment, will be beneficial.

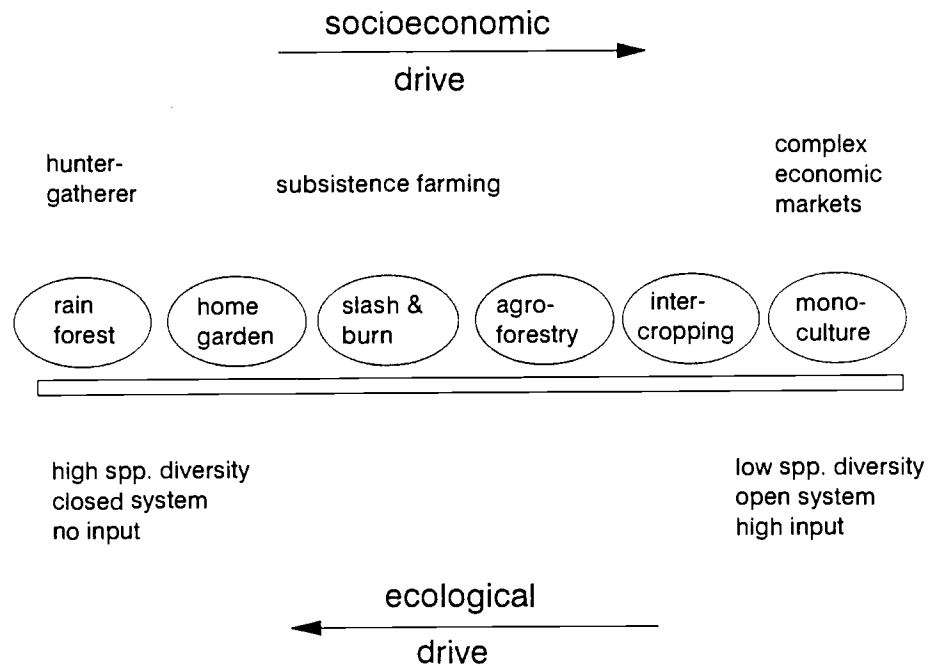


Figure 11. A continuum in species diversity and land occupations.

The concept of 'environmental grain' (MacArthur & Levins 1964) may thus be important in the spatial design of an agroforestry system. If a plant of species A interfaces or 'experiences' the vegetation in the proportions in which its component species (B, C, D etc.) occur, it is behaving in a fine-grained manner, whereas if the distribution of individuals is ordered in some way so that a plant of species A has many neighbours of species B and few of species C, D, E, etc., species A is said to behave in a coarse-grained manner. In a natural ecosystem the ordering may be caused by some heterogeneity in the physical conditions of the environment (Harper 1977). Local variation in soil resource supply rates can be caused by a variety of factors, including differences in soil permeability to water, exchange sites for nitrogen and phosphorus, effects of herbivore excretion, soil erosion, topographic variability, and feedback from plants (Jenny 1980).

In a sense the gardener's allotment is an artificial point somewhere between the home garden, with its complexity of species interactions, and the uniformity of large scale monocultures in Europe and America. It is possible to visualize (Figure 11) a continuum from rain forest to monoculture running left to right, with home gardens, slash-and-burn, agroforestry and intercropping as successive points in between these two extremes. The ecological drive is from right to left, reflecting increasing species diversity (numbers of tree species in particular) and, in terms of nutrient cycling, a move from open, leaky systems towards

closed systems. The socioeconomic drive occurs in the reverse direction (left to right), and reflects a move from 'hunter-gatherer' occupations through subsistence farming towards the complexities of economic markets where crops are sold for money with which to buy other goods. The socioeconomic shift is linked to increase in population density, again left to right, with urbanization as a consequence of large populations at the extreme, resulting in dependence on others for the provision of agricultural produce.

The gardener's allotment involves growing crops as a series of monocultures; this is a system that is considerably easier to manage than the home garden, where crop species are dispersed throughout the plot of land; it also requires less labour input. The allotment is also flexible, because temporal spread of harvesting times permits maximum utilization of the land, with the same piece of land being used to grow more than one crop in a season, possibly adjacent to a slow growing perennial crop. It also allows continual rotation of the faster growing crops. In conclusion, both land use systems are species diverse, and thus overall are potentially more stable (less variable) than a one or two species system, but the home garden, whilst being more labour intensive and temporally less flexible, could show an advantage in terms of enabling niche differentiation to occur, particularly when the distribution of resources in the environment is patchy at the fine scale.

3. Maintenance of resources

Whilst stability can be equated with short-term environmental or economic fluctuations, sustainability concerns the effects of long-term fluctuations or stresses on the agroecosystem's ability to maintain productivity (Figure 12). Any agroecosystem may be sustainable, so long as inputs and outputs (water, nutrients, energy) are in balance; the more that is removed by cropping (i.e. the larger the losses), the larger the inputs (i.e. sources) required to maintain the balance. In natural ecosystems, such as a tropical rain forest, the dynamics of the plant community have reached a state of equilibrium, and thus the rate of resource consumption is equal to the rate of resource supply (Tilman 1988). In order to examine the question of sustainability, an examination will first be made of what is known about such systems, and the effects of disturbance on their functioning.

Nutrient and hydrological cycling in tropical forests have been extensively reviewed (Jordan 1985; Vitousek & Sanford 1986; Proctor 1987; Bruijnzeel 1990), as have the hydrological and soil chemical responses to disturbance (deforestation) in moist tropical forests (Bruijnzeel 1990). Field methods and applications for nutrient cycling in terrestrial ecosystems have also been reviewed (Harrison *et al.* 1990).

A useful summary of the major pathways linking the various nutrient storage pools in a tropical forest has been provided by Proctor (1987), quoted by Bruijnzeel (1990): 'Nutrients enter the ecosystem with the rain, deposition of dust and aerosols, (in the case of nitrogen) by fixation by micro-organisms above and below ground, and (except for nitrogen) by weathering of the underlying rock. The major above-ground pool of nutrients is the canopy (defined as the total plant community) and there is a flow of nutrients from this to the forest floor in small and large litterfall and in throughfall and stemflow of rainwater, which usually becomes enriched by nutrients from leaves and bark. A proportion of the above-ground nutrients is in dead organic matter such as standing dead trees and small and large litter lying on the forest floor. Nutrients are gradually released from the dead matter by decomposition mediated by soil animals and micro-organisms. Decomposition is complex and can involve immobilization of nutrients as well as their release. Nutrients are taken up from the exchange complexes of the soil by roots (probably usually in association with mycorrhizal fungi) which provide a living below-ground pool and which export them to the canopy. The roots release nutrients to the soil as secretions and by the death and decomposition of their parts. Permanent loss of nutrients occurs through surface erosion, fires, loss in drainage water and in the case of nitrogen by abiotic or microbial denitrification. Some, particularly phosphorus, may effectively leave the system by conversion into insoluble inorganic forms within the soil'.

Regarding the dynamics of nutrient cycling and maintenance of forest productivity, nutrient conserving mechanisms are a feature of tropical forests growing on nutrient poor substrates which maintain themselves at a high biomass level (Bruijnzeel 1990). These mechanisms permit a relatively 'tight' or 'closed' nutrient cycle with minimum leakage of nutrients from the system (Herrera *et al.* 1978; Brinkmann 1985). Conversely, forests growing on more fertile substrates exhibit a more 'open' type of nutrient cycle (Baillie 1989).

A distinction can also be drawn between forests that have reached a state of dynamic equilibrium and young forests or plantations which rapidly incorporate large amounts of nutrients into their biomass. For young trees net uptake rates exceed supply from litterfall and canopy wash, and the extra nutrients have to be supplied by the soil (Bruijnzeel 1990). As nutrient demand declines with age, gradual increase in nutrient losses can occur as tree demands progressively fall below the rate of soil nutrient supply (Vitousek & Reiners 1975). Thus in the short term 'nutrient availability is regulated by the balance between processes releasing nutrients into available forms and those removing them. In the long term the nutrient status of a forest ecosystem depends on the balance, at the landscape level, between nutrient inputs [wet and dry deposition, mineral weathering, gas absorption and fixation] and outputs [mainly leaching and volatilization]' (Bruijnzeel 1990).

A nutrient cycling model which simulates vegetation growth, litterfall and decomposition, soil biogeochemical processes, and pathways for moisture has been described (Gherini *et al.* 1989). Available nutrients in the soil strata and vegetation pools, and the fluxes between pools, are traced, and the

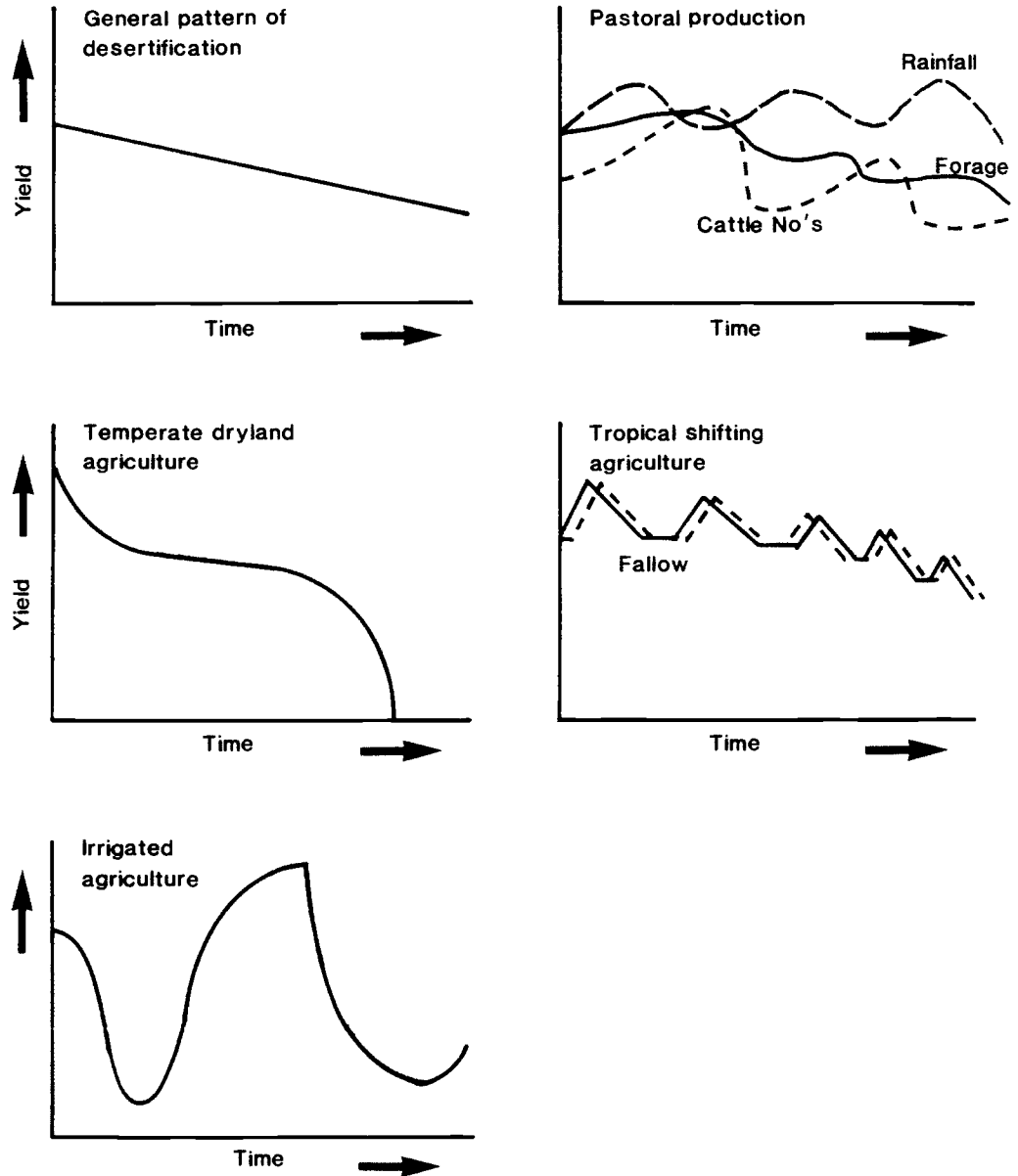
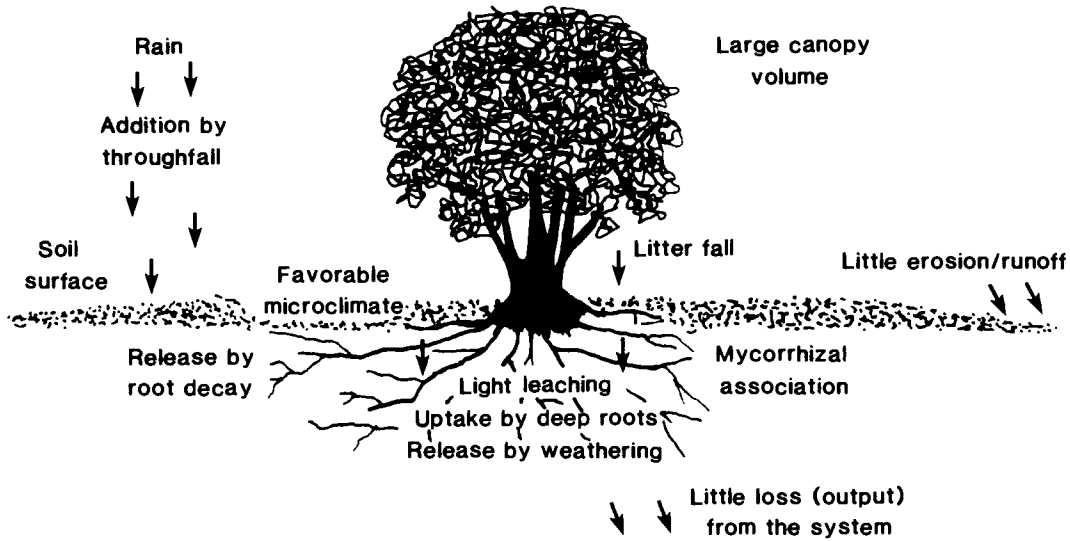


Figure 12. Changes in productivity with time associated with land degradation. Changes in yield during desertification for different land uses: (a) general pattern; (b) approximation to situation under pastoral production; (c) approximation to pattern in drylands where persistent cropping overtakes the soil nutrients, reduces organic matter content and causes erosion; (d) pattern where drylands shifting cultivation has degenerated; and (e) a generalization of what happens in irrigation projects, a pattern of rising yields, breakdown, possible rehabilitation and so on. Source: UN 1977; redrawn from Barrow 1991.

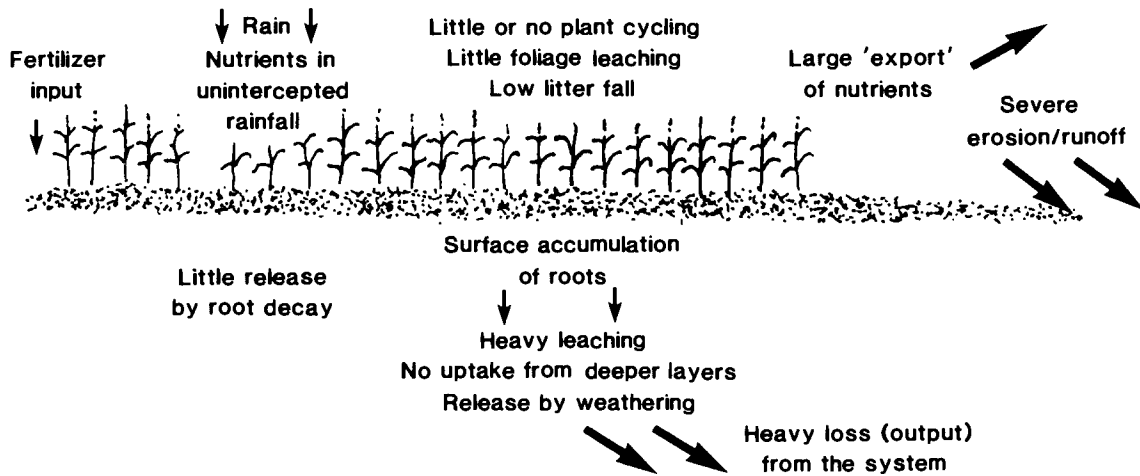
interaction of processes occurring in these pools used to resolve nutrient status and hence the health and productivity of the forest (Liu *et al.* 1992).

Hunter-gatherer societies have lived in tropical rain forest regions for thousands of years without destroying the forest (Lea 1975), whilst 'shifting cultivation', or 'slash and burn agriculture' (Whitmore 1990) as a farming system in rain forests throughout the tropics is said to have been responsible for 35% of the deforestation in Latin America, 70% in Africa and 50% in Asia (Bruijnzeel 1990). This system of agriculture is characterized by clearing and burning of forest vegetation, growing crops in the ashes for one or two harvests, then abandoning the area to forest regrowth or 'bush fallow'. It is sustainable under the climatic and edaphic conditions of the humid tropics provided the cropping period is not extended too long or the bush fallow period made too brief, in which case the system will degrade because forest succession is hindered and insufficient time is allowed for build-up of nutrients in the vegetation (Sanchez 1976; Scott 1987). The decline in yields during the cropping period is due to many factors, including soil fertility depletion, increased weed infestation, deterioration of soil physical properties, and increased

FOREST ECOSYSTEM



AGRICULTURAL SYSTEM



AGROFORESTRY SYSTEM

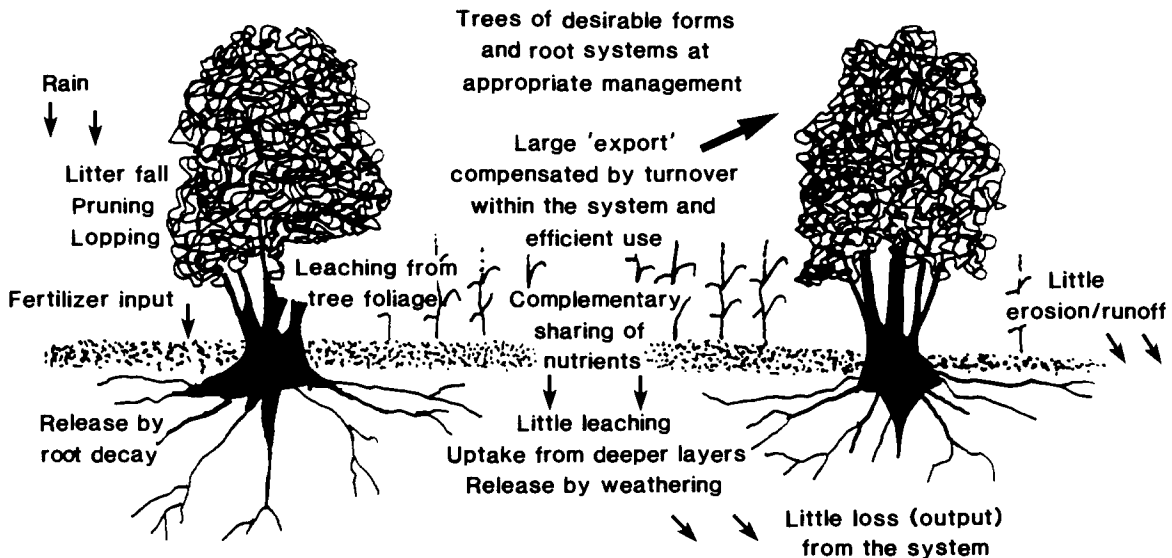


Figure 13. Agroforestry as a system combining the benefits of forest ecosystems with agricultural practice. Source: redrawn from Mainguet 1991.

insect and disease attack (Sanchez 1976). The period of fallow required to restore fertility is longer in areas of high erosion and leaching potential (Bruijnzeel 1990).

In a study comparing nutrient dynamics and productivity in undisturbed natural forest and newly created pasture in Venezuela (Buschbacher 1984) it was observed that cutting and burning produced large initial increases in topsoil available nutrients, which rapidly declined during the first year of pasture use, then more slowly subsequently. It was concluded that once all the woody material had decomposed, soil nutrient stores could probably not be maintained and the site would then need to be fertilized or abandoned.

What can be concluded about the sustainability of an agroforestry system given the state of knowledge concerning forest and grassland systems (Figure 13), and the effects of disturbance by conversion to farming land? Clearly biogeochemical cycling, the cycling of elements continuously within the ecosystem from non-living components to living organisms and back (Odum 1971), is an important concern. In this context scale (landscape factors) become important; where are the boundaries of the system? If, as has been suggested (Calder *et al.* 1992), trees can tap ground water reserves, then studies at the catchment scale will be necessary with regard to sustaining productivity of the trees. There is little information on absolute inputs and outputs at the catchment scale for tropical environments, yet it is vital to know whether resource accumulation is occurring or not if the aim is to 'cream off the profit' in terms of cropping levels.

In any system which is cropped, the resources that are taken off must be replaced if yield is to be sustained. Again this can be considered as an optimization problem where the amount that can be cropped off is maximized for minimum inputs whilst maintaining resource pools. Crop rotation, which enables resource sharing in time rather than space, may efficiently exploit the resources available provided suitable combinations of crops are used. This extends the length of time before additions of resources have to be made. It cannot, *per se*, maintain or restore the levels of all resources unless one of the rotation components is a period of fallow during which water and nutrients can accumulate, refilling the system pools to pre-cropping volumes.

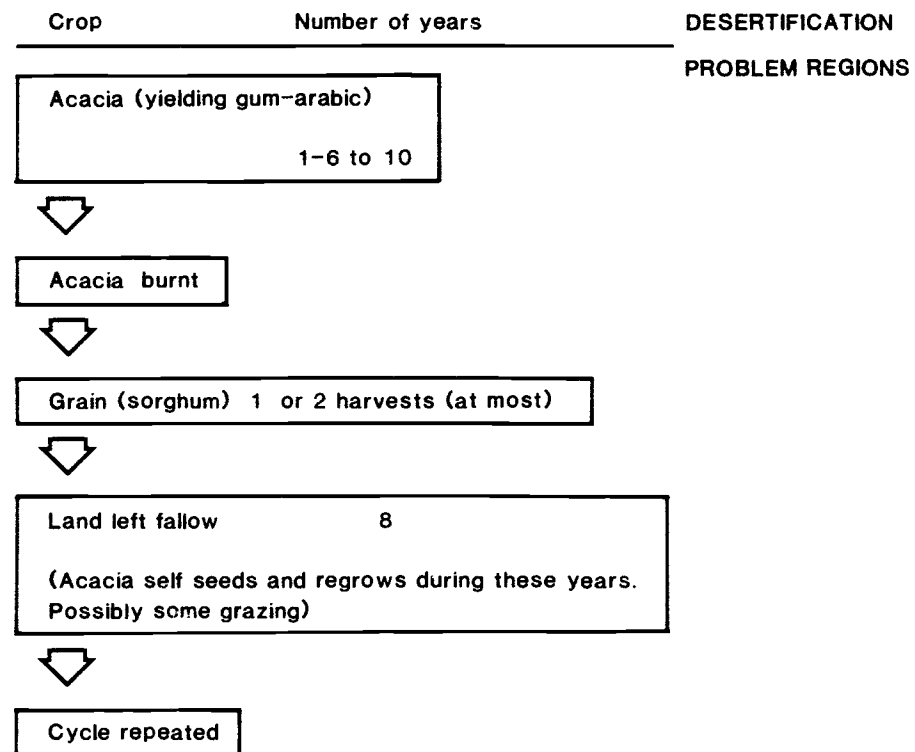


Figure 14. Land use based on improved fallow: a gum arabic (*Acacia senegal*)/grain/fallow cropping cycle.

Source: redrawn from Barrow 1991.

Improved fallow (Figure 14) is thus perhaps the most realistic management option for sustaining agroforestry systems when desired cropping levels will exceed input levels and lead to depletion of the resource base. It enables periodic resetting of the resource levels, provided the cropping phase has not carried on too long and led to irreversible environmental changes. Biogeochemical studies would be essential in determining the optimal relative lengths of the cropping and fallow phases of the land use cycle.

One final point, noted in the introduction, concerns the effects of resource depletion on the species interactions occurring in an agroforestry system, and competition for limiting resources in particular. It can be reasoned, from the argument put forward by Tilman (1988), that the species which is able to

maintain the highest growth rate at the lowest level of a limiting resource will be superior in competition with other species that have higher requirements. The intensity of competition will increase as the resource becomes progressively more scarce (i.e. plants should compete strongly in habitats with low resource levels; c.f. Grime 1979), and it is not possible to view either the flows of resources through the environment or competition between species in isolation.

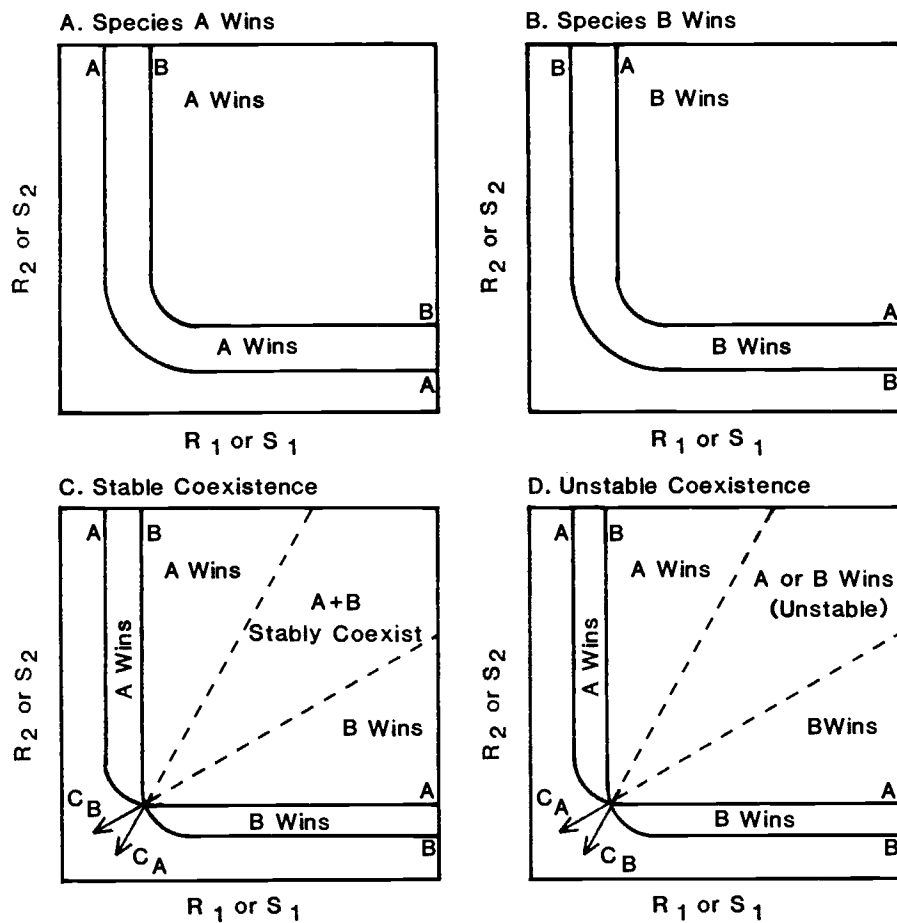


Figure 15. Four possible outcomes of competition between two species for two limiting resources. The solid, thick lines labelled A and B are resource (R_1 and R_2) dependent zero net growth isoclines for species A and B. The positions of these isoclines and of the resource consumption vectors (broken and thin lines, C_A and C_B) determine the equilibrial outcome of competition in each habitat. (A) Species A is a superior competitor for both resources in all habitats (resource supply points) in which either species can survive, and it displaces B. (B) Species B is a superior competitor for both resources, and displaces A. (C) The isoclines cross at a two-species equilibrium point. In combination with the resource consumption vectors of the two species, these isoclines determine the habitat conditions for which species A wins, both species coexist, or species B wins. Each habitat is defined by its resource supply point, (S_1, S_2). The labelled regions show the outcome of competition expected for supply points that fall in each region. For this case, the equilibrium point is stable. (D) Here, the consumption vectors are reversed. This causes the two-species equilibrium point to be unstable. Either A or B wins in this region, with the winner determined by initial conditions. Source: redrawn from Tilman 1988.

Tilman's proposals concern plant populations whose dynamics are in equilibrium, where population size can be expressed as biomass per unit area, and the growth rate for a given species is dependent on resource level. The resource level at which gain (from vegetative and reproductive growth) balances loss (from disturbance, predation and other mortality sources), and thus there is zero net rate of population change for a species, is denoted R^* . This resource level can be resolved, either by allowing the species to attain its equilibrial biomass in a monospecific stand and assessing the level to which it reduces the limiting resource at equilibrium (i.e. where the rate of resource supply and consumption are matched), or by determining the dependence of the species' growth rate on the resource levels, i.e. constructing resource dependent growth curves. If the resource level in the niche is $>R^*$, population size can increase, thus reducing the resource level towards R^* , whereas if the resource level is $<R^*$, population size will decrease, allowing the resource level to increase because of decreased consumption rates. Using this equilibrium approach (Figure 15), competition between two species for two limiting resources can have one of four possible outcomes: (i) species A wins and displaces species B; (ii) species B wins and

displaces A; (iii) there is stable coexistence; and (iv) there is unstable coexistence. Two factors strongly influence the availability of resources at equilibrium, (1) the loss rate of the species, and (2) the rate of supply of the limiting resource. The maximal vegetative growth rate of a species is thus the greatest rate of growth in a habitat which is not limited for any resource.

V. Conclusions and summary

1. Agroforestry is primarily considered as a set of land use practices which aim to realize the benefits from growing woody and herbaceous species together, commonly by the addition of trees to land already being used for pasture or for growing crops.

2. Most experimental field studies in agroforestry to date have reported net effects on productivity, so that the result of plant-plant interactions can be described as a positive, negative or nil effect on each species in the combination. These phenomenological studies do not state the mechanisms involved, and are highly site specific.

3. In order to focus on the fundamental processes operating in agroforestry systems, a mechanistic approach is required. The plant and its environment modify one another so that the environment causes a response in plant function and growth, and the plant then has an effect upon the environment by changing one or more of its factors. Agroforestry thus concerns the ways in which a plant can influence its neighbours by changing their environment. Mechanistic studies, which explicitly state the processes whereby individuals of one species influence individuals of that and other species, produce results that are amenable to modelling and are of more general applicability.

4. Species interactions can be advantageous, leading to an increase in total yield, reduced yield variability, and protection of the resource base. These ecological issues are analogous to socio-economic concepts concerning productivity, vulnerability and sustainability in marginal land use systems.

5. Future research should concentrate on the tree-crop interface, and specifically consider (i) below-ground studies, (ii) nutrient and water cycling, and (iii) traditional practices in agroforestry. Process-based models should be a central feature of the research, and a knowledge base should be constructed to assist the research effort.

References

- Aiyer, A. K. Y. N. (1949) Mixed cropping in India. *Indian Journal of Agricultural Sciences* 19, 439-543.
- Allen, J. H. Jnr. (1974) Model of light penetration into a wide-row crop. *Agronomy Journal* 66, 41-47.
- Anderson, J. M. (1987) Plant nutrient-use efficiencies and soil processes in natural and agricultural ecosystems. In *Amelioration of soil by trees: a review of current concepts and practices* [edited by Prinsley, R. T.; Swift, M. J.]. London, UK; Commonwealth Secretariat, Commonwealth Science Council. 20-29.
- Anderson, J. M.; Spencer, T. (1991) Carbon, nutrient and water balances of tropical rain forest ecosystems subject to disturbance: management implications and research proposals. *MAB Digest* No. 7, 95 pp.
- Anderson, R. C.; Loucks, O. L.; Swain, A. M. (1969) Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. *Ecology* 50, 255-263.
- Anderson, T. R. (1991) Computer modelling of agroforestry systems Ph.D. Thesis, University of Edinburgh, UK.
- Aspinal, D. (1960) An analysis of competition between barley and white persicaria. II. Factors determining the course of competition. *Annals of Applied Biology* 48, 637-654.
- Ayeni, A. O.; Duke, W. B.; Akobundu, I. O. (1984) Weed interference in maize, cowpea and maize/cowpea intercrop in a subhumid tropical environment. I. Influence of cropping season. *Weed Research (Oxford)* 24, 269-279.
- Azam-Ali, S. N.; Gregory, P. J.; Monteith, J. L. (1984) Effects of planting density on water use and productivity of pearl millet (*Pennisetum typhoides*) grown on stored water. II. Water use, light interception and dry matter production. *Experimental Agriculture* 20, 215-224.
- Baillie, I. C. (1989) Soil characteristics and classification in relation to the mineral nutrition of tropical wooded ecosystems. In *Mineral nutrients in tropical forest and savanna ecosystems* [edited by Proctor, J.]. Oxford, UK; Blackwell Scientific Publications. 15-26.
- Ballare, C. L.; Sanchez, R. A.; Scopel, A. L.; Casal, J. J.; Ghersa, C. M. (1987) Early detection of neighbor plants by phytochrome perception of spectral change in reflected sunlight. *Plant, Cell and Environment* 10, 551-558.
- Barber, S. A. (1984) Soil nutrient bioavailability: a mechanistic approach. New York, USA; John Wiley & Sons, Inc.
- Barrow, C. J. (1991) Land degradation: development and breakdown of terrestrial environments. Cambridge, UK; Cambridge University Press.
- Beer, J. (1988) Litter production and nutrient cycling in coffee (*Coffea arabica*) or cacao (*Theobroma cacao*) plantations with shade trees. *Agroforestry Systems* 7, 103-114.
- Bergh, J. P. van den (1968) An analysis of yields of grasses in mixed and pure stands. *Verslagen van Landbouwkundige Onderzoekingen* 714, 1-71.

- Bezdicsek, D. F.; Kennedy, A. C. (1988) Symbiotic nitrogen fixation and nitrogen cycling in terrestrial environments. In *Micro-organisms in action: concepts and applications in microbial ecology* [edited by Lynch, J. M.; Hobbie, J.E.]. Oxford, UK; Blackwell Scientific Publications. 241-260.
- Blackman, F. F. (1905) Optima and limiting factors. *Annals of Botany* 19, 281-295.
- Bleasdale, J. K. A. (1967) Systematic designs for spacing experiments. *Experimental Agriculture* 3, 73-85.
- Bradshaw, A. D.; Chadwick, M. J. (1980) The restoration of land: the ecology and reclamation of derelict and degraded land. Oxford, UK; Blackwell Scientific Publications.
- Brenner, A. (1991) Millet growth behind shelter in the Sahel. *Agroforestry in the UK* 2, 30-38.
- Brinkmann, W. L. F. (1985) Studies on hydrobiogeochemistry of a tropical lowland forest system. *GeoJournal* 11, 89-101.
- Brown, D. P.; Pratum, T. K.; Bledsoe, C.; Ford, E. D.; Cothorn, J.S.; Perry, D. (1991) Noninvasive studies of conifer roots: nuclear magnetic resonance (NMR) imaging of Douglas-fir seedlings. *Canadian Journal of Forest Research* 21, 1559-1566.
- Bruijnzeel, L. A. (1990) Hydrology of moist tropical forests and effects of conversion: a state of knowledge review. Amsterdam, Netherlands; Free University Press.
- Budelman, A. (1989) Effect of the application of the leaf mulch of *Gliricidia sepium* on early development, leaf nutrient contents and tuber yields of water yam (*Dioscorea alata*). *Agroforestry Systems* 8, 243-256.
- Burley, J.; Hughes, C. E.; Styles, B. T. (1986) Genetic systems of tree species for arid and semiarid regions. *Forest Ecology and Management* 16, 317-344.
- Buschbacher, R. J. (1984) Changes in productivity and nutrient cycling following conversion of Amazonian rainforest to pasture. Ph.D. Thesis, University of Georgia, Athens, USA.
- Cadisich, G.; Sylvester-Bradley, R.; Nosberger, J. (1989) ¹⁵N based estimation of nitrogen fixation of eight tropical forage legumes at two levels of P:K supply. *Field Crops Research* 22, 181-194.
- Caemmerer, S. von; Farquhar, G. D. (1984) Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced p(CO₂) on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. *Planta* 160, 320-329.
- Calder, I. R. (1977) A model of transpiration and interception loss from a spruce forest in Plynlimon, central Wales. *Journal of Hydrology (Amsterdam)* 33, 247-265.
- Calder, I. R. (1991) Deuterium tracing for the estimation of transpiration from trees. Part 2. Estimation of transpiration rates and transpiration parameters using a time-averaged deuterium tracing method. *Journal of Hydrology (Amsterdam)* 130, 27-35.
- Calder, I. R. (1992) A model of transpiration and growth of *Eucalyptus* plantation in water-limited conditions. *Journal of Hydrology (Amsterdam)* 130, 1-15.
- Calder, I. R.; Narayanswamy, M. N.; Srinivasalu, N. V.; Darling, W. G.; Lardner, A. J. (1986) Investigation into the use of deuterium as a tracer for measuring transpiration from eucalypts. *Journal of Hydrology (Amsterdam)* 84, 345-351.
- Calder, I. R.; Kariyappa, G. S.; Srinivasalu, N. V.; Murthy, K. V. S. (1991) Deuterium tracing for the estimation of transpiration from trees. Part 1. Field calibration. *Journal of Hydrology (Amsterdam)* 130, 17-25.
- Calder, I. R.; Swaminath, M. H.; Kariyappa, G. S.; Srinivasalu, N. V.; Murthy, K. V. S.; Mumtaz, J. (1992) Deuterium tracing for the estimation of transpiration from trees. Part 3. Measurements of transpiration from *Eucalyptus* plantation, India. *Journal of Hydrology (Amsterdam)* 130, 37-48.
- Cameron, G. N.; Spencer, S. R. (1989) Rapid leaf decay and nutrient release in a chinese tallow forest. *Oecologia* 80, 222-228.
- Campbell, C. D. (1989) The importance of root interactions for grass and trees in a silvopastoral system. *Aspects of Applied Biology* 22, 255-261.
- Campbell, C. D.; Dawson, L. A. M. (1991) Below-ground competition between trees and grass in a silvopastoral system. *Agroforestry in the UK* 2, 39-43.
- Carlisle, A.; Brown, A. H. F.; White, E. J. (1967) The nutrient content of tree stem flow and ground flora litter and leachates in a sessile oak (*Quercus petraea*) woodland. *Journal of Ecology (Oxford)* 55, 615-627.
- Casal, J. J.; Smith, H. (1988) Persistent effects of changes in phytochrome status on internode growth in light-grown mustard: occurrence, kinetics and locus of perception. *Planta* 175, 214-220.
- Charles-Edwards, D. A.; Thornley, J. H. M. (1973) Light interception by an isolated plant, a simple model. *Annals of Botany* 37, 919-928.
- Charles-Edwards, D. A.; Thorpe, M. R. (1976) Interception of diffuse and direct-beam radiation by a hedgerow apple orchard. *Annals of Botany* 40, 603-613.
- Clatworthy, J. N. (1960) Studies on the nature of competition between closely related species. D.Phil. Thesis, University of Oxford, UK.
- Clements, F. E. (1928) Plant succession and indicators. New York, USA; H. W. Wilson Co.
- Colwell, R. K.; Fuentes, E. R. (1975) Experimental studies on the niche. *Annual Review of Ecology and Systematics* 6, 281-310.
- Conway, G. R. (1987) The properties of agroecosystems. *Agricultural Systems* 24, 95-117.
- Corlett, J. E.; Ong, C. K.; Black, C. R. (1989) Microclimate modification in intercropping and alley-cropping. In *Meteorology and agroforestry. Proceedings of an international workshop on the application of meteorology to agroforestry systems planning and management, Nairobi 9-13 February 1987* [edited by Reifsnyder, W. S.; Darnhofer, T.O.]. Nairobi, Kenya; ICRAF. 419-430.
- Corlett, J. E.; Ong, C. K.; Black, C. R.; Monteith, J. L. (1992a) Above- and below-ground interactions in a leucaena/millet alley cropping system. I. Experimental design, instrumentation and diurnal trends. *Agricultural and Forest Meteorology* 60, 53-72.
- Corlett, J. E.; Black, C. R.; Ong, C. K.; Monteith, J. L. (1992b) Above- and below-ground interactions in a leucaena/millet alley cropping system. II. Light interception and dry matter production. *Agricultural and Forest Meteorology* 60, 73-91.
- Crawley, M. J. (1986) Plant ecology. Oxford, UK; Blackwell Scientific Publications.
- Cuevas, E.; Medina, E. (1986) Nutrient dynamics in Amazonian forest ecosystems. I: Nutrient flux in fine litter fall and efficiency of nutrient utilisation. *Oecologia* 68, 466-472.
- Davis, J. E.; Norman, J. M. (1988) Effects of shelter on plant water use. *Agriculture, Ecosystems & Environment* 22-23, 393-402.
- Dhileepan, K. (1991) Insect pests of intercrops and their potential to infest oil palm in an oil palm based agroforestry system in India. *Tropical Pest Management* 37, 57-58.
- Dixon, D. (1992) Can agroforestry meet Indias needs? Farming World, BBC World Service broadcast.
- Donald, C. M. (1958) The interaction of competition for light and for nutrients. *Australian Journal of Agricultural Research* 9, 421-435.
- Dudman, W. F. (1977) Serological methods and their application to dinitrogen-fixing organisms. In *A treatise on dinitrogen fixation. Section IV: agronomy and ecology* [edited by Hardy, R.; Gibson, A.]. New York, USA; John Wiley. p.487.
- Dunham, K. M. (1989) Litterfall, nutrient fall and production in an *Acacia albida* woodland in Zimbabwe. *Journal of Tropical Ecology* 5, 227-238.

- Eaglesham, A. R. J.; Anyanaba, A.; Rao, V. R.; Eskew, D. L. (1981) Improving the nitrogen nutrition of maize by intercropping with cowpea. *Soil Biology & Biochemistry* 13, 169-171.
- Eason, W. R. (1988) Effect of tree litter on sward botanical composition and growth. In *Proceedings of a Research Meeting held at the Welsh Agricultural College, Aberystwyth, 13-15 September 1988*. Hurley, UK; British Grassland Society.
- Eason, W. R. (1991) The effect of tree leaf litter on sward botanical composition and growth. In *Agroforestry: principles and practices. Proceedings of an international conference 23-28 July 1989 at the University of Edinburgh, UK* [edited by Jarvis, P. G.]. Amsterdam, Netherlands; Elsevier. 165-172. Also *Forestry Ecology and Management* 45, 165-172.
- Eason, W. R.; Newman, E. I.; Chuba, P. N. (1991) Specificity of interplant cycling of phosphorus: the role of mycorrhizas. *Plant and Soil* 137, 267-274.
- Eastham, J.; Rose, C. W. (1988) Pasture evaporation under varying tree planting density in an agroforestry experiment. *Agricultural Water Management* 15, 87-105.
- Eastham, J.; Rose, C. W.; Charles-Edwards, D. A.; Cameron, D. M.; Rance, S. J. (1990) Planting density effects on water use efficiency of trees and pasture in an agroforestry experiment. *New Zealand Journal of Forestry Science* 20, 39-53.
- Eimern J. van; Karschon, R.; Razumova, L. A.; Robertson, G. W. (1964) Windbreaks and shelterbelts. *WMO Technical Note* No. 59.
- Epila, J. S. O. (1988) Wind, crop pests and agroforest design. *Agricultural Systems* 26, 99-110.
- Ewel, J.; Benedict, F.; Berish, C.; Brown, B.; Gliessman, S.; Amador, M.; Bermudez, R.; Martinez, A.; Miranda, R.; Price, R. (1982) Leaf area, light transmission, roots and leaf damage in nine tropical plant communities. *Agro-Ecosystems* 7, 305-326.
- Fahey, T. J.; Hughes, J. W.; Pu, M.; Arthur, M. A. (1988) Root decomposition and nutrient flux following whole-tree harvesting of northern hardwood forest. *Forest Science* 34, 744-768.
- Faris, M. A.; Araujo, M. R. A. de; Lira, M. de A.; Arcovere, A. S. S. (1983) Yield stability in intercropping studies of sorghum or maize with cowpea or common beans under different fertility levels in northeastern Brazil. *Canadian Journal of Plant Science* 63, 789-799.
- Fassbender, H. W.; Alpizar, L. (1987) Criteria for the evaluation of organic matter and nutrient cycling in agroforestry systems. In *Advances in agroforestry research. Proceedings of a seminar held in CATIE, Turrialba, Costa Rica from September 1-11th, 1985, and sponsored by CATIE and GTZ* [edited by Beer, J. W.; Fassbender, H. W.; Heuvelodp, J.]. *Serie Técnica: Informe Técnico - Centro Agronómico Tropical de Investigación y Enseñanza* No. 117. 91-103.
- Fassbender, H. W.; Beer, J.; Heuvelodp, J.; Imbach, A.; Enríquez, G.; Bonnemann, A. (1991) Ten year balances of organic matter and nutrients in agroforestry systems at CATIE, Costa Rica. In *Agroforestry: principles and practice. Proceedings of an international conference 23-28 July 1989 at the University of Edinburgh, UK* [edited by Jarvis, P. G.]. Amsterdam, Netherlands; Elsevier. 173-183. Also *Forest Ecology and Management* 45, 173-183.
- Finlay, R. D.; Read, D. J. (1986) The structure and function of the vegetative mycelium of ectomycorrhizal plants. I. Translocation of ¹⁴C-labelled carbon between plants interconnected by a common mycelium. *New Phytologist* 103, 143-156.
- Fitter, A. H. (1986) Acquisition and utilisation of resources. In *Plant ecology* [edited by Crawley, M. J.]. Oxford, UK; Blackwell Scientific Publications. 375-405.
- Ford, E. D.; Deans, J. D. (1977) Growth of a Sitka spruce plantation: spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine roots. *Plant and Soil* 47, 463-486.
- Ford, E. D.; Deans, J. D. (1978) The effects of canopy structure on stemflow, throughfall and interception loss in a young Sitka spruce plantation. *Journal of Applied Ecology* 15, 905-917.
- Franco, M.; Harper, J. L. (1988) Competition and the formation of spatial pattern in spacing gradients: an example using *Kochia scoparia*. *Journal of Ecology (Oxford)* 76, 959-974.
- Gash, J. H. C.; Morton, A. J. (1978) An application of the Rutter model to the estimation of the interception loss from Thetford Forest. *Journal of Hydrology (Amsterdam)* 38, 49-58.
- Gherini, S.; Munson, R.; Altwicker, E.; April, R.; Chen, C.; Clesceri, N.; Cronan, C.; Driscoll, C.; Johannes, A.; Newton, R.; Peters, N.; Schofield, C. (1989) Regional Integrated Lake-Watershed Acidification Study (RILWAS): summary of major findings. *EPRI Report - Electric Power Research Institute, Palo Alto, California* No. EN-6641.
- Gill, M.; Wood, C. D. (1992) Animal production in developing countries. *Proceedings - British Society of Animal Production* No. 16.
- Giller, K. E.; Ormesher, J.; Awah, F. M. (1991) Nitrogen transfer from *Phaseolus* bean to intercropped maize measured using ¹⁵N-enrichment and ¹⁵N-isotope dilution methods. *Soil Biology and Biochemistry* 23, 339-346.
- Giller, K. E.; Wilson, K. J. (1991) Nitrogen fixation in tropical cropping systems. Wallingford, UK; CAB International.
- Gillespie, A. R. (1989) Modelling nutrient flux and interspecies root competition in agroforestry interplantings. *Agroforestry Systems* 8, 257-265.
- Glover, N. L.; Beer, J. W. (1984) Spatial and temporal fluctuations of litterfall in the agroforestry associations *Coffea arabica/Erythrina poeppigiana* and *C. arabica/E. poeppigiana/Cordia alliodora*. In *CATIE UN University Agroforestry Project*. Turrialba, Costa Rica; CATIE.
- Goh, K. M. (1980) Dynamics and stability of organic matter. In *Soils with variable charge* [edited by Theng, B. K. B.]. *New Zealand Society of Soil Science Proceedings*.
- Goldberg, D. E.; Werner, P. A. (1983) Equivalence of competitors in plant communities: a null hypothesis and a field experiment approach. *American Journal of Botany* 70, 1098-1104.
- Goto, M.; Simada, E.; Sugawara, K. (1986) The relation between palatability and chemical composition of herbage cultivated in the shading condition. *Bulletin of the Faculty of Agriculture, Mie University* No. 72, 81-85.
- Grace, J. (1977) Plant responses to wind. London, UK; Academic Press.
- Grace, J. (1983a) Plant-atmosphere relationships. In *Outline studies in ecology* [edited by Dunnett, G. M.; Gimingham, C. H.]. London, UK; Chapman and Hall. 92 pp.
- Grace, J. (1983b) Plant-animal relationships. London, UK; Chapman and Hall.
- Greb, B. W.; Black, A. L. (1961) Effects of windbreak plantings on adjacent crops. *Journal of Soil & Water Conservation* 16, 223-227.
- Green, S. R.; Hutchings, N. J.; Grace, J.; Greated, C. (1991) Shelter effects in agroforestry. *Agroforestry in the UK* 2, 14-17.
- Grewal, S. S.; Abrol, I. P. (1986) Agroforestry on alkali soils: effects of some management practices on initial growth, biomass accumulation and chemical composition of selected tree species. *Agroforestry Systems* 4, 221-232.
- Grime, J. P. (1979) Plant strategies and vegetation processes. London, UK; John Wiley.

- Grime, J. P.; Hodgson, J. G.; Hunt, R. (1988) Comparative plant ecology: a functional approach to common British species. London, UK; Unwin Hyman Ltd. ix + 742 pp.
- Gurbachan Singh; Abrol, I. P.; Cheema, S. S. (1988) Forage production and nutrient cycling through Karnal (*Diplachne fusca*) grass planted with mesquite (*Prosopis juliflora*) in a highly sodic soil. In *Rangelands resource and management. Proceedings of the National Rangeland Symposium, IGFR, Jhansi, November 9-12, 1987* [edited by Panjab Singh; Patnak, P. S.]. 322-332.
- Hairiah, K.; Noordwijk, M. van (1986) Root studies on a tropical ultisol in relation to nitrogen management. Report of field work at IITAs high rainfall substation at Onne (Port Harcourt, Nigeria) in 1985. *Rapport - Instituut voor Bodemvruchtbaarheid, Netherlands* No. 7. 121 pp.
- Hairiah, K.; Noordwijk, M. van (1989) Root distribution of leguminous cover crops in the humid tropics and effects on a subsequent maize crop. In *Nutrient management for food crop production in tropical farming systems* [edited by Heide, J. van der]. Haren, Netherlands; Institute for Soil Fertility. 157-169.
- Hamilton, W. A. (1988) Microbial energetics and metabolism. In *Micro-organisms in action: concepts and applications in microbial ecology* [edited by Lynch, J. M.; Hobbie, J. E.]. Oxford, UK; Blackwell Scientific Publications. 75-100.
- Harding, R. J.; Rosier, P. T. W. (1989) Water use of fast growing tree species. *Journal of Applied Hydrology* 2, 9-25.
- Hardy, R. W. F. (1975) Fertiliser research with emphasis on nitrogen fixation. In *Proceedings of 24th Annual Meeting of Agriculture Research Institute*. Washington, DC, USA; National Academy of Sciences.
- Harley, J. L.; Smith, S. E. (1983) Mycorrhizal symbioses. London, UK; Academic Press.
- Harper, J. L. (1961) Approaches to the study of plant competition. In *Mechanisms in biological competition* [edited by Milthorpe, F. L.]. *Symposia of the Society of Experimental Biology* 15, 1-39.
- Harper, J. L. (1967) A Darwinian approach to plant ecology. *Journal of Ecology (Oxford)* 55, 247-270.
- Harper, J. L. (1977) Population biology of plants. London, UK; Academic Press.
- Harrison, A. F.; Ineson, P.; Heal, O. W. (1990) Nutrient cycling in terrestrial ecosystems: field methods, application and interpretation. Barking, UK; Elsevier Applied Science Publishers Ltd. xvii + 454 pp.
- Hawke, M. F. (1991) Pasture production and animal performance under pine agroforestry in New Zealand. *Forest Ecology and Management* 45, 109-118.
- Heichel, G. H.; Barnes, D. R. (1984) Opportunities for meeting crop nitrogen needs from symbiotic nitrogen fixation. In *Organic farming: current technology and its role in a sustainable agriculture* [edited by Bezdicsek, D. F.; Powers, J. F.; Keeney, D. R.; Wright, M. J.]. Madison, Wisconsin, USA; American Society of Agronomy. *ASA Special Publication* No. 46, 49-59.
- Henzell, E. F.; Vallis, I. (1977) Transfer of nitrogen between legumes and other crops. In *Biological nitrogen fixation in farming systems in the tropics* [edited by Ayanaba, A.; Dart, P. J.]. New York, USA; John Wiley. p.73.
- Herrera, R.; Jordan, C. F.; Klinge, H.; Medina, E. (1978) Amazon ecosystems: their structure and functioning with particular emphasis on nutrients. *Interciencia* 3, 223-232.
- Holt, R. D. (1977) Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* 11, 197-229.
- Huxley, P. A. (1967) The effects of artificial shading on some growth characteristics of arabica and robusta coffee seedlings: 1. The effects of shading on dry weight, leaf area and derived growth data. *Journal of Applied Ecology* 4, 291-308.
- Huxley, P. A.; Maingu, Z. (1978) Use of a systematic design as an aid to the study of intercropping: some general considerations. *Experimental Agriculture* 14, 49-56.
- Ingestad, T. (1987) New concepts on soil fertility and plant nutrition as illustrated by research on forest trees and stands. *Geoderma* 40, 237-252.
- Jackson, J. E.; Palmer, J. W. (1979) A simple model of light transmission and interception by discontinuous canopies. *Annals of Botany* 44, 381-383.
- Jackson, J. E.; Middleton, S. G. (1988) Modelling of orchards for maximum productivity and fruit quality. [Progettazione del frutteto per la massima produttività e qualità]. In *Coltura del melo verso gli anni '90. Conference, Cordenons, Italy, 18-20 December 1986* [coordinated by Youssef, J.]. Florence, Italy; Società Orticola Italiana. 309-320.
- Jarvis, P. G. (1989) Atmospheric carbon dioxide and forests. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 324, 369-392.
- Jarvis, P. G.; Sinclair, F. L. (1990) Priorities in farm forestry research. In *Marginal agricultural land and efficient afforestation. Proceedings of a workshop in the CEC land and water use research programme, held in Gembloux (Belgium), 20 and 21 October 1988* [edited by Bock, L.; Rondeux, J.]. Luxembourg; Office for Official Publications of the European Communities. No. EUR 10841
- Jenny, H. (1980) Soil genesis with ecological perspectives. *Ecological Studies* 37. New York, USA; Springer-Verlag.
- Jimenez Otarola, F. (1989) Water balance with an emphasis on infiltration in two agroforestry systems in Turrialba, Costa Rica: coffee/poro and coffee/laurel. Thesis, Universidad de Costa Rica/Centro Agronómico Tropical de Investigación y Enseñanza. xvii + 104 pp.
- Jonsson, K.; Fijdeland, L.; Maghembe, J. A.; Högberg, P. (1988) The vertical distribution of fine roots of five tree species and maize in Morogoro, Tanzania. *Agroforestry Systems* 6, 63-69.
- Jordan, C. F. (1985) Nutrient cycling in tropical forest ecosystems. Chichester, UK; John Wiley & Sons. 190 pp.
- Kang, B. T.; Wilson, G. F.; Sipkens, L. (1981) Alley cropping maize (*Zea mays* L.) and leucaena (*Leucaena leucocephala* Lam.) in southern Nigeria. *Plant and Soil* 63, 165-179.
- Kang, B. T.; Grimme, H.; Lawson, T. L. (1985) Alley cropping sequentially cropped maize and cowpea with leucaena on a sandy soil in southern Nigeria. *Plant and Soil* 85, 267-277.
- Karim, A. B.; Savill, P. S.; Rhodes, E. R. (1991) The effect of young *Leucaena leucocephala* (Lam.) de Wit hedges on the growth and yield of maize, sweet potato and cowpea in an agroforestry system in Sierra Leone. *Agroforestry Systems* 16, 203-211.
- Kass, D. C. (1978) Polyculture cropping systems: review and analysis. *Cornell Institute Agricultural Bulletin* No. 32, 69 pp.
- Kass, D. L.; Jimenez H., M. (1986) Effects of applying prunings of *Gliricidia sepium* to maize and beans on an oxic dystropept in San Carlos, Costa Rica. *Nitrogen Fixing Tree Research Reports* 4, 11-12.
- Kessel, C. van; Roskoski, J. P. (1988) Row spacing effects on N₂-fixation, N-yield and soil N uptake of intercropped cowpea and maize. *Plant and Soil* 111, 17-23.
- Kira, T.; Kumura, A. (1983) Dry matter production and efficiency in various types of plant canopies. In *Plant research and agroforestry* [edited by Huxley, P. A.]. Nairobi, Kenya; ICRAF. 347-363.
- Kort, J. (1988) Benefits of windbreaks to field and forage crops. *Agriculture, Ecosystems & Environment* 22-23, 165-190.

- Kronenberg, G. H. M.; Kendrick, R. E. (1986) The physiology of action. In *Photomorphogenesis in plants* [edited by Kendrick, R. E.; Kronenberg, G. H. M.]. Dordrecht, Netherlands; Martinus Nijhoff. 99-114.
- Kummerow, J. (1981) Carbon allocation to root systems in Mediterranean evergreen sclerophylls. In *Tasks for vegetation science, Volume 4. Components of productivity of Mediterranean-climate regions: basic and applied aspects* [edited by Margariš, N. S.; Mooney, N. S.]. The Hague, Netherlands; Dr. W. Junk Publishers. 115-120.
- Lal, R. (1987) Earthworms; Termites; Ants. In *Tropical ecology and physical edaphology*. Chichester, UK; John Wiley. 285-336; 340-422; 423-441.
- Lal, R. (1988) Effects of macrofauna on soil properties in tropical ecosystems. *Agriculture, Ecosystems & Environment* 24, 101-116.
- Lal, R. (1989) Agroforestry systems and soil surface management of a tropical alfisol. *Agroforestry Systems* 8, 1-6.
- Lal, R.; Wilson, G. F.; Okigbo, B. N. (1978) No-till farming after various grasses and leguminous cover crops in a tropical Alfisol. I. Crop performance. *Field Crops Research* 1, 71-84.
- Lang, A. R. G.; Xiang Y. Q. (1986) Estimation of leaf area index from transmission of direct sunlight in discontinuous canopies. *Agricultural and Forest Meteorology* 37, 229-243.
- Lang, A. R. G.; Xiang Y. Q.; Norman, J. M. (1985) Crop structure and the penetration of direct sunlight. *Agricultural and Forest Meteorology* 35, 83-101.
- Lang, A. R. G.; McMurtrie, R. (1991) Total leaf areas of single trees of *Eucalyptus grandis* estimated from transmittances of the sun's beam in discontinuous canopies. *Agricultural and Forest Meteorology* 58, 79-92.
- Lawton, J. H. (1989) Food webs. In *Ecological concepts: the contribution of ecology to an understanding of the natural world* [edited by Cherrett, J. M.]. Oxford, UK; Blackwell Scientific Publications. 43-78.
- Lea, D. A. M. (1975) Human sustenance and the tropical forest. In *Ecological effect of increasing human activities on tropical and subtropical forest ecosystems*. Canberra, Australia; Australian UNESCO/MAB Committee. 141-151.
- Leakey, R. R. B. (1987) Clonal forestry in the tropics — a review of developments, strategies and opportunities. *Commonwealth Forestry Review* 66, 61-75.
- Leakey, R. R. B.; Last, F. T. (1980) Biology and potential of *Prosopis* species in arid environments, with particular reference to *P. cineraria*. *Journal of Arid Environments* 3, 9-24.
- Leakey, R. R. B.; Ladipo, D. O. (1987) Selection for improvement in vegetatively-propagated tropical hardwoods. In *Improvement of vegetatively propagated plants*. London, UK; Academic Press. 324-336.
- Lee, D. W. (1989) Canopy dynamics and light climates in a tropical moist deciduous forest in India. *Journal of Tropical Ecology* 5, 65-79.
- Legg, J. O.; Meisinger, J. J. (1982) Soil N budgets. In *Nitrogen in agricultural soils* [edited by Stevenson, F. J.]. Madison, Wisconsin, USA; American Society of Agronomy. p.503.
- Levine, S. H. (1976) Competitive interactions in ecosystems. *American Naturalist* 110, 903-910.
- Leibman, M. Z. (1986) Ecological suppression of weeds in intercropping systems: experiments with barley, pea, and mustard. Ph.D. Thesis, University of California, Berkeley, USA.
- Liu, S.; Munson, R.; Johnson, D. W.; Gherini, S.; Summers, K.; Hudson, R.; Wilkinson, K.; Pitelka, L. F. (1992) The nutrient cycling model (NuCM): overview and application. In *Atmospheric deposition and forest nutrient cycling* [edited by Johnson, D. J.; Lindberg, S. E.]. New York, USA; Springer-Verlag. 583-609.
- Lundgren, B. O. (1987) Institutional aspects of agroforestry research and development. In *Agroforestry: a decade of development* [edited by Steppeler, H. A.; Nair, P. K. R.]. Nairobi, Kenya; ICRAF. 43-51.
- MacArthur, R. H. (1972) Geographical ecology. New York, USA; Harper & Row.
- MacArthur, R. H.; Levins, R. (1964) Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the United States of America* 51, 1207-1210.
- McMurtrie, R.; Wolf, L. (1983) A model of competition between trees and grass for radiation, water and nutrients. *Annals of Botany* 52, 449-458.
- Mainguet, M. (1991) Desertification: natural background and human mismanagement. Berlin, Germany; Springer-Verlag. xvi + 306 pp.
- Mann, J. E.; Curry, G. L.; Sharpe, P. H. (1979) Light interception by isolated plants. *Agricultural Meteorology* 20, 205-214.
- Mann, J. E.; Curry, G. L.; Michele, D. W. de; Baker, D. N. (1980). Light penetration in a row-crop with random plant spacing. *Agronomy Journal* 72, 131-142.
- Marshall, B.; Willey, R. W. (1983) Radiation interception and growth in an intercrop of pearl millet/groundnut. *Field Crops Research* 7, 141-160.
- Marshall, K. C. (1964) Survival of root-nodule bacteria in dry soils exposed to high temperatures. *Australian Journal of Agricultural Research* 15, 273-281.
- Mason, S. C.; Leihner, D. E.; Vorst, J. J. (1986) Cassava-cowpea and cassava-peanut intercropping. III. Nutrient concentrations and removal. *Agronomy Journal* 78, 441-444.
- Mathai, C. K.; Chandy, K. C. (1988) Yield response of black pepper varieties to varying growth light regimes. *Indian Cocoa, Arecanut and Spices Journal* 11, 85-88.
- Maxwell, T. J. (1990) Plant-animal interactions in northern temperate sown grasslands and semi-natural vegetation. In *Systems theory applied to agriculture and the food chain* [edited by Jones, G. W.; Street, P. R.]. Amsterdam, Netherlands; Elsevier Applied Science Publishers. 23-60.
- May, R. M. (1974) Stability and complexity in model ecosystems. Princeton, New Jersey, USA; Princeton University Press.
- May, R. M. (1976) Models for two interacting populations. In *Theoretical ecology: principles and applications* [edited by May, R. M.]. Oxford, UK; Blackwell Scientific Publications. 78-104.
- Mead, R. (1979) Competition experiments. *Biometrics* 35, 41-54.
- Mead, R.; Willey, R. W. (1980) The concept of a 'Land Equivalent Ratio' and advantages in yields from intercropping. *Experimental Agriculture* 16, 217-228.
- Minchin, F. R.; Pate, J. S. (1974) Diurnal functioning of the legume root nodule. *Journal of Experimental Botany* 14, 483-495.
- Monteith, J. L. (1981) Does light limit crop production? In *Physiological processes limiting plant productivity* [edited by Johnson, C. B.]. London, UK; Butterworths. 23-28.
- Monteith, J. L. (1990) Conservative behaviour in the response of crops to water and light. In *Theoretical production ecology: reflections and prospects* [edited by Rabbinge, R.]. Wageningen, Netherlands; PUDOC. *Simulation Monographs* 34, 3-14.
- Monteith, J. L.; Ong, C. K.; Corlett, J. E. (1991) Microclimatic interactions in agroforestry systems. In *Agroforestry: principles and practices. Proceedings of an international conference 23-28 July 1989 at the University of Edinburgh, UK* [edited by Jarvis, P. G.]. Amsterdam, Netherlands; Elsevier. 31-44. Also *Forestry Ecology and Management* 45, 31-44.

- Morgan, D. C.; Smith, H. (1981) Non-photosynthetic responses to light quality. In *Encyclopedia of plant physiology, Volume 12a: Physiological plant ecology I. responses to the physical environment* [edited by Lange, O. L.; Nobel, P. S.; Osmond, C. B.; Zeigler, H.]. Berlin, Germany; Springer-Verlag. 109-134.
- Morris, D. R. (1986) Studies on competition for N between arrowleaf clover and Gulf ryegrass by using ^{15}N depleted ammonium nitrate. *Dissertation Abstracts International. B, Sciences and Engineering* 46, 3275B.
- Mozheiko, G. A.; Semyakin, V. A. (1984) Effect of protective shelterbelts and type of soil cultivation on the yield of agricultural crops in southern Ukraine. *Lesovodstvo i Agrolesomeliatsiya* No. 69, 23-28.
- Murray, D. B.; Nichols, R. (1966) Light, shade and growth in some tropical plants. In *Light as an ecological factor* [edited by Bainbridge et al.]. Oxford, UK; Blackwell Scientific Publications. 249-263.
- Nair, P. K. R. (1991) State-of-the-art of agroforestry systems. In *Agroforestry: principles and practices. Proceedings of an international conference 23-28 July 1989 at the University of Edinburgh, UK* [edited by Jarvis, P. G.]. Amsterdam, Netherlands; Elsevier. 5-29. Also *Forest Ecology and Management* 45, 5-29.
- Natarajan M.; Willey, R. W. (1980) Sorghum-pigeonpea intercropping and the effects of plant population density. *Journal of Agricultural Science, UK* 95, 59-65.
- Neelam Saharan; Singh, R. P. (1988) Influence of earthworm activity on soil fertility in agroforestry systems. *Annals of Arid Zone* 27, 81-85.
- Nelder, J. A. (1962) New kinds of systematic spacing designs for spacing experiments. *Biometrics* 18, 283-307.
- Newman, E. I. (1988) Mycorrhizal links between plants: their functioning and ecological significance. *Advances in Ecological Research* 18, 243-270.
- Newson, M. D.; Calder, I. R. (1989) Forests and water resources: problems of prediction on a regional scale. *Philosophical Transactions at the Royal Society of London. Series B, Biological Sciences* 324, 283-298.
- Noordwijk, M. van (1989) Rooting depth in cropping systems in the humid tropics in relation to nutrient use efficiency. In *Nutrient management for food crop production in tropical farming systems* [edited by Heide, J. van der]. Haren, Netherlands; Institute for Soil Fertility. 129-144.
- Norman, J. M.; Jarvis, P. G. (1975) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). IV. Radiation penetration theory and a test case. *Journal of Applied Ecology* 12, 839-878.
- Nye, P. H. (1955) Some soil-forming processes in the humid tropics. IV. The actions of soil fauna. *Journal of Soil Science* 6, 73-83.
- Odum, E. P. (1971) Fundamentals of ecology (3rd edition). Philadelphia, USA; W. B. Saunders.
- Ofori, F.; Pate, J. S.; Stern, W. R. (1987) Evaluation of N_2 -fixation and nitrogen economy of a maize/cowpea intercrop system using ^{15}N dilution methods. *Plant and Soil* 102, 149-160.
- Okeke, A. J.; Omaliko, C. P. E. (1991) Nutrient accretion to the soil via litterfall and throughfall in *Acioa barteri* stands at Ozala, Nigeria. *Agroforestry Systems* 16, 223-229.
- Ong, C. K.; Monteith, J. L. (1985) Response of pearl millet to light and temperature. *Field Crops Research* 11, 141-160.
- Ong, C. K.; Corlett, J. E.; Singh, R. P.; Black, C. R. (1991a) Above and below ground interactions in agroforestry systems. In *Agroforestry: principles and practices. Proceedings of an international conference 23-28 July 1989 at the University of Edinburgh, UK* [edited by Jarvis, P. G.]. Amsterdam, Netherlands; Elsevier. 45-57. Also *Forest Ecology and Management* 45, 45-57.
- Ong, C. K.; Odongo, J. C. W.; Marshall, F.; Black, C. R. (1991b) Water use by trees and crops: five hypotheses. *Agroforestry Today* 3, 7-10.
- Ong, C. K.; Subrahmanyam, P.; Khan, A. A. H. (1991c) The microclimate and productivity of a groundnut/millet intercrop during the rainy season. *Agricultural and Forest Meteorology* 56, 49-66.
- Ong, C. K.; Black, C. R. (in press) Complementarity in resource use in intercropping and agroforestry systems.
- Park, T. (1962) Beetles, competition and populations. *Science (Washington)* 138, 1369-1375.
- Passioura, J. B. (1982) The role of root system characteristics in the drought resistance of crop plants. In *Symposium on drought resistance in crops with emphasis on rice*. Manila, Philippines; International Rice Research Institute. 71-82
- Paul, E. A. (1984) Dynamics of organic matter in soil. *Plant and Soil* 76, 275-285.
- Penman, H. C. (1948) Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society of London. Series A* 193, 120-146.
- Perrin, R. M. (1977) Pest management in multiple cropping systems. *Agro-Ecosystems* 3, 93-118.
- Pierce, N. E. (1989) Butterfly-ant mutualisms. In *Towards a more exact ecology* [edited by Grubb, P. J.; Whittaker, J. B.]. Oxford, UK; Blackwell Scientific Publications. 299-324.
- Post, W. M.; Pastor, J.; Zinke, P. J.; Stangenberger, A. G. (1985) Global patterns of soil nitrogen store. *Nature (London)* 317, 613-616.
- Proctor, J. (1987) Nutrient cycling in primary and old secondary rain forests. *Applied Geography* 7, 135-152.
- Pugashetti, B. K.; Angle, J. S.; Wagner, G. H. (1982) Soil microorganisms antagonistic towards *Rhizobium japonicum*. *Soil Biology & Biochemistry* 14, 45-49.
- Rao, M. R.; Willey, R. W. (1980) Evaluation of yield stability in intercropping: studies on sorghum/pigeonpea. *Experimental Agriculture* 16, 105-116.
- Rao, N. G. P.; Rana, B. S.; Tarhalker, P. P. (1981) Stability, productivity, and profitability of some intercropping systems in dryland agriculture. In *Proceedings of the international workshop on intercropping* [edited by Willey, R. W.]. Hyderabad, India; ICRISAT. 292-298.
- Rao, M. R.; Sharma, M. M.; Ong, C. K. (1990) A study of the potential of hedgerow intercropping in semiarid India using a two-way systematic design. *Agroforestry Systems* 11, 243-258.
- Rice, W. A.; Penney, D. C.; Nyborg, M. (1977) Effects of soil acidity on rhizobia numbers, nodulation and nitrogen fixation by alfalfa and red clover. *Canadian Journal of Soil Science* 57, 197-203.
- Risch, S. J.; Andow, D.; Altieri, M. A. (1983) Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. *Environmental Entomology* 12, 625-629.
- Ritz, K.; Newman, E. I. (1985) Evidence for rapid cycling of phosphorus from dying roots to living plants. *Oikos* 45, 174-180.
- Root, R. (1973) Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43, 95-124.
- Rout, S. K.; Gupta, S. R. (1987) Effect of chemical composition on leaf litter decomposition in forest soil. *Proceedings of the Indian Academy of Sciences, Plant Sciences* 97, 399-400.

- Russell, G.; Marshall, B.; Jarvis, P. G. (Editors) (1989) Plant canopies: their growth, form and function. Cambridge, UK; Cambridge University Press. *Society for Experimental Biology Series No. 31*, ix + 178 pp.
- Russo, R. O.; Budowski, G. (1986) Effect of pollarding frequency on biomass of *Erythrina poeppigiana* as a coffee shade tree. *Agroforestry Systems* 4, 145-162.
- Rutter, A. J.; Kershaw, K. A.; Robins, P. C.; Morton, A. J. (1971) A predictive model of rainfall interception in forests. I. Derivation of the model from observations in a plantation of Corsican pine. *Agricultural Meteorology* 9, 367-383.
- Rutter, A. J.; Morton, A. J.; Robins, P. C. (1975) A predictive model of interception loss in forests: II. Generalization of the model and comparison with observations in some coniferous and hardwood stands. *Journal of Applied Ecology* 12, 367-380.
- Rutter, A. J.; Morton, A. J. (1977) A predictive model of rainfall interception in forests: III. Sensitivity of the model to stand parameters and meteorological variables. *Journal of Applied Ecology* 14, 567-588.
- Sanchez, P. A. (1976) Properties and management of soils in the tropics. New York, USA; John Wiley.
- Sanchez, P. A. (1987) Soil productivity and sustainability in agroforestry systems. In *Agroforestry: a decade of development* [edited by Stepler, H. A.; Nair, P. K. R.]. Nairobi, Kenya; ICRAF. 205-233.
- Schoener, T. W. (1983) Field experiments on interspecific competition. *American Naturalist* 122, 240-285.
- Schoener, T. W. (1988) Ecological interactions and biogeographic patterns. In *Analytical biogeography: an integrated approach to the study of animal and plant distribution* [edited by Myers, A. A.; Giller, P. S.]. London, UK; Chapman & Hall. 255-297.
- Schultz, B. B. (1984) Ecological aspects of stability in polycultures versus sets of monocultures of annual crops. Ph.D. Thesis, University of Michigan, USA.
- Scott, G. A. J. (1987) Shifting cultivation where land is limited. Case study no.3: Campa Indian agriculture in the Gran Pajonal of Peru. In *Amazonian rain forests. Ecosystem disturbance and recovery. Case studies of ecosystem dynamics under a spectrum of land-use intensities* [edited by Jordan, C. F.]. New York, USA; Springer. 34-35.
- Sharma, S. C.; Pande, P. K. (1989) Patterns of litter nutrient concentration in some plantation ecosystems. *Forest Ecology and Management* 29, 151-163.
- Shparik, Yu. S. (1988) Biomass in the roots and litter in protection forest stands in the upper reaches of the river Dnestr basin. *Lesovodstvo i Agrolessomeliorsiya* No. 77, 26-31.
- Sidhu, D. S.; Hans, A. S. (1988) Preliminary studies on the effect of *Eucalyptus* leaf-litter on accumulation of biomass in wheat. *Journal of Tropical Forestry* 4, 328-333.
- Sinclair, F. L. (1992) Advances in agroforestry: project design, selection and management of components, and system evaluation. British Council short course, 29 March - 10 April 1992.
- Singh, R. P.; Ong, C. K.; Saharan, N. (1989) Above and below ground interactions in alley cropping in semi-arid India. *Agroforestry Systems* 9, 259-274.
- Sivakumar, M. V. K.; Virmani, S. M. (1980) Growth and resource use of maize, pigeonpea and maize/pigeonpea intercrop in an operational research watershed. *Experimental Agriculture* 16, 377-386.
- Snaydon, R. W. (1971) An analysis of competition between plants of *Trifolium repens* L. populations collected from contrasting soils. *Journal of Applied Ecology* 8, 687-697.
- Snaydon, R. W.; Harris, P. M. (1981) Interactions below ground — the use of nutrients and water. In *Proceedings of an international workshop on intercropping*. Hyderabad, India; ICRISAT. 188-201.
- Soria, J. R.; Bazan, J. R.; Pinchinat, A. M.; Paez, G.; Mateo, N.; Moreno, R.; Fargas, J.; Forsythe, W. (1975) Investigación sobre sistemas de producción agrícola para el pequeño agricultor del tropico. *Turrialba* 25, 283-293.
- Sparling, G. P.; Hart, P. B. S.; Hawke, M. F. (1989) Influence of *Pinus radiata* stocking density on organic matter pools and mineralizable nitrogen in an agroforestry system. In *Nitrogen in New Zealand agriculture and horticulture*. Palmerston North, New Zealand; Massey University. 186-195.
- Sprent, J. I. (1979) The biology of nitrogen-fixing organisms. New York, USA; McGraw Hill.
- Srinivasan, V. M.; Subramanian, S.; Rai, R. S. V. (1990) Studies on intercropping with multipurpose trees — resource sharing ability of the trees. In *Advances in casuarina research and utilization. Proceedings of the Second International Casuarina Workshop, Cairo, Egypt, January 15-20, 1990* [edited by El-Lakany, M. H.; Turnbull, J. W.; Brewbaker, J. L.]. Cairo, Egypt; Desert Development Center, American University in Cairo.
- Stirling, C. M.; Williams, J. H.; Black, C. R.; Ong, C. K. (1990) The effect of timing of shade on development, dry matter production and light use efficiency in groundnut (*Arachis hypogaea* L.) under field conditions. *Australian Journal of Agricultural Research* 41, 633-644.
- Swift, M. J. (1977) The roles of fungi and animals in the immobilisation and release of nutrient elements from decomposing branchwood. In *Soil organisms as components of ecosystems* [edited by Lohm, U.; Persson, T.]. *Ecological Bulletin (Sweden)* No. 25. 193-202.
- Swift, M. J.; Sanchez, P. A. (1984) Biological management of tropical soil fertility for sustained productivity. *Nature and Resources* 20, 2-10.
- Szott, L. T.; Fernandes, E. C. M.; Sanchez, P. A. (1991) Soil-plant interactions in agroforestry systems. In *Agroforestry: principles and practices. Proceedings of an international conference 23-28 July 1989 at the University of Edinburgh, UK* [edited by Jarvis, P. G.]. Amsterdam, Netherlands; Elsevier. 127-152. Also *Forest Ecology and Management* 45, 127-152.
- Teklehaimanot, Z.; Jarvis, P. G. (1991a) Modelling of rainfall interception loss in agroforestry systems. *Agroforestry Systems* 14, 65-80.
- Teklehaimanot, Z.; Jarvis, P. G. (1991b) Direct measurement of evaporation of intercepted water from forest canopies. *Journal of Applied Ecology* 28, 603-618.
- Teklehaimanot, Z.; Jarvis, P. G.; Ledger, D. C. (1991) Rainfall interception and boundary layer conductance in relation to tree spacing. *Journal of Hydrology (Amsterdam)* 123, 261-278.
- Tilman, D. (1982) Resource competition and community structure. Princetown, New Jersey, USA; Princeton University Press.
- Tilman, D. (1986) Resources, competition and the dynamics of plant communities. In *Plant ecology* [edited by Crawley, M. J.]. Oxford, UK; Blackwell Scientific Publications. 51-75.
- Tilman, D. (1988) Plant strategies and the dynamics and structure of plant communities. New Jersey, USA; Princeton University Press. 360 pp.
- Toft, C. A. (1986) Communities of species with parasitic lifestyles. In *Community ecology* [edited by Diamond, J.; Case, T. J.]. New York, USA; Harper & Row. 445-463
- Toit, J. J. du; Bryant, J. P.; Frisby, K. (1990) Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. *Ecology, USA* 71, 149-154.
- Tomlinson, H. F.; Eason, W. R. (1990) Sward type affects tree root distribution. *Agroforestry in the UK* 1, 17-18.

- UK, Overseas Development Administration (ODA) (1990) A strategy for research on renewable natural resources. London, UK; Overseas Development Administration.
- Unamma, R. P. A.; Ene, L. S. O. (1984) Weed interference in cassava-maize intercrop in the rain forest of Nigeria. In *Tropical root crops production and uses in Africa* [edited by Terry, E. R.; Doku, E. V.; Arene, O. B.; Mahungu, N. M.]. Ottawa, Canada; IDRC. 59-62.
- Upadhyay, M. S.; Sharma, R. A.; Yadav, S.; Gupta, R. K.; Billore, S. (1990) Studies on population densities of component crops in sorghum/pigeonpea intercropping. *Indian Journal of Agronomy* 35, 60-66.
- VanDenBeldt, R. J.; Brenner, A. J.; Sinclair, F. L. (1990) Tree/crop interactions in agroforestry systems. In *Congress report: Volume B. Proceedings, 19th IUFRO World Congress, Montreal, Canada, 5-11 August 1990*. Montreal, Canada; Canadian IUFRO World Congress Organizing Committee. 292-303.
- Vandermeer, J. (1989) The ecology of intercropping. Cambridge, UK; Cambridge University Press. 237 pp.
- Vincent, J. B. (1970) A manual for the practical study of root-nodule bacteria. Oxford, UK; Blackwell Scientific Publications. *IBP Handbook* No. 15.
- Vitousek, P. M.; Reiners, W. A. (1975) Ecosystem succession and nutrient retention: a hypothesis. *Ecology, USA* 65, 285-298.
- Vitousek, P. M.; Sanford, R. L. Jr. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17, 137-167.
- Wahua, T. A. T.; Miller, D. A. (1978) Effects of intercropping on soybean N₂-fixation and plant composition on associated sorghum and soybeans. *Agronomy Journal* 70, 292-295.
- Walker, D. H.; Sinclair, F. L.; Muetzelfeldt, R. I. (1991) Formal representation and use of indigenous ecological knowledge about agroforestry: pilot phase report. Bangor, UK; University of Wales. 111 pp.
- Wang, Y. P.; Jarvis, P. G. (1990) Description and validation of an array model — MAESTRO. *Agricultural and Forest Meteorology* 51, 257-280.
- Watkinson, A. R. (1986) Plant population dynamics. In *Plant ecology* [edited by Crawley, M. J.]. Oxford, UK; Blackwell Scientific Publications. 137-184.
- Weaver, R. W.; Frederick, L. F. (1974) Effect of inoculum rate on competitive nodulation of *Glycine max* (L.) Merr. II. Field studies. *Agronomy Journal* 66, 233-236.
- Weber, D. F.; Miller, V. L. (1972) Effect of soil temperature on *Rhizobium japonicum* serogroup distribution in soybean nodules. *Agronomy Journal* 64, 796-798.
- Whitmore, T. C. (1990) An introduction to tropical rain forests. Oxford, UK; Clarendon Press. xi + 226 pp.
- Whitney, A. S. (1977) Contribution of forage legumes to the nitrogen economy of mixed swards. A review of the relevant Hawaiian research. In *Biological nitrogen fixation in farming systems in the tropics* [edited by Ayanaba, A.; Dart, P. J.]. New York, USA; John Wiley. p.89
- Wilkinson, G. E. (1975) Effects of grass fallow rotations on the infiltration of water into a savanna zone soil of northern Nigeria. *Tropical Agriculture* 52, 97-103.
- Willey, R. W. (1979) Intercropping — its importance and research needs. Part 1. Competition and yield advantages. *Field Crop Abstracts* 32, 1-10.
- Willey, R. W.; Rao, M. R. (1981) A systematic design to examine effects of plant populations and spatial arrangements in intercropping, illustrated by an experiment on chickpea/safflower. *Experimental Agriculture* 17, 63-73.
- Willey, R. W.; Natarajan, M.; Reddy, M. S.; Rao, M. R. (1986) Cropping systems with groundnut: resource use and productivity. In *Agrometeorology of groundnut. Proceedings of an international symposium, ICRISAT Sahelian Center, 21-26 August 1985*. Patancheru, Andhra Pradesh, India; ICRISAT. 193-205.
- Williamson, M. H. (1972) The analysis of biological populations. London, UK; Arnold.
- Willigen, P. de; Noordwijk, M. van (1987) Roots, plant production and nutrient use efficiency. Ph.D. Thesis, Wageningen Agricultural University, Netherlands.
- Wilson, J. R.; Catchpool, V. R.; Weir, K. L. (1986) Stimulation of growth and nitrogen uptake by shading a rundown green panic pasture in Brigalow clay soil. *Tropical Grasslands* 20, 134-144.
- Wit, C. T. de (1960) On competition. *Verslagen van Landbouwkundige Onderzoekingen* 66, 1-82.
- Wood P. (1989) Planning and the potential of agroforestry. In *Agroforestry. Potential, current UK expertise, and research needs: a guide to ODA strategy. Papers and proceedings of expert seminar for the UK Government's Overseas Development Administration* [compiled by Burley, J.; Wilson, N.]. Oxford, UK; Oxford Forestry Institute, University of Oxford. p.1.
- Young, A. (1989a) Agroforestry for soil conservation. Wallingford, UK; CAB International. *Science and Practice of Agroforestry* No. 4, vii + 276 pp.
- Young, A. (1989b) The environmental basis of agroforestry. In *Meteorology and agroforestry. Proceedings of an international workshop on the application of meteorology to agroforestry systems planning and management, Nairobi 9-13 February 1987* [edited by Reifsnnyder, W. S.; Darnhofer, T. O.]. Nairobi, Kenya; ICRAF. 29-48.
- Zohar, Y.; Brandle, J. R. (1978) Shelter effects on growth and yield of corn in Nebraska. *La-Yaaran* 28, 11-20.