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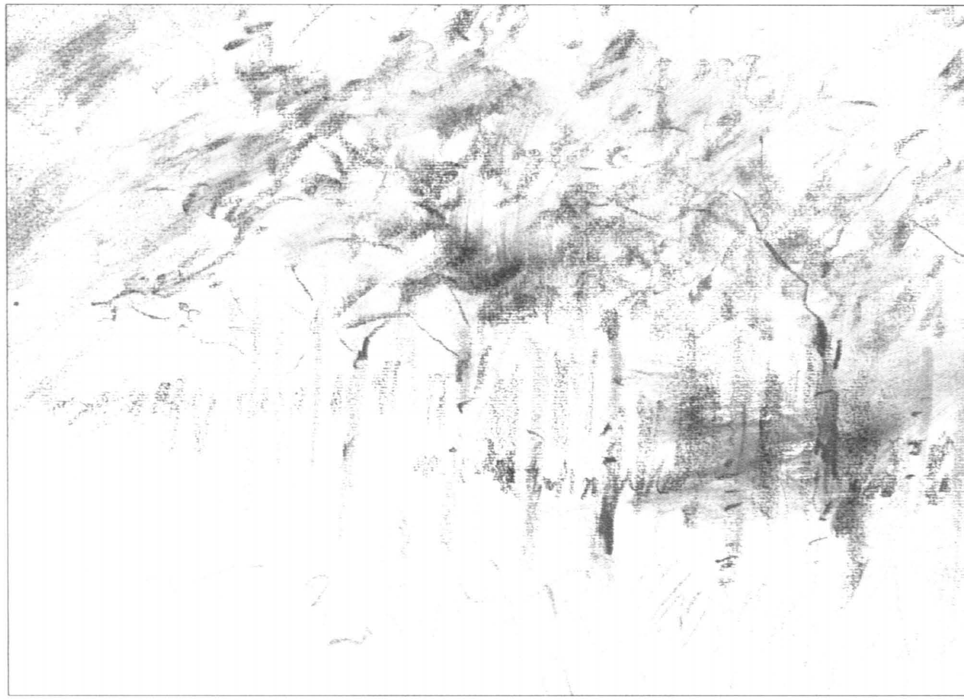

Wending Huang

Productive Coexistence and Gain in Agroforestry Systems

260 · 1998

ACTA FORESTALIA FENNICA

Publishers The Finnish Society of Forest Science
The Finnish Forest Research Institute

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Production editors Seppo Oja, Tommi Salonen

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To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public discussion in Auditorium XII at the University Main Building, Aleksanterinkatu 5, on Friday, 13 March 1998 at 12 o'clock noon

Wending Huang

Productive Coexistence and Gain in Agroforestry Systems

The Finnish Society of Forest Science — The Finnish Forest Research Institute

Huang, W. 1998. Productive coexistence and gain in agroforestry systems. Acta Forestalia Fennica 260. 72 p.

Productive coexistence and coexistence gain of populations were studied using nine years' data from field experiments of *Taxodium ascendens*-intercrop systems in Lixiahe, Jiangsu Province, China. A theoretical framework for productive coexistence in agroforestry was developed. Interaction patterns between trees and intercrops were presented within this framework. A model framework was developed to describe the coexistence gain and interaction of populations in *T. ascendens*-intercrop systems. Facilitation and resource sharing were identified as main contribution to the advantage of species combination in agroforestry. The model of population interaction developed in the present study was accepted for describing the interaction of populations in *T. ascendens*-intercrop systems, because it explained a high proportion of the variance of experimental data and fitted well the observations in most intercropping types. The model developed in the present study provides flexibility for describing different patterns of intra- and inter-specific interactions. Model coefficients were applied to the determination of the ecological compatibility of species.

Managed *T. ascendens*-intercrop systems were advantageous as compared to a monoculture of trees or arable crops. In *T. ascendens* stands up to the age of three, arable crops contributed about 50–80 % of the total biomass yield of agroforestry. The diameter or height growth of *T. ascendens* was not significantly influenced by intercrops, indicating that intercropping under trees produced extra yields but did not depress the tree growth. When the trees were young (during the first three years), *T. ascendens* did not depress the crop yields, and a land equivalent ratio greater than unity was obtained together with a high yield of both components. The diameter and height of the trees were similar in four spacing configurations with an equal number of trees per hectare up to the age of eight, but wider between-rows open range were beneficial for the intercrops. The relationship between open-ranges and species coexistence was also analysed and the distribution of soil nutrients studied.

Keywords agroforestry, coexistence gain, facilitation, interaction model, productive coexistence, resource sharing, *Taxodium ascendens*.

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Accepted 30 January 1998.

ISBN 951-40-1603-3
ISSN 0001-5636
Tampere 1998, Tammer-Paino Oy

Contents

Preface

The present work has been carried out at the Tropical Silviculture Unit, Department of Forest Ecology, University of Helsinki. This is one part of the Agroforestry Project in Lixiahe Wetlands, Jiangsu Province, China. The present study was funded by the Academy of Finland, University of Helsinki, the Chinese Education Commission, and the Center for International Mobility of the Finnish Ministry of Education (CIMO).

I express my sincere appreciation to my supervisor Prof. Olavi Luukkanen. His significant help, constant encouragement and guidance have played a decisive role in the completion of the present study. I am grateful to Prof. Matti Leikola and Prof. Juhani Päivänen, the former and present Head of the Department, respectively, for their support in my work. I wish to thank Prof. Pertti Hari for his kind assistance in my study. It is deeply in my mind that the late Dr. Jussi Kuusipalo, as acting professor, offered great help and encouragement to me. In addition, my sincere gratitude goes to Dr. Markku Kanninen, who also as acting professor gave considerable support to my work, and to Dr. Vesa Kaarakka, for his kind assistance in many various ways.

The manuscript was reviewed by Prof. Juha Helenius and Dr. Pekka Nygren. I highly appreciate their valuable comments and practical suggestions that helped to improve the manuscript. An earlier version of the manuscript was reviewed by Dr. Annikki Mäkelä. Her detail and considerable comments improved my work.

Consultations with Dr. Kari Tuomela, Jarkko Koskela and Li Chunyang gave much help for the improvement of the present thesis. I express my special gratitude to Aija Niskanen and Jörn Laxén for their zeal to help me and my family. I would like to acknowledge all colleagues at my department in Helsinki for providing assistance on many occasions as well as a pleasant atmosphere. I wish to thank Zhang Lijun, Hua Baiyin and Wang Nian for field assistance in China.

Finally, I am in debt to my wife, Qifen, and my son, Tianyu. They have always been so patient and understanding in help to my work over the years. My wife, even though she has had to finish her own study, not only took up most house work but also contributed greatly to my research with assistance in data input and analysis.

Helsinki, January 1998

Wending Huang

List of Symbols and Abbreviations

A	yield of agroforestry
$ACDR$	asymmetric crown development ratio
C	competition loss
Cr_r	crown width of between-rows (m)
Cr_p	crown width of within-rows (m)
C_{tr}	competition loss of trees (effect of intercrops on trees) (tons/ha)
E_c	profit index which denotes ratio ($E_c = 1$) of output to input of arable crops in agroforestry
E_f	profit index which denotes ratio ($E_f = 1$) of output to input of forest management in agroforestry
F_{tr}	facilitation gain of trees (increased tree growth) (facilitative effect of arable crops on trees)
GA	ground area under tree stands (m^2)
GA model	Gilpin-Ayala model
GSV	space volume of forest ground (m^3)
IPA	area between within-rows (m^2)
$IPCA$	projected areas of within-row crowns (m^2)
I_{tr}	overall interaction of arable crops on tree species
K_c	maximum yield of arable crops
K_i	carrying capacity of species *i*
K_s	maximum biomass yield of soybean in monoculture.
K_{tr}	final maximum biomass in stands of *T. ascendens* in monoculture (tons/ha)
K_w	maximum biomass of wheat in monoculture (tons/ha)
L	Land Equivalent Ratio
L_{cr}	crown length of trees (m)
LV model	Lotka-Volterra model
M_i	yield of species *i* in monoculture
M_{tr}	tree growth in monoculture (sole-trees)
N_{tr}	number of tree individuals per unit
O_c	tree canopy open-range in tree stands (m^2)
O_p	within-rows open-range of tree stands (m^2)
O_r	between-rows open-range of tree stands (m^2)
O_s	space-volumed open-range (m^3)
P_i	production of species *i* in the multi-species system
PI	profit index in productive coexistence
R_i	relative yield of species i
RA	area between two rows of trees (m^2)
RCA	projected area of within-row tree crowns on ground (m^2)
r_0	initial growth rate of species
RO_c	relative tree canopy open-range
RO_p	relative tree within-row open-range
RO_r	relative between-rows open-range in tree stands
RO_s	relative space-volumed open-range
r_{s0}	initial annual increase or decrease rate of soybean by years
r_{tr0}	initial growth rate of *T. ascendens*
r_{w0}	initial annual increase or decrease rate of wheat by years
Spac I	tree spacing 1.5 × 4 m
Spac II	tree spacing 1.2 × 5 m
Spac III	tree spacing 2 × 3 m
Spac IV	tree spacing 1.5 × 2 × 6 m
S_{tr}	gain of resource sharing under tree stands (tons/ha)
V	tree crown volume (m^3)
W_a	growth of tree species (or arable crops) in agroforestry
$W_{a,tr}$	tree growth in agroforestry
$W_{a,trf}$	tree growth in fertilisation plots in agroforestry
W_c	yields of arable crops
W_m	growth of tree species (or arable crops) in monoculture
$W_{m,tr}$	tree biomass in monoculture (tons/ha)
W_s	biomass of soybean in tree+soybean system (tons/ha)
W_{s2}	soybean biomass in tree+wheat+soybean system (tons/ha)
W_{total}	total yield in agroforestry
W_{tr}	tree biomass in agroforestry (tons/ha)
W_{trs}	tree biomass in tree+soybean system (tons/ha)
W_{trw}	tree biomass in tree+wheat system (tons/ha)
W_{tws}	tree biomass in unfertilised tree+wheat+soybean system (tons/ha)
W_w	biomass of wheat in tree+wheat system (tons/ha)
W_{w2}	wheat biomass in tree+wheat+soybean system (tons/ha)
W_j'	differences between the maximum yields (K_j) of arable crops (j = wheat and soybean) in fertilised monoculture and those (W_j) in fertilised intercropping regime at age *i* (i.e. $W_j' = K_j - W_j$)
α_{ct}	competition coefficient of *T. ascendens* on intercrops
α_{st}	competition coefficient of *T. ascendens* on soybean in tree+soybean system
α_{trs}	competition coefficient of soybean on *T. ascendens* in tree+soybean system
α_{trw}	competition coefficient of wheat on *T. ascendens* in tree+wheat system
α_{wt}	competition coefficient of *T. ascendens* on wheat in tree+wheat system
α'	joint effect coefficient of wheat and soybean on tree species
β_{ij}	coefficient of management facilitation due to fertilisation
γ_{tr}	facilitation coefficient of fertilised intercropping regime on *T. ascendens*
λ_i	feedback rate of management facilitation
λ_{tr}	rate of facilitation feedback of fertilised intercropping regimes on *T. ascendens*
θ	density-feedback rate of intraspecific interaction
θ_c	density-feedback rate of intraspecific competition of arable crops
θ_s	feedback rate of soybean in tree+soybean system
θ_{s2}	feedback rate of soybean in tree+wheat+soybean system
θ_{ts}	density-feedback rate of *T. ascendens* in tree+soybean system
θ_{tr}	density feedback rate of trees
θ_{tw}	density-feedback rate of *T. ascendens* in tree+wheat system
θ_{tws}	density-feedback rate of *T. ascendens* in tree+wheat+soybean system
θ_w	density-feedback rate of wheat in tree+wheat system
θ_{w2}	density-feedback rate of wheat in tree+wheat+soybean system
ψ	any asymmetry in curve of interspecific interaction
ψ_c	feedback rate of interspecific competition of trees on arable crops
ψ_{st}	rate of interspecific competition feedback of *T. ascendens* on soybean in tree+soybean system
ψ_{st2}	rate of interspecific competition feedback of *T. ascendens* on soybean in tree+wheat+soybean system
ψ_{ts}	rate of interspecific competition feedback of soybean on *T. ascendens* in tree+soybean system
ψ_{ts2}	rate of interspecific competition feedback of soybean on *T. ascendens* in tree+wheat+soybean system
ψ_{tw}	rate of interspecific competition feedback of wheat on *T. ascendens* in tree+wheat system
ψ_{tw2}	rate of interspecific competition feedback of wheat on *T. ascendens* in tree+wheat+soybean system
ψ_{wt}	rate of interspecific competition feedback of *T. ascendens* on wheat in tree+wheat system
ψ_{wt2}	rate of interspecific competition feedback of *T. ascendens* on wheat in tree+wheat+soybean system
ψ'	feedback rate of joint effect of interspecific competition
ψ'_{tws}	feedback rate of joint effect of wheat and soybean on trees in tree+wheat+soybean system

1 Introduction

1.1 Background

At the present time, the forests in China cover only 14 % of the country's total territory. Annual deforestation is 0.44 million hectares (Ministry of Forestry of China 1993). Heavy pollution and other environmental degradation are caused by rapid economic development. Since the 1980s, increases in food production in China have barely kept up with the annual population growth, and there is little unoccupied land to fill with productive agriculture. The food that will be required to feed a population of 1.6 billion or more in the next century will have to come almost entirely from today's farmland.

Agroforestry is a land-use system in which woody perennials are intentionally grown in association with agricultural crops and pastures as well as with livestock, and in which there is both ecological and economic interaction between trees and other components (ICRAF 1979, Nair 1985, Rule et al. 1994, King 1979, Gholz 1987). Agroforestry is expected to be an alternative for the increase of the forest cover and food production, to slow the environmental degradation and to contribute to the natural heritage of plants and animals. Agroforestry has been practised for several thousand years in China (Hsiung and Yiang 1992, Huang and Wang 1992, Huang et al. 1993, Lei 1992). In recent decades, agroforestry has been rapidly developed in order to increase overall production by harnessing the potential of the various resources involved.

Primary agroforestry systems are estimated to cover 45.24 million hectares in China (Huang et al. 1997). Agrosilviculture is a dominant practice (Fig. 1). Aquasilviculture, e.g. tree-fish-arable crop and tree-fish-livestock systems, is an alternative for land use in the wetlands. Silvopastoral systems are popular in the northern and western regions. Compared to monocultures, well managed systems have many extra benefits. The recycling of residues is expected to increase the efficient use of natural resources. The C sink in the vegetation of major agroforestry systems in China is estimated as 179 Tg/yr (Huang et al. 1997), and agroforestry is reported to have a positive effect on soil conservation and biodiversity. Tree species are very diversified in agroforestry systems, especially in the tropical and subtropical areas (Huang 1985). Nearly 75 % of major plantation species are involved in the practice of agroforestry (Table 1). Most arable crop, livestock and aquacultural species are integrated with tree species.

Agrosilviculture denotes the combination of arable crops and trees, including intercropping, shelterbelts, and home gardens (Nair 1985, Huang and Wang 1992). In intercropping, arable crops are intentionally grown between the rows of trees. It is intensive management under trees. Intercropping is dominant in hilly and mountainous areas in southern China, which are situated in the tropical and subtropical zones. Intercropping is also popular in the central and northern plains. The traditional practice usually intercrops arable crops between tree rows for 1–3 years. This is about the same as 'Taungya', which indicates a system of planting forest trees in combination with agricultural crops during the early stages of plantation establishment. The origin of Taungya can be traced back to the 1850s in Burma, where it was used as a means of replanting teak on badly degraded land (King 1968). In China, intercropping systems, e.g. mulberry trees combined with arable crops, have been practised for at least 2000 years (Zhang 1993). A major improvement in intercropping in recent decades has been the widening of the distance between tree rows and a reduction in tree plantation density in order to extend the intercropping period or to intercrop permanently, or to make the systems compatible with mechanized methods (Table 2). One example is the intercropping of paulownia (*Paulownia tomentosa*) in the Henan and Shandong provinces, in which the distance between tree rows is 18–80 metres. Similar designs can be found in the intercroppings of poplars, maidenhair tree (*Ginkgo biloba*), and common jujube (*Zizyphus jujuba*).

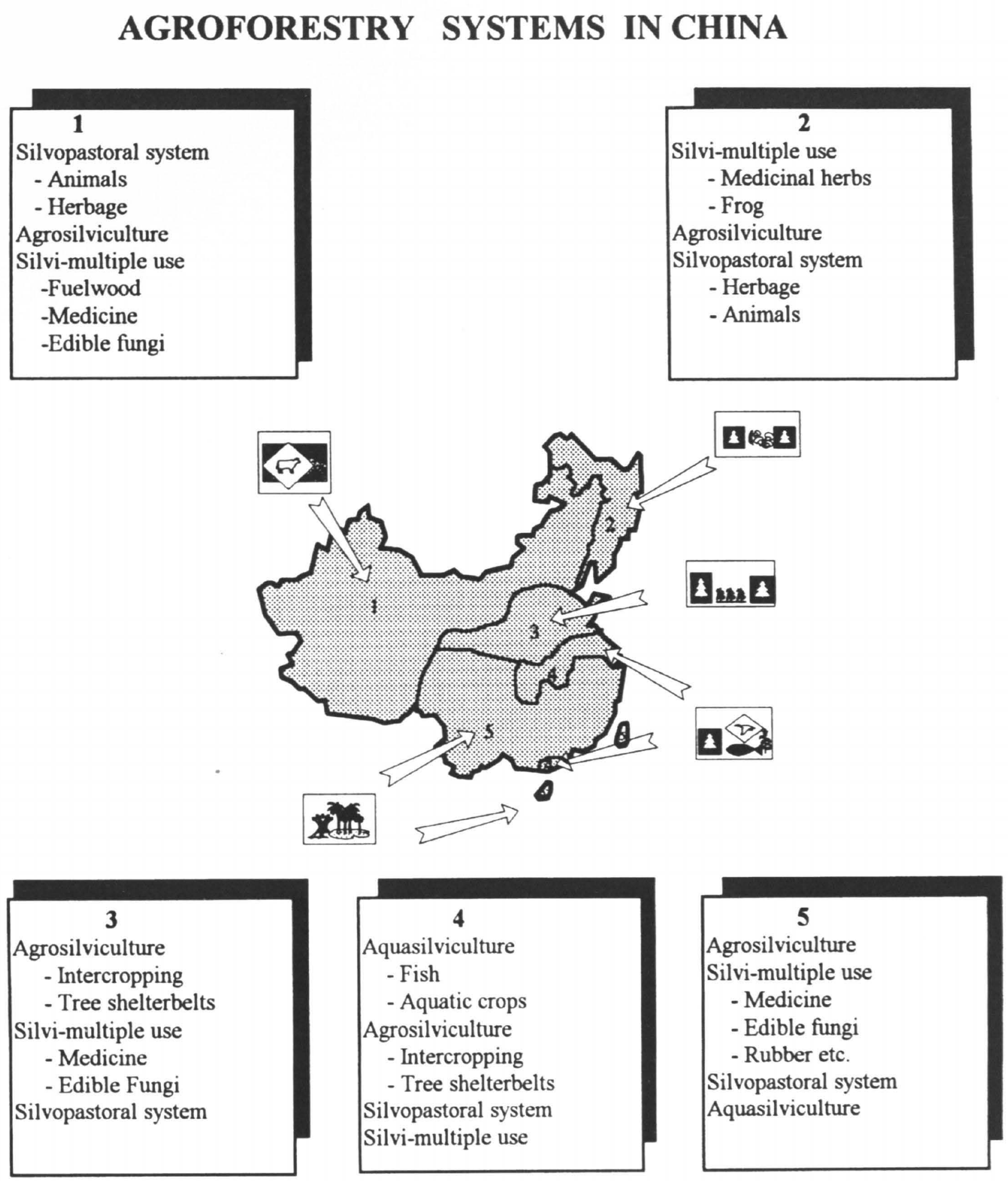

Fig. 1. Distribution of the main agroforestry systems in China (Huang et al 1997). (1) The agricultural and pastoral regions of the Three-North and Qin-Tibet Plateaus. (2) The northeastern forest region. (3) The central plains. (4) The wetlands or low lands. (5) The southern hilly and mountain regions.

Home gardening consists of the multi-species, multi-storey association of trees with herbaceous crops or livestock (Yun 1987). Home gardening in the rural areas of China covers 3.44 million hectares, making up 3.6 % of the arable land (Hu

1993). What distinguishes the home gardening system from other land use is the intensive utilisation of the above-ground and the below-ground resources resulting from high species diversity. Usually, the upper storey consists of trees that produce timber, fuelwood, fruit and fodder. The middle storey consists of shrubs. The understorey includes vegetables, other annual crops, or animals (Hu 1992, Wang 1993). However, most home gardens are randomly or haphazardly arranged, and the individual components are not very productive. The introduction of highly productive species and the use of efficient management patterns are positive ways for the improvement of home garden production. One example is the use of recycled residues in Jiangsu Province (Hu 1993). The excrement of chickens and pigs, and the leaves of trees and crops are placed in a biogas pool for the production of biogas. The residues of the biogas pool are used to produce mushrooms. The residues of the mushrooms are used to grow earthworms, which in turn are fed to chickens. Organic matter is also used as fertiliser for tree and crop growth (Yun 1984).

A shelterbelt comprises strips of trees planted in fields to reduce soil erosion, wind speed, sand encroachment, and the drought stress. It may take the form of a windbreak, which is useful in checking drifting sands in desert areas (Fullen and Mitchell 1994) and along the coasts. Shelterbelts are especially effective in protecting the farmland and for producing high-quality timber in the central and northern plains (including Hebei, Henan, Shandong, Shanxi, Jiangsu and Anhui provinces) (Zhao 1989, 1993). The farmlands protected by tree shelterbelts cover 10.7 million hectares and take up 45.7 % of the arable land in these areas (Zhen 1989). In the northern parts of China, windbreaks offer a major alternative for the control of desertification and protection of pasture and farmland. Shelterbelts have been recently established to enhance soil and water conservation in the upper-middle reaches of the Yangtze River and other hilly areas. For maximum efficiency, the upper to middle part of the hill is forested, the lower slope consists of bench-terraced horticulture, and the bottom is farmland (Huang, 1987, Huang and Wang 1992).

Aquasilviculture is a land use system linking trees with fish or other aquatic species. Intensive aquasilviculture systems is found in the middle and lower reaches of the Yangtze River, the Huihe River, the Zhujiang River and along the coasts. Virgin swamps, abandoned arable, coastal wastelands, and forest lands constitute the major land resources for aquasilviculture (Huang and Huang

Table 1. Distribution of some common tree species in agroforestry systems of China (Huang, unpublished).

Scientific name	Regions[1]	IC[2]	TS	SP	AS	HA
Ailanthus altissima	3,4	+				+
Aleurites fordii	5	+				
A. montana	5	+				
Alnus japonica	4,5		+			
Amorpha fruticosa	3	+	+			
Camellia oleosa	5	+				
Caragana arborescens	1			+		
Castanea mollissima	3,5	+				+
Catalpa speciosa	3	+				
Cedrela sinensis	3	+				
Cedrus deodara	4,5					+
Cinnamomum camphora	5	+	+			+
Citrus microcarpa	5	+				+
Cocos nucifera	5	+				
Crataegus	1,3	+				
Crytomeria japonica	5	+	+			
Cunninghamia lanceolata	4,5	+	+			+
Diospyros kaki	1,3,5	+				+
Elaeagnus angustifolia	1	+	+	+		
Eriobotrya japonica	5	+				+
Eucalyptus exserta	5	+	+			
E. citriodora	5	+	+			
Eucommia ulmoides	4,5	+				
Fraxinus americana	3	+	+			
Ginkgo biloba	1,4,5	+	+			+
Juglans regia	3,5	+				+
Juniperus chinensis	5	+	+			+
Litchi chinensis	5	+				+
Larix dahurica	2	+				
Lycium chinense	1	+		+		
Machilus pauhoi	5	+				
Malus pumila	1,3,5	+				+
Metasequoia glyptostroboides	4,5	+	+		+	+
Morus alba	1,4,5	+			+	

Table 1. Continued

Scientific name	Regions[1]	IC[2]	TS	SP	AS	HA
Musa paradisiaca	5	+				+
Olea europaea	5	+				
Paulownia tomentosa	1,3,4	+	+			+
Picea obovata	1,2	+				
Phoebe nanmu	5	+				
Pinus massoniana	4,5	+				
P. elliottii	4,5	+	+			
P. koraiensis	2	+				
P. taeda	5	+	+			
P. thunbergii	1,5	+			+	
Populus deltoides	4,5	+	+			+
P. diversifolia	1	+				
P. tomentosa	1,3	+	+			+
Populus × euramericana	1,3,4,5	+	+	+	+	+
Prunus armeniaca	1,3,5	+		+		+
P. mume	5	+				
P. yedoensis	5					+
Pseudolarix amabilis	5	+				
Robinia pseudoacacia	1,3	+		+		
Salix babylonica	4,5		+		+	+
S. purpurea	1,3,4					
S. viminalis	3,4	+				
Sapium sebiferum	5	+	+			
Sassafras officinale	5	+				
Taxodium ascendens	4	+	+		+	+
T. distichum	4	+	+		+	+
Thea sinensis	5	+				+
Tilia mandshurica	2	+				
Torreya grandis	5	+				
Trachycarpus excelsa	4,5	+				+
Ulmus pumila	1,3,4	+				
Zanthoxylum	3	+				
Zizyphus jujuba	1,2,3,5	+		+		+

[1] The numbers in the column of "regions" refer to Fig. 1

[2] IC: intercropping system; TS: tree shelterbelt system; SP: silvopastoral system; AS: aquasilviculture; HA: home-garden system

Table 2. Planting density of some tree species in agroforestry systems in China (Huang and Wang 1992).

Tree species	Density (stem ha^{-1})	Spacing (m)
Cunninghamia lanceolata	1111–1667	2×3, 1.5×4, 3×3
Crytomeria japonica	833–1667	2×3, 3×3, 3×4
Metasequoia glyptostroboides	833–1667	2×3, 1.5×4, 3×3.5, 3×4
Taxodium ascendens	272–1667	2×3, 1.5×4, 3×3, 3×4, 4×6, 3.5×10.5, 1.5×2×6
T. distichum	833–1667	2×3, 1.5×4, 3×4
Pinus koraieensis	1667–3855	1.3×2, 1.5×2, 1.5×2.8 (silvi-ginseng), 2×3
P. elliottii	180–1667	2×3, 3×3, 3×4, 7×8
P. taeda	833–1667	2×3, 3×3, 3×4
Ginkgo biloba	179–500	4×5, 5×6, 7×8
Populus	156–1000	2×5, 2×6, 3×4.5, 3.4×5, 2×8, 6×6, 4×10, 5×10, 6×10, 8×8
Paulownia	50–417	4×6, 5×5, 4×8, 4×16, 5×10, 6×10, 5×16, 5×20, 4×30, 5×40
Tilia	833–5783	1.3×1.33, 1.5×2.8, 1.6×1.3×2.4 (silvi-ginseng), 2×3, 3×4
Eucalyptus	833–1667	2×3, 1.5×4, 3×3, 3×4
Cinnamomum	833–1667	2×3, 2×3.5, 3×3, 3×4
Sassafras	417–500	4×5, 4×6
Camellia oleosa	833–1333	2.4×3, 3×4
Juglans regia	156–364	5×5.6, 6×6, 6×8, 7×9, 8×8
Olea europaea	278–333	5×6, 6×6
Aleurites fordii	625–833	3×4, 3×5, 4×4
A. montana	333–714	3.5×4, 5×6
Sapium sebiferum	333–833	3×4, 3.5×4, 5×6
Castanea mollissima	167–833	3×4, 4×10, 6×10
Zizyphus jujuba	125–333	3×10, 4×10, 5×10, 4×15, 4×20

1987b, 1991a). Aquasilviculture is practised in areas with a high water table. Ditching and terracing are employed for lowering the water level. The ponds are made on one side and the terraces on the other by removing soil from moist lands (Huang and Huang 1990). Fish are bred in the ponds, while trees are planted on terraces and intercropped with arable crops. A successful example is the fish pond-mulberry system widely used in the wetlands (Tan 1993, Zhong 1980). Mulberry trees and arable crops are interplanted on the dikes. Fish are bred in the ponds. The mulberry leaves are fed to silkworms, whose excreta are used as fish food. The pond mud fertilised by organic matter and fish excreta is put up on the dikes as manure for the mulberry trees and the arable crops.

Other similar examples are the tree-fish-arable crop and tree-fish-animal systems in the middle and lower reaches of the Yangtze River. The tree species are *Taxodium ascendens*, *T. distichum* (Huang 1988) and *Metasequoia glyptostroboides*. Aquatic species include silver carp, crab, turtle and shrimp (Zhao 1993). The animals include geese, ducks and sheep. The various species in the system can satisfy their growth requirements in the different niches and realize their functional potential to produce by-products and benefit the environment.

In the tree-aquatic crop systems, a combination of rice and *T. ascendens* is practised in the wetlands of the lower reaches of the Yangtze River. Trees are planted in the rice fields or on the dikes with a row distance of 5–12 m (Huang and Huang 1987a). Other types include lotus-trees, arrow head-trees and wild rice-trees. However, the shade from the trees reduces the temperature, light, and wind velocities. Exposure to wind is important because the resulting waves produce oxygen for the fish. A high oxygen level is necessary in the summer in ponds with a high fish population density. Thus, the wind direction and structure of tree stands or belts must be carefully considered in the design of aquasilviculture.

The silvopastoral system is a form of land use in which forest and pasture are simultaneously managed for wood production and domestic animals (King 1979, Byington 1990). The silvopastoral system is dominant in the Three-North region (northern, northwestern and northeastern parts of China). This region covers 1.49 million km^2 of desert and vast drought areas. The silvopastoral system is noted for its spatial arrangement of multi-storeyed vegetation. The upper storey consists of arboreal species, the middle storey of shrubs, and the understorey of forage or grazing land (Wang 1993). The primary use of trees for pasture and livestock is to produce fodder, provide shade and serve as a windbreak. A common practice is to give priority to forage production by using widened tree spacing. Forage production can usually be maintained by tree harvesting. The variations range from planting trees in widely spaced rows in existing pastures to thinning of existing tree stands. Another alternative regards wood production as the primary objective: grazing is not permitted until the planted trees are tall enough to avoid damage by animals.

Silvi-multiple use systems are popular in the northeastern forest areas. This region includes the provinces of Helongjiang, Jilin, Liaoning and parts of the Inner Mongolia Autonomous Region. One of most noted examples of a silvi-multiple use system is the tree-ginseng (*Panax ginseng*) system. Ginseng root is widely regarded as a valuable medicinal product, with a large market in China (Li 1986, Huang and Wang 1992). Another example of integration is the silvi-frog system. Forest frogs can produce frog oil, which is a kind of crude drug used widely in the Helongjiang and Jilin provinces.

Agrosilviculture and silvi-edible fungus cultures are also popular. In southern China, the silvi-medicinal herb culture (Liu 1991, Yiong 1992, Zhou 1991) and silvi-edible fungus management are notable for their high profitability. Rubber, tea, coffee and coconut trees intercropped with arable crops are very popular for increasing the production of multiple products. The silvi-medicinal herb culture is widely practised in the Henan, Anhui and Shandong provinces. The major species are gastrodia (*Gastrodia elata*), ballonflower (*Platycodon grandiflorum*), large-headed atractylodes (*Atractylodes macrocephala*), and tree peony (*Paeonia suffruticosa*). The maidenhair tree, mulberry (*Morus alba*), persimmon (*Diospyros kaki*), apricot (*Prunus armeniaca*), Chinese chestnut (*Castanea mollissima*), hawthorn (*Crataegus pinnatifida*), and walnut (*Juglans regia*) associated with arable crops make up the main part of the intercropping systems in northern China (Zhou 1993).

However, there are many constraints on agroforestry development because of the shortage of technical support (Huang et al. 1997). Most agroforestry systems still use traditional or old agroforestry methods with a low level of benefits, and they have been improved very little. The plant arrangement usually gives inadequate attention to growth requirements and species interaction, primarily because of a lack of understanding of the mechanisms of the production system. This leads to a reduction in yield and land-use efficiency. In addition, the present agroforestry systems are often not suitable for mechanization of management. It is thus clear that new production systems should be developed.

In Lixiahe region, Jiangsu province, under the pressure of population expansion and land limit in the early 1980s, more efficient economic exploitation of degraded marshlands without causing environmental degradation was suggested, due to the existing resources of water and fertile soil (cf. Huang and Huang 1985, 1991a). This area used to be a part of the flood-diversion in the lower reaches of the Huai River. There has been a lot of ecological concern because of the reduced flood-resistant capacity and declined biological diversity resulting from a surrounding dam-dependent agricultural reclaim (Hsiung 1991, Huang and Huang 1991a). In the recent decades, the irrigation-drainage systems have been significantly rebuilt, and they have much improved the environment for both agriculture and flood prevention. With artificial re-routing of the waterways leading to the sea or bigger rivers (e.g. the Yangtze River), many lakes and marshes in the area become dry or seasonally dry. As reed production drops significantly, the annual profit decreases correspondingly. In order to make a reasonable exploitation of the long-slumbering marshland, some alternatives were put forward (Huang and Huang 1985) of which agroforestry was considered very advantageous.

Agroforestry is a proper way to solve the contradiction between land use and water conservation, and the conflict in land use between agriculture and forestry in wetlands. In wetland agroforestry systems, networks of irrigation ditches or canals are built so that the excess water can be stored or discharged when necessary. Hydrophilous tree species are selected, since they are able to grow normally even while the land is flooded. Furthermore, both social and economic conditions are taken into account, so as to build different agroforestry models to suit different areas. Forestry, fishery, agriculture, and animal husbandry are wholly or partly combined to form various agroforestry systems, e.g. forest-fish, forest-fish-crop, forest-fish-aquatic crop, forest-fish-animal, forest-crop, forest-fungus and forest-sideline production systems (Huang and Huang 1991b).

1.2 Ecological Interactions

1.2.1 Interaction Among Species

Managing the interaction in agroforestry systems aims at maximizing the positive interaction and minimizing the negative interaction. Socioeconomic and ecological complexity is typical of agroforestry systems (Sanchez 1993, 1995), and an interdisciplinary approach is taken to land use by the combination of ecological with social and economic factors.

Agroforestry research is being transformed from a collection of largely descriptive studies into more scientific approaches based on process-oriented research (Sanchez 1995). Agroforestry systems represent a move away from the markedly artificial systems of monocultural production towards mimicking aspects of a natural ecosystem, with an emphasis on species diversity and resource conservation, and from zoned agroforestry arrangements using exotic woody perennials to more intimately mixed combinations involving dispersed indigenous trees (Anderson and Sinclair 1993). The theory from population and community ecology should thus be used with caution.

Interactions among species or populations are mediated by the environment through the 'response and effect' principle, which states that 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 (Goldberg and Werner 1983, Anderson and Sinclair 1993). There is an extensive ecological literature which describes the outcomes of the interactions among species, and at least six resultant interactions can be listed: neutralism (0, 0), competition (–,–), amensalism (–,0), compensation (+,–), commensalism (+,0), and mutualism (+,+). Table 3 presents a framework for the classification of ecological interactions in agroforestry using existing concepts from population and community ecology regarding ecological interactions (Anderson and Sinclair 1993). In this framework, the ecosystem is split into components and relationships. The components of the system are separated into physical and biological environments. 'Relationships' cover interactions between the physical and biotic components, and amongst biotic components. Using this type of categorization, agroforestry constitutes a set of land use practices which aims to encourage a favorable combination of the ecological interactions, thus enhancing productivity of land and conserving resources (Anderson and Sinclair 1993).

In agroforestry systems, the tree species, competition winner, is purposely introduced to the management systems, and compensation is thus dominant in alley cropping and other related systems. Since overyielding, stability and sustainability are the primary objectives of agroforestry management (Anderson and Sinclair 1993, Nair 1991, Huang and Huang 1991a, Conway 1987), agroforestry management emphasises maximising the positive interactions and minimising the negative ones (Young 1989b). Managing the positive interaction is thus one of key issues in the theory development of agroforestry.

Table 3. A system for the classification of ecological interactions in agroforestry systems (Anderson and Sinclair 1993).

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 interaction (intraspecific & interspecific)
    a. competition
      consumptive
      pre-emptive
      interference
    b. predation
      predation proper
      herbivory
      parasitism
    c. mutualism
      facultative
      obligatory
    d. commensalism

Competition

Competition occurs when two or more organisms or other organism units such as populations, interfere with or inhibit one another (Pianka 1981), causing demonstrable reductions in each other's fitness (Begon and Mortimer 1981). According to this definition, the word competition is reserved for mutually deleterious interactions (–,–). Some ecologists prefer to use competition to cover both the mutually deleterious interactions (–,–) and asymmetric interaction (or called amensalism) (0,–) (Crawley 1986, Vandermeer 1989), "because: 1) a great many plant-plant interactions are asymmetric; and 2) we often do not know the fitness implication of particular interactions in advance, so that calling them amensal rather begs the question" (Crawley, 1986).

Competition can be divided into interference competition (e.g. allelopathic competition) and exploitation competition (resource competition), in terms of competition mechanisms. Interference occurs when one species interferes with the well-being of the other, e.g. in the production of allelochemicals or shading. Exploitation competition occurs when species reduce the availability of limiting resources below the level that is required for normal growth of another by exploiting the same or similar resources. However, 'interference' has been frequently used as the general term for negative interaction (Harper 1961, 1977, Vandermeer 1981, 1989). In interspecific resource competition, changes in the density of one species may influence the availability of resources, e.g. light, water and nutrients, thus affecting the growth of the other components. As the density of one species increases, there is an increased rate of consumption of the resources and the availability of resources for the other species is reduced (Anderson and Sinclair 1993).

There is a continuum of exploitation competition from highly asymmetric (contest) to rather symmetric (scramble) (Crawley 1986). In contest competition there are winners and losers. One gets all the resources which it requires while another gets only the left-over. In scramble, the limited resources are divided equally between the competitors (Crawley 1986). These two kinds of competition have different effects on population dynamics. In terms of dynamics, scramble competition is more destabilising as compared with contest competition.

Competitive effects on a species which derive indiscriminately from all or many of the other species in a community have been described as diffuse competition (MacArthur 1972). More or less weak diffuse competition between plant species in a community is probably common, with more severe interference occurring between particular species for particular limiting factors (Silvertown 1987). Removal experiments can be used to investigate diffuse competition. Many experiments of this kind have been performed (Mack and Harper 1977, Fowler 1981, Davidson et al. 1985). They demonstrate that the behaviour of a plant in a mixture of two species may be quite different from its behaviour in more diverse mixtures. On the whole, field experiments involving species removal usually demonstrate that competition is local and not specific (i.e. it is "diffuse"), though exceptions to this do occur (Silvertown 1987).

The biological processes responsible for the deviation of component performance in polyculture from that expected in monoculture are complex and varied. The best understood mechanism that can cause the yield of plants to differ between polyculture and monoculture is the process of competition (Trenbath 1974, Baeumer and Wit 1968). Plants are conceived as 'competing' for the limited supplies of environmental resources necessary. In a mixture, differences in morphology and physiology between the components cause their individuals to experience different microenvironments and hence different resource availabilities from those experienced by the plants in monoculture.

The most important aspect for managing the competition in agroforestry systems is to weaken the competition. Plant competition for limiting nutrients has been widely studied (Tilman 1982, 1988, 1990, Berendse 1985, 1990, Silander and Pacala 1990). Berendse and Elberse (1990) relate plant growth to the nutrient supply and consider the 'relative nutrient requirement', defined as the amount of nutrients needed to maintain each unit of biomass during a given time period, as a major determinant of competitive success. Tilman (1990) relates plant growth to the nutrient concentration in soil solution and emphasises nutrient reduction as the mechanism of nutrient competition. According to this explanation, R*, 'critical nutrient concentration' is the key parameter of competitive success, which can be measured in the soil in which a limiting nutrient is reduced by a steady-state monoculture. The species with lower R* to the limiting resource (often N in terrestrial plant community) always has a competitive advantage. The same author emphasised that it is not necessary to perform competition experiments to estimate 'competition coefficients' or other interaction terms, if species only interact via shared resources. According to him, all relevant parameters concerned with resource utilisation should be measurable in monoculture. There is an interesting contrast between the approaches of Berendse (1985) and Tilman (1990). These two models, which seem to represent two completely different perspectives on plant competition, have been represented as having 'indeed much in common' according to Huisman (1994).

Concerning the resource competition in agroforestry, plenty of research has demonstrated the reduction in the yields of intercrops due to the underground competition for water and nutrients (Singh et al. 1989, Ong et al. 1991, Akbar et al. 1990, Huang et al. 1993). The hypothesis initiated in the early 1980's in agroforestry was that trees extend their roots into deeper soil layers and hence do not compete with arable crops for nutrients and water (Kang et al. 1981, Schroth and Zech 1995). Jonsson (1995) studied the root distribution under five species (*Cassia siamea, Eucalyptus camaldulensis, E. tereticornis, Leucaena leucocephala, Prosopis chilensis*) with potential for agroforestry, and observed that 80 % of the root biomass occurred in the upper 60 cm of the soil. It is therefore relevant to assume competition with arable crops for nutrients and water.

Competition between root systems for nitrogen is likely to start earlier in growth than the competition for phosphorus or potassium, because nitrogen is much more mobile in the soil than phosphorus and potassium (Trenbath 1974). Zones of nitrogen depletion around individual roots therefore begin to overlap relatively early. In connection with this proposition, it was observed that the competition for nitrogen was intense, whilst the competition for phosphorus was indeed slight (Trenbath 1974). Since the mobilities of nitrogen and water in soil are similar, the soil resources most likely to be subject to competition are nitrogen and /or water (Trenbath 1974).

There are many experiments on the competition for light in agroforestry (cf. Huang et al. 1993, Huang and Wang 1992). It has been frequently reported that arable crop yields are depressed by competition with trees for light (Srinivanet et al. 1990). In alley cropping systems, the fraction of available light which would reach the arable crops is controlled by the dimensions and orientations of the tree rows, and by the latitude and time of day and year. If the tree rows are from N to S, the lower the latitude is, the greater the relative irradiance reaching crops. In a continuous upper-storey canopy, the light transmission to the crops will be controlled by tree LAI (leaf area index) and light extinction coefficient (Jackson and Palmer 1989, Tan 1987).

Near the equator the solar radiation reaching the centre of the open row will depend on the orientation of the rows. With the N-S rows, the centre of the pen space will receive direct-beam sunlight for a period in the middle of the day, the exact duration depending on the ratio of the tree height to the width of the rows. With E-W rows, the centre spot will be typically exposed to nearly full sunlight throughout the day, missing only the skylight obscured by the nearby trees. By contrast, a random orientation of tree rows will result in an irregular pattern of sunfleck and shade (Reifsnyder 1989). However, the shade that is given by the various orientations (N-S, E-W, random etc.) of the tree rows will relieve the intercrops from extra heat and respiration in corresponding way in the afternoon during the summer. For managing the species composition in agroforestry systems, it is useful to know the understorey crop light requirements.

At the crop level, Sale (1974) studied the productivity of vegetable crops in a region of high solar light input (the Murrumbidgee irrigation area of New South Wales, Australia, where solar input is often up to 1000 Wm^{-2}), and showed that potato was unable to use a large proportion of the photosynthetically active radiation (PAR), light saturation of the canopy occurring at about 450 Wm^{-2}. Light saturations of French bean and cabbages occurred at 600–650 Wm^{-2} and at about 800 Wm^{-2} respectively (Sale 1975, Jackson 1983). Thus, it seems that crops with low light saturation levels are most suitable as understorey crops.

The relationship between yield and population density have been widely observed for crop plants. A reciprocal relationship exists between plant size and density. At low densities there are plastic responses of plant size as plants grow, and at high densities mortality occurs and plants tend to follow the –3/2 thinning law (Silvertown, 1987). The reciprocal and hyperbolic functions are frequently used to fit this linear relationship between the reciprocal of mean plant weight and density, even though it is open to the criticism that unless properly weighted, very small plants at high densities contribute disproportionately large amounts of information to the regression analyses (Harper, 1977).

Facilitation

Facilitation is the process in which two individual plants or two populations interact in such a way that at least one exerts a positive effect on the other (Vandermeer 1989). Mutualism is a symmetric positive 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). 'Facilitation' has been used as a single term to describe interactions between plants with a positive result (Vandermeer 1989). Commensalism is equivalent to single facilitation, and mutualism is equivalent to reciprocal facilitation (Anderson and Sinclair 1993).

Using ecological concepts concerning interactions, Anderson and Sinclair (1993) suggested that published studies can be simply separated in terms of the observed net result or effect of the interactions occurring, i.e. competition, mutualism and commensalism, and considered as evidence which can be used to support or refute the advantage of agroforestry. In terms of the above definition, facilitation also includes mutualism and commensalism. Reducing the competition is one part of managing positive interactions.

Several authors have reported facilitative interactions (Huang and Wang 1992, Huang et al. 1993, Vandermeer 1989, Feng 1990). Jonsson (1995) found that the maize biomass production was higher in plots with *Leucaena leucocephala* and *Prosopis chilensis* (both N$_2$-fixing), as compared to grass plots. The percentage of N was higher and the natural abundance of ^{15}N in total N in the soil was lower under *Prosopis* than under other tree species. This indicated an input of fixed N under *Prosopis*.

Competition and Facilitation

In agroforestry, asymmetric facilitation and competition (Weiner 1990) may occur concurrently. This point is often not emphasised sufficiently (Anderson and Sinclair 1993). For example, trees improve soil fertility (Campbell et al. 1994, Sanchez 1987, Huang and Wang 1992), and also compete with arable crops for nutrients and light (Breman and de Ridder 1991, Huang et al. 1993).

Competition occurs when two species occupy the same ecological niche and interfere with each other's activities. On the other hand, when the two species have similar but distinct requirements, they may coexist in the same environment for some time or indefinitely. Vandermeer (1989) suggested a 'competitive togetherness principle', because they cannot both persist when competing intensely (which has been referred to as the competitive exclusion principle), although it is obvious that the emphasis could have been placed on their coexistence.

Much of the initial enthusiasm in agroforestry was based on the assumption that when trees and crops are brought together they complement rather than compete with each other in their capture of growth resources (Sanchez 1995). Young (1989b) transformed a soil-agroforestry hypothesis into ten hypotheses and Sanchez (1995) listed 17 biophysical hypotheses, nearly all of which dealt with facilitation or complementarity.

Ong (1995, 1996) proposed a tree-crop interaction equation for quantifying the crop and the tree component effect (Sanchez 1995),

overall interaction = fertility effect – competition effect,

where the fertility effect is the percentage of crop-yield increase caused by soil fertility improvements, and the competition effect is the crop-yield decrease caused by competition with trees for light, water and nutrients etc. (Sanchez 1995). A positive value of overall interaction in this equation means net complementarity, the desired outcome of agroforestry, and a negative value of overall interaction means net competition to the detriment of crop yields.

In terms of analyses from the available literature comprising over 100 alley-cropping experimental data sets (Sanchez 1995) in a alley-cropping system of *Leucaena leucocephala* and maize in Nigeria, the effect of competition was strong (–54), and a fertility effect (+58) and an overall interaction value (+4) were observed (Kang et al. 1981, 1985). Other similar results have been also analysed from numerous research reports in the semiarid (Rao et al. 1991, ICRAF 1993) and humid tropics (Szott et al. 1991, Kass 1987, Van Noordwijk et al. 1992), but many negative overall interactions were also observed because there were stronger competitions than fertility effects. Minimizing the competition is the paramount objective in simultaneous agroforestry, in which the tree and the crop components grow at the same time and in close enough proximity for interactions to occur, e.g. alley cropping (hedgerow intercropping), contour hedges, parklands, boundary plantings, home-gardens and several silvopastoral systems (Sanchez 1995).

1.2.2 Resource Sharing

Managing the resource sharing in agroforestry systems is concerned with minimising the mutual interference and maximising the potential of resource sharing. In a monoculture, one species cannot utilise all the available ecological resources, and thus other species can fit in without excessively disturbing the first one. In this case, two species growing together will overyield if there exist resources enough for both of them to grow. Growth implies resource use, and hence, gradual decreasing of the size of resource pools (Buck 1986). The growth of species requires continuous and balanced access to resources, e.g. light, water and nutrients. The quality and quantity of light are affected by the composition of coexistent systems, e.g. plant stature, canopy closure and canopy structure. Water and nutrients, unlike light, are available to plants to a limited extent, even though they can be compensated for from external input.

Sharing of resource pools in agroforestry encompasses competitive, differential, and complementary aspects (Buck 1986). In the present study, it was preferred to classify the competitive and complementary aspects as ecological interaction among species or populations in terms of their definitions (see above). The differential aspect occurs when access to resource pools is partitioned in space or time (e.g. different effective root depths, deciduous trees in overstorey, etc.) (Buck 1986).

In general, resource sharing can be divided into differential and bio-cycle sharing. The former can be sub-divided into spatial and temporal sharing. The spatial sharing includes above- and underground resource use. The temporal resource sharing concerns phenological mechanisms, e.g. components growing at different times or at widely different rates, and leads to enhanced productivity due to the capture of more resources rather than changes in the efficiency of resource utilisation (Willey et al. 1986). The efficiency in resource sharing increases simply because the peak demand of each component for resources occurs at different time. In this paper, bio-cycle resource sharing refers to the cycle use of resources. The well-known example is the mulberry-fish or dike-pond system in China.

In the differential aspect, resources can be shared horizontally by managing the spatial dispersion and regulating the composition of coexistent systems. The boundary between trees and arable crops is often considered as an important factor for maximizing the beneficial area (Trenbath 1976, Buck 1986). However, this depends on the objective of management. For example, intercropping or alley cropping aims at maximizing the area of the interface, whereas windbreaks aim at maximizing the protective function against wind. In alley cropping, additional production of wood would be obtained by increasing the within-row density of trees or by planting double rows of trees.

Resource sharing in the vertical dimension, e.g. light, has been widely studied, because light is one of the primary limiting resources in agroforestry management. Light distribution in agroforestry systems is more complicated than that in monoculture. Light levels in the understorey can be adjusted by controlling the overstorey strata. The resource capture ratio, which is analogous to the land equivalent ratio, has been used to determine the difference of radiation interception in monoculture and mixtures (Marshall and Willey 1983, Stirling et al. 1990).

In underground resource use, root distribution of plants in soil can influence the efficiency of resource sharing. Optimal spatial distribution is conceived as requiring deep root development for 'nutrient pumping' and limited horizontal development in order to reduce competition with arable crops (Hairiah and Noodwijk 1986). This will promote effective resource sharing in most agroforestry systems. However, roots of trees and arable crops, e.g. maize, are likely to share the same space in the soil (Jonsson 1995, Toky and Bisht 1992). Water stress can be a limiting factor in agroforestry systems. Soil moisture depletion mainly occurs in the top meter of the soil (Leyton 1983). As soil depth increases, the evergreen forest causes the greatest depletion at depths between two and three meters, whereas tea, which presumably is more shallow-rooted, takes up relatively little water below the depth of two meters (Eales 1980).

In temporal resource sharing, increased use efficiency can be achieved by planting the components at different times or planting them at the same time when one component grows rapidly while the other grows slowly (Sanchez 1995). The former is called relay intercropping (Andrews and Kassam 1976), and the latter is usually called mixed intercropping. The temporal dimension is considered seasonally, annually, and over the life span of the longest-living component. In the phenological patterns, optimising production in agroforestry by knowing the requirements and timing of nutrient demand offers great potential for total system yield increase. For example, fertiliser application or harvesting and planting of understorey crops could be synchronised with the nutrient demands of the overstorey crop (Buck 1986).

1.2.3 Competition, Facilitation and Resource Sharing

Coexistence is crucial to the success of any agroforestry programme designed to produce overyielding or other advantages, because it enables components to adapt not only to the environment which they share, but also to each other. Within a community, species maintain a coexistence by niche differentiation, where a niche is defined as 'the range of values of environmental factors' that are necessary and sufficient to allow a species to carry out its life history (James et al. 1984). Competitive stress for a limiting resource must be withstood before species can coexist within a community. This is accomplished by a process of niche diversification, arising from temporal or spatial differences between species (Hill 1990).

The effect of one species on another by affecting the environment is related to the theory of the ecological niche. A state in which a species lives in an unmodified environment is called the fundamental niche, while a state in which a species lives in an environment modified by other species represents the realised niche. If facilitation is operative and dominates competition, the general expectation is that the realised niche will be broader than the fundamental niche (Vandermeer 1989). This hypothesis can be tested by studying the facilitative benefit to trees from intercrops, with well designed experiments.

The aim of good agroforestry is to weaken the competition by planting combinations of species which allow niche differentiation to occur, e.g. root systems exploiting different soil depths and hence different parts of the resource base (Anderson and Sinclair 1993). A practice which avoids competition results in a greater productivity per unit of land from mixtures of species than from pure stands.

Coexistence gains for populations can be obtained by maximizing facilitation and niche differentiation. In order to predict the outcome and interactive process of coexistence gain of species or populations in agroforestry systems, an approach must be introduced that can relate the coexistence gain to the resource sharing which depends on the availability of limiting resources, and to the facilitation which depends on the positive interaction within and between species.

1.3 *Taxodium ascendens*

Taxodium ascendens Brongn, *Taxodium distichum* L. Rich., and *Metasequoia glyptostroboides* Hu et Cheng were selected as primary tree species in agroforestry management in the Lixiahe wetlands (Huang and Huang 1985). Of these, *T. ascendens* has performed perfectly in the marshland with a high water table, due to the species' water-tolerance (Fig. 2). *T. ascendens* is a deciduous conifer that grows on saturated and seasonally inundated soils of the south-eastern and Gulf Coastal plains of North America. The native range extends from southern Virginia to southern Florida, and then along the Gulf Coast to south-eastern Louisiana. The species grows almost always at elevations below 30 m. Humid and moist subhumid climatic types occur within the range of *T. ascendens*.

Typical specimens of *T. ascendens* have nearly scale-like leaves, which are appressed along the twig in several ranks (Fig. 3). However, fast-growing shoots often have distichous (two-ranked) leaves. *T. ascendens* is monoecious. The cones turn from green to brownish purple as they mature from September to October. The globose cones are 20 to 30 mm in diameter. The irregular seeds have thick, horny, warty and projecting flanges.

T. ascendens was first introduced to China at the beginning of the 1900s. It was planted in Nanjing, Nantong of Jiangsu Province, and Jigong Mountain of Henan Province. Today, *T. ascendens* is one of the best-known introduced plantation species in China. The main areas of introduction include Hubei, Jiangsu, Anhui, Guandong, Hunan, Zhejiang, Fujian, Jiangxi, Henan, Shandong, Shaanxi, Guangxi, and Sichuan provinces. It grows well in southern China, especially in the wetlands and plains, due to the high precipitation and warm climate, but poorly along the Yellow River valley. *T. ascendens* is used as one of the major species for timber plantations, shelterbelts, windbreaks and agroforestry in China, but in North America it is not widely accepted as a forestry species because of its small stature and slow growth in natural sites. Many forestry professionals from North America have been surprised at the good performance of this species in China. It can in fact grow fast in suitable sites. In Wuhan of Hubei Province, the mean tree height is 7.9 m and mean diameter (DBH) 10.9 cm at the age of ten years in a fertile site, whilst the values are 5.9 m and 8.3 cm respectively in a poor site (Huang 1978). The primary reasons for the good performance of this species in China are that most tree stands are set up in fertile soil with intensive or agroforestry management (Fig. 2).

In China, plantations of *T. ascendens* are usually established in the wetlands, plains and hilly areas at elevations below 100 m. This species can be grown at elevations higher than 1000 m, e.g. in Lushan Mountain of Jiangxi Province (1200 m), and in Jiansi County of Hubei Province (1600 m); however, the growth in these regions is quite poor. In the areas of good growth the mean annual temperature is 12–20 °C, but the tree can also endure low temperature. It was not damaged during a transient heavy frost (–17.3 °C) in Wuhan of Hubei Province in 1969. Annual precipitation higher than 1000 mm together with a thermic temperature form good climatic conditions for the growth of *T. ascendens*.

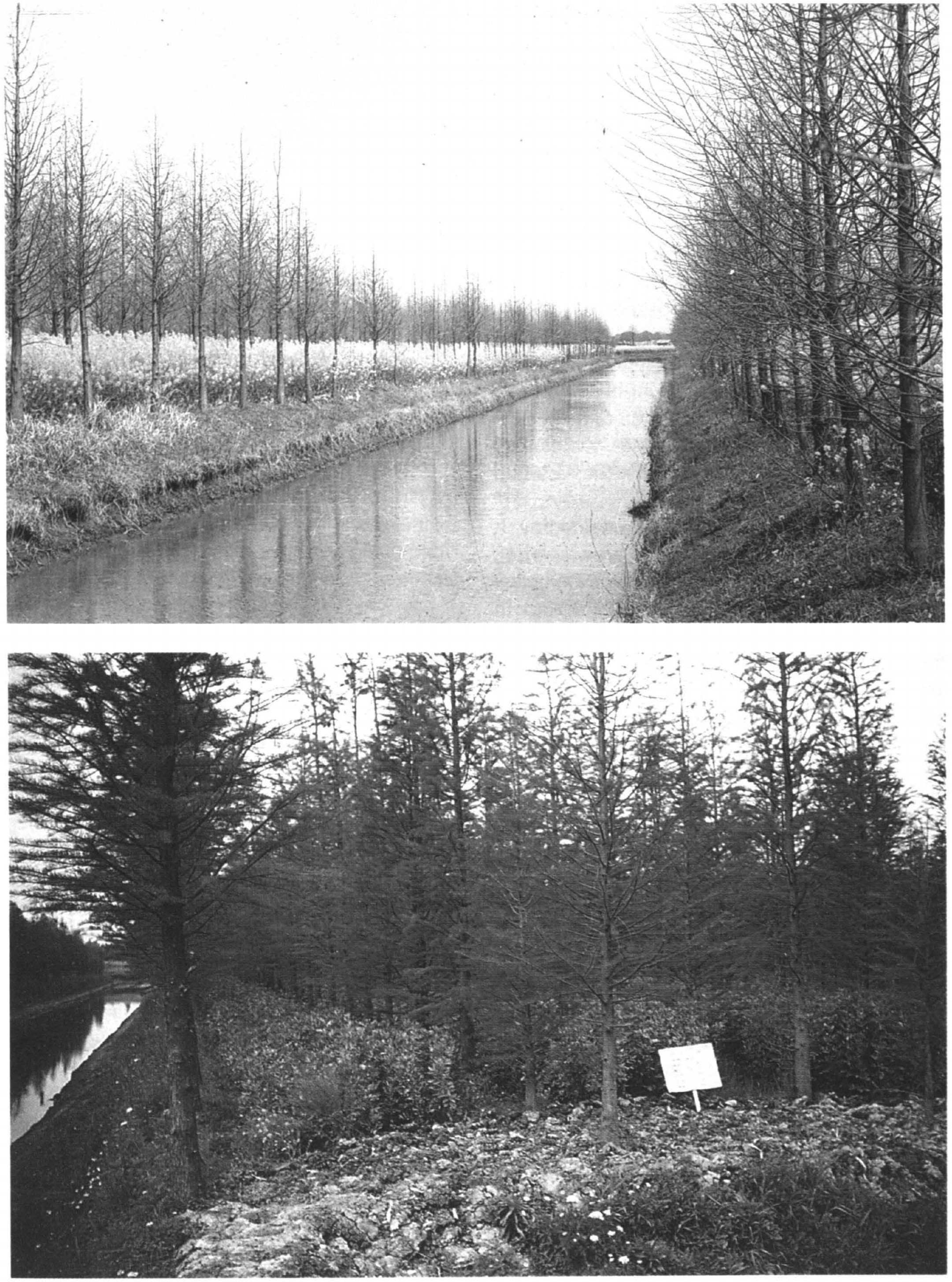

Fig. 2. *Taxodium ascendens* grown in wetlands. (Above) Trees without leaves in *T. ascendens*-fish-rape system. (Below) Trees with leaves in *T. ascendens*-fish-broadbean system.

T. ascendens sites are characterised by frequent, prolonged flooding. The native range of the species is in the thermic and hyperthermic soil temperature regimes. It can grow on intermittently flooded and very poorly drained lands or wetlands where soils range from heavy clays to peats. The species prefers acidic soils.

T. ascendens develops a taproot; in swamps it develops several descending roots that provide anchorage and numerous lateral roots from which rise peculiar structures known as 'knees'. These knees vary in height from several centimetres to several meters depending on the mean water level of the site. Knees are less likely to form in the absence of flooding or permanent high water table. The knees have been believed to be beneficial as aeration organs (Eyre 1980). Knees may also help to anchor the trees because they develop large masses of roots.

T. ascendens can endure prolonged flooding. It was observed that the species had grown well in water for two or three months during the heavy flooding in Xinhua County of Jiangsu Province in 1989, whilst most of the other species died in similar conditions. The species has high wind resistance. For example, over 20-year-old Chinese redwood trees (*Metasequoia glyptostroboides*) were heavily damaged by a violent typhoon but *T. ascendens* grew well in Hangzhou of Zhejiang Province and Nanjing of Jiangsu Province in 1974 (Huang 1978). *T. ascendens* wood has a multitude of uses and is resistant to decay. It has been favoured in building construction, planking in boats, furniture, sills, rafters, and many other uses.

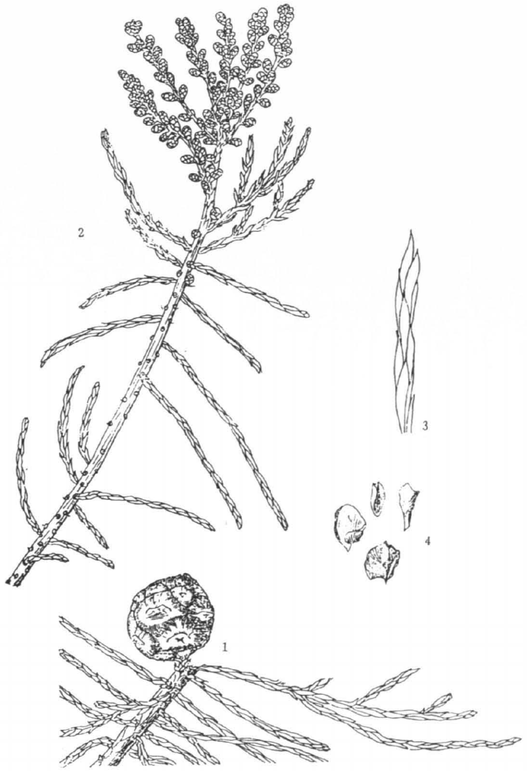

Fig. 3. *Taxodium ascendens*. (1) Twig with fruit; (2) twig with staminate flowers; (3) green twig; (4) seeds.

1.4 Objectives of the Study

The principal aim of the present research was to study the productive coexistence and interactions among selected species in agroforestry, with consideration both of agroforestry which is to obtain the maximum economic and environmental benefits, and of improving the understanding of interactions in agroforestry. Specific objectives were as follows:

(1) To identify the effects of different tree spacing configurations on the open ranges, so as to determine how the open ranges influence the intercrop growth and to examine the relationship between open-ranges and species coexistence for better intercropping management;

(2) To develop a theoretical framework for productive coexistence in agroforestry, to determine whether the yield advantage (overyielding) of a species combination is evident in *T. ascendens* intercropping systems, and to investigate the possible mechanisms of overyielding; and

(3) To develop a model framework for describing the coexistence gain in agroforestry and to derive more flexible interaction models for complex agroforestry systems; these models were to be judged against the biological realism of their parameters, and the fit of the models was to be tested using nine years' data from field experiments of *T. ascendens*-intercrop systems.

2 Theoretical Framework

2.1 Productive Coexistence

Facilitation and resource sharing lead to an economically beneficial coexistence in multi-species systems. Generally it can be evaluated by the Land Equivalent Ratio (L) (Mead and Willey 1980):

$$L = \Sigma P_i M_i^{-1} \qquad (1)$$

where P_i is the production of species i in the multi-species system, and M_i is the production of species i in the monoculture. The Land Equivalent Ratio can be defined as the amount of land needed to produce as much in monocultures as can be produced on the same area for a polyculture.

To determine whether each species is facilitated, the relative production, R_i, (or relative yield) can be calculated as:

$$R_i = P_i M_i^{-1} \qquad (2)$$

Productive coexistence is a concept describing the performance of a productive system with at least two managed species or populations. The existence or removal of one species or population is limited by the balance of its output and input (Fig. 4). The line $T_m - C_m$ is the criterion where the land equivalent ratio (L) equals 1.0. If L is higher than 1.0, it indicates overyielding (i.e. the polyculture is more productive than monoculture). The quadrant I (+,+) shows that the yield of each species in agroforestry is higher than that in monoculture. III (–,–) denotes that the yield of each of them in agroforestry is lower than that in monoculture, but it is still advantageous if the L is above 1.0. II (–,+) and IV (+,–) show the total yield is higher than that in monoculture, but while the former implies that the forest is facilitated and its yield is higher than that in monoculture, the intercrop is not, the latter denotes that the crop is improved and its yield is higher than that in monoculture but the forest is not. E_f is the profit index (PI) which denotes the ratio ($E_f = 1$) of the output of production to the input of the forest management in agroforestry systems, and E_c is that due to intercropping. The line $E_f - E_c$ denotes the critical risk criterion where output and input are equal in economic value. If PI is below line $E_f - E_c$, it shows that both or one of the components are in negative profit, which is unacceptable in practice. It is only acceptable if both components are above 1.0, defining the region of productive coexistence (Fig. 4).

2.2 Coexistence Gain and Model Construction

In order to describe the yield composition and performance of productive coexistence in *T. ascendens*-intercrop system, let us make the following assumptions:

(1) The competition loss of *T. ascendens* (or intercrops) is caused by intercrops (or *T. ascendens*) exerting negative effects on the other, covering mutually deleterious interaction (–,–) and asymmetric interaction (–,+). The yield loss due to the presence of the arable crops (or tree species), C, could be determined by comparing the differences between their growths at the same density but with and without arable crops (or tree species):

$$C = W_m - W_a \qquad (3)$$

where W_a is the yields of tree species (or arable crops) with arable crops (or tree species), W_m that without arable crops (or tree species) at the same density in the same environment. The competition effect of intercrops on tree species could be demonstrated in the quadrant III (–,–) and IV (+,–) of the region of productive coexistence, and that of tree species on intercrops in the quadrant II (–,+) and III (–,–) (Fig. 4).

(2) The coexistence gain of species, which could be defined as a system's over-yielding or advantage, is partly created from facilitation in a coexistent community. Facilitation could be thought of as engaging in the following process: tree species and arable crops exert an effect on the mutual environment and respond to the affected environment positively (Vandermeer 1989). The over-yielding could result from the positive ecological interaction (ecological facilitation) and management effect (management facilitation). As arable crops are grown under trees, application of nutrients to these crops is quite common in China, because farmers expect to obtain high yields of intercrops due to limited arable lands and population pressure. The applied nutrients are also facilitating the tree growth (management facilitation). If we consider this effect as one of facilitations of arable crops on tree, the yield increase of tree species, F_{tr}, could be determined by

$$F_{tr} = W_{a,trf} - W_{m,tr} + W_{m,tr} - W_{a,tr} = W_{a,trf} - W_{a,tr} \quad (4)$$

where $W_{a,trf}$ is the tree yield in fertilisation plots in agroforestry at the same tree density, Wa,tr the tree yield in agroforestry, and $W_{m,tr}$ the tree yield without arable crops (in the absence of its competitors). The term, $W_{m,tr} - W_{a,tr}$, is added to the right side of equation because the yield loss of trees would, in the same time, be caused by the competition effect of intercrops on tree species for nutrients, water and light etc. The expression using plain yield difference here is for easier use for the predictive purpose of tree or arable crop yield dynamics in the models, compared to the relative yield loss due to competition (e.g. $RC = 1 - W_a / W_m$) or relative yield increase due to management facilitation (e.g. $RF = 1 - W_{a,trf}/W_{a,tr}$). The management facilitation of intercrops on tree species could be demonstrated in the quadrant I (+,+) and II (–,+) of the region of productive coexistence , and that of tree species on intercrops in the quadrant I (+,+) and IV (+,–) (Fig. 4).

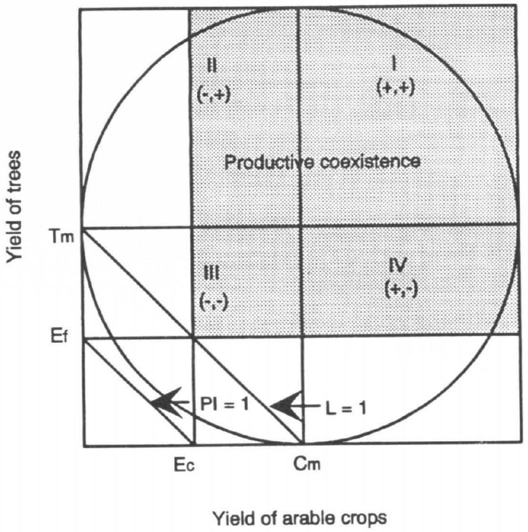

Fig. 4. Productive coexistence in agroforestry systems. Quadrant I, II, III and IV are the facilitation types. T_m is the yield of tree species in monoculture, C_m the yield of arable crop in monoculture, L the land equivalent ratio, PI the profit index, E_f and E_c are the profit indexes (see text).

(3) The coexistence gain of species is partly created from resource sharing. A monoculture, under certain conditions, can not utilise all available ecological space, and a second crop species can fit in without excessively disturbing the first crop. In this case, two crop species growing together will overyield if there are enough resources for the growth of both of them. For example, in a plantation of *T. ascendens* (sole-trees) that has timber as the only product, it is possible to produce x tons of tree biomass in a unit of land. In order to enhance the biomass production by utilising the available resources under trees, soybean or wheat is intercropped and produces y tons/unit of land of crop biomass, receiving a total of x + y tons/unit of land in this new system. Compared to the sole-tree plantation, this extra crop yield, y, is a result of additional use of available resources (or complementary use of resources by soybean or wheat) under trees. The usual practice is to introduce high light-requiring crops (e.g. wheat and soybean) under young tree plantations and low light-requiring species (e.g. medicine herbs and mushrooms) under older tree plantations (Huang and Wang 1992), resulting in an increase in the productivity of land. The land productivity increase due to complementary use of resource compared to the sole-tree plantation, S_{tr}, could be determined by

$$S_{tr} = W_{total} - W_{a,tr} \quad (5)$$

where W_{total} is the total yield in agroforestry. Compared to the sole-tree plantation at the same density, the productivity increase of land is due to introducing arable crops under the tree plantation. In practice, it is difficult to extract the exact benefit that is specifically from the mechanism of resource-sharing because of shortage of well designed experiments. In the present study, the yield of intercropped arable crops was used as an approximation to the yield increase that is a result of additional use of available resources.

Ong (1995, 1996) proposed a tree-crop interaction equation for quantifying the crop and the tree component effect (Sanchez 1995),

$$I_c = F_c - C_c \quad (6)$$

where I_c is the overall interaction, as a percentage of sole-crop yields free from interference with trees; F_c is the fertility effect, i.e. the percentage of crop-yield increase caused by soil fertility improvements (nutrient inputs from tree pruning and microclimate modifications such as less soil evaporation, lower soil temperatures); and C_c is the competition effect, i.e. the crop-yield decrease caused by competition with trees for light, water and nutrients. A positive value of overall interaction in this equation means net complementarity, the desired outcome of agroforestry, and a negative value of overall interaction means net competition to the detriment of crop yields (Sanchez 1995). It is claimed that this equation differs from the classic intercropping ones of land equivalent ratios or relative yield totals in that the complementary and competition effects are not separated (see Sanchez 1995).

The value of the parameters can be obtained from the following treatments: (1) Co = sole crop; (2) Cm = sole crop + mulch from pruned trees; (3) Ho = crop + tree with mulch removed; (4) Hm = crop + tree with its mulch. F_c can be measured as $Cm - Co$, that is the effect of tree prunings due to their nutrient input upon decomposition plus microclimatic changes on the soil surface. F_c is therefore the fertility effect in its broadest sense, involving both nutrient availability and soil physical changes (Sanchez 1995). C_c can be obtained by $Hm - Cm$ or $Ho - Co$, that is the effect of trees on arable crop yields separate from the fertility effect. Therefore it makes the determination of crop-yield effects operational (Ong 1995, 1996; Sanchez 1995):

$$I_c = (Cm - Co) - (Hm - Cm) \quad (7)$$

The units of interaction, e.g. fertility effect and competition, are presented as the percentage of sole-crop yield. In the present study, the tree-crop interaction equation was tried to be employed to describe the interaction types and to help to understand the model of coexistence gain. In order to describe and predict the outcome of coexistence gain simply, the units of the present model were used in a different way (i.e. as yield per unit land instead of the percentage of Ong's tree-crop equation). This is easier in a complex model because it is not necessary to exchange the units (e.g. percentage vs. yield per unit land) frequently.

The coexistence gain in a deliberately designed agroforestry system could be expected to be obtained by exploiting the positive interaction and by complementing in resource use, or in other words, by separating the interaction effect and complementary use of resources. The development of coexistence gain of populations can be simply expressed as shown in Fig. 5. In agroforestry systems, sharing a resource covers the sharing of economic, ecological and social resources. Facilitation appears in the procedure of interaction between components, e.g. trees and intercrops.

The theoretical framework of the yield dynamics of individual species (tree species or arable crops) in *T. ascendens*-intercrop systems could be expressed as:

$$\frac{dW_i}{dt} = M_i(W_i,t) - C_i(W_i,t) + F_i(W_i,t) \quad (8)$$

where W_i is the yield variable of species i (i = tree species, wheat, soybean, ...); t is the time variable; Function $M_i(W_i, t)$ describes the rate of yield change of species i in monoculture; Function $C_i(W_i, t)$ that of yield loss of species i due to competition, and $F_i(W_i, t)$ that of yield increase of species i due to management facilitation in agroforestry. Eq. 8 only describes the yield change process of individual species (e.g. *T. ascendens* or soybean) in agroforestry systems, thus without "resource-sharing" term.

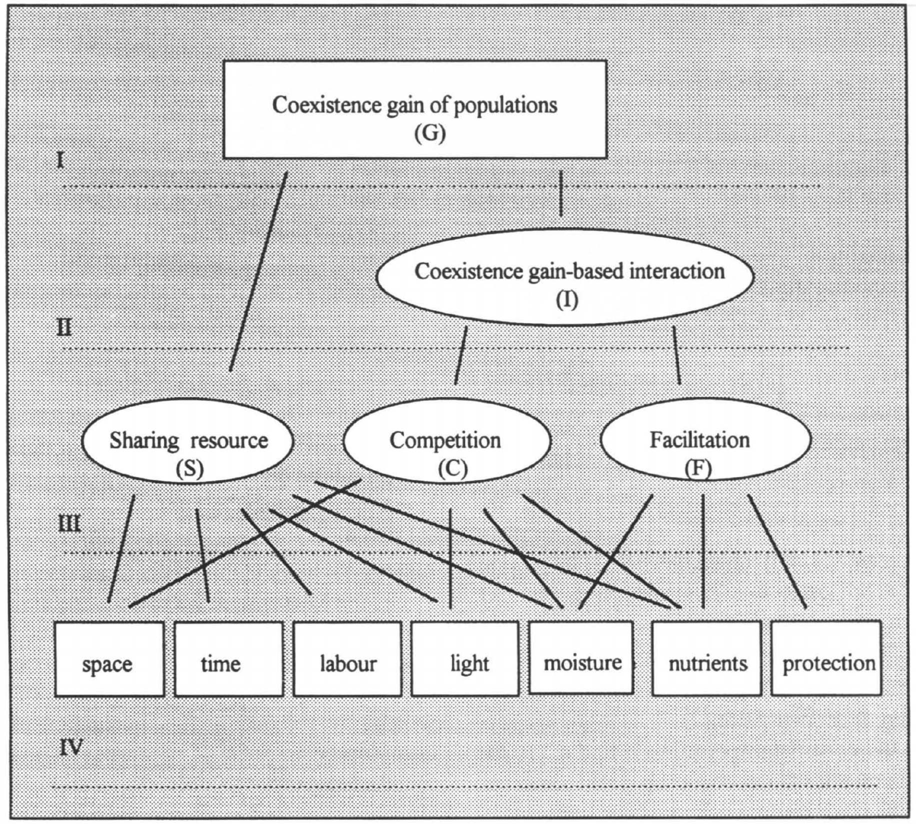

Fig. 5. Diagrammatic illustration of the coexistence gain of populations in *T. ascendens*-intercrop systems.

The theoretical framework of yield change of *T. ascendens*-intercrop systems is expressed as:

$$A(W,t) = M_{tr}(W,t) - C_{tr}(W,t) + F_{tr}(W,t) + S_{tr}(W,t) \qquad (9)$$

where term M_{tr} describes the yield change process of tree species in sole-tree plantation; C_{tr} describes the change process of yield loss of tree species due to the presence of arable crops, F_{tr} that of yield increase of tree species due to management facilitation in agroforestry, and S_{tr} that of resource-sharing gain due to complementary use of resources compared to the sole-tree plantation, which is a considerable advantage in agroforestry systems for efficient use of environmental resources (Huang and Wang 1992, Huang et al. 1993). Eq. 9 describes the dynamic process of whole yield (including trees and intercrops) in agroforestry, obviously the term $S_{tr}(W, t)$ should be added. Eq. 8 and 9 will be determined by the following interaction equations.

2.3 Interaction Model and Analyses

2.3.1 Model Structure

Gilpin and Ayala (1973) proposed a general competition model (including that of Lotka and Volterra as a special case when ($\theta_i = 1$)

$$\frac{dW_i}{dt} = r_{i0}W_i\left[1-\left(\frac{W_i}{K_i}\right)^{\theta_i} - \alpha_{ij}\frac{W_j}{K_i}\right] \qquad (10)$$

where W_i represents the density of population for species i, and W_j that for species j; θ_i describes any asymmetry in the growth curve of the single species i; K_i is the carrying capacity of species i and α_{ij} the competition coefficient of species j on species i; and r_{i0} is the intrinsic rate of increase of species i. The Lotka-Volterra model is admittedly very simple and might not reflect all the complexities suggested by our knowledge of the mechanisms of competition (Roughgarden 1979, Pascual and Kareiva 1996). Gilpin and Ayala (1973, 1976) attempted to construct a general, yet accurate competition model, used Ayala's input/output data on *Drosophila pseudoobscura* and *D. willistoni*, and found them to agree well with the model. The Gilpin-Ayala model (GA model) could usefully be studied with a variety of other organisms (Harper 1977, Emlen 1984). But it is not so certain that this model may well fit the competition process as it occurs in nature. In the field, more than two species may often compete for the same resources, and additional complexities are likely to occur which do not exist in the laboratory.

The Lotka-Volterra model (LV model) is based on the logistic theory of population growth and is subject to the same criticisms as the logistic theory which is far from perfect for reflecting all the complexities because of its simplification (Emlen 1984, Renshaw 1991, Pascual and Kareiva 1996). It also assumes that competitive interactions, both intra- and inter-specific, are linear (Ayala et al. 1973). The GA model assumes that the competitive effect of one species on the growth of another is linearly proportional to the density of the first, and α_{ij} and α_{ji} are invariant with W_i and W_j, a simplification that is almost surely inaccurate (Emlen 1984). Adding ψ_i, an exponent that permits the interaction curve of inter-species to vary in any asymmetry, to the above equation will change the model relating growth rate of one species to the density of another species. This appears to increase the range of accurate representation since the approximation is performed in logarithmic space with power-law representations (Voit and Sands 1996, Peschel and Mende 1986).

Compared with the LV model and GA model, an alternative approach is the hyperbolic yield-density model (or reciprocal equation), which was first proposed by Shinozaki and Kira (1956). This equation was derived from a simple logistic growth curve and the law of constant final yield (Willey and Heath 1969). The relationship assumes a linear relationship between the reciprocal of yield per plant and density. Afterwards, this approach has been applied in many studies and different equations have been proposed (Holliday 1960, Wright 1981, Spitters 1983). Following these studies, this relationship was introduced to analyse the competitive phenomena in mixtures (Wright 1981, Spitters 1983, Helenius and Jokinen 1994). Spitters (1983) expanded the reciprocal yield model for multiple species: $1/w_i = A_i + B_{ii}N_i + B_{ij}N_j$. In this model, w_i is the plant weight of component i in mixture, N_i and N_j are the plant densities of i and j respectively, B_{ii} and B_{ij} are intra- and inter-specific competition coefficients. The reciprocal of average yield per plant of species i ($1/w_i$) is described by a theoretical maximum yield per plant ($1/A$), by its own density and by the density of a second species. This model has many advantages: first, it can realistically describe the parabolic yield-density situation; second, parameters have a good deal of biological meaningfulness; and third, parameters can be easily estimated by regression analysis. Obviously, this model also assumes that the reciprocal of average yield per plant of species i ($1/w_i$) is linearly proportional to its own and the second species densities. It seems likely that the inevitable interactions in mixture are a far more complex situation than can be described by a few simple constants with linearly proportional relationship. The coefficient of variation of $1/w_i$ is assumed to be constant over the density range. This is also somewhat unrealistic, as the size inequality between plants in most cases increases with increasing density (Weiner 1990).

In the present study it was assumed that competitive interactions in nature, both intra- and inter-specific, were not linearly proportional due to resource interactions and environmental uncertainty involved, and exponents θ_i and ψ_i were added to describe any asymmetry in the growth curve of the single species and the interaction curve of inter-species. Thus this model perhaps gives a more flexible, realistic and precise representation in complex ecosystems. The new model is expressed as follow:

$$\frac{dW_i}{W_i dt} = r_{i0}\left[1-\left(\frac{W_i}{K_i}\right)^{\theta_i} - \alpha_{ij}\left(\frac{W_j}{K_i}\right)^{\psi_i}\right] \qquad (11)$$

In the logistic equation $(dW/dt)/W = r_0(1 - W/K)$, r_0/K is the density-feedback term: the addition

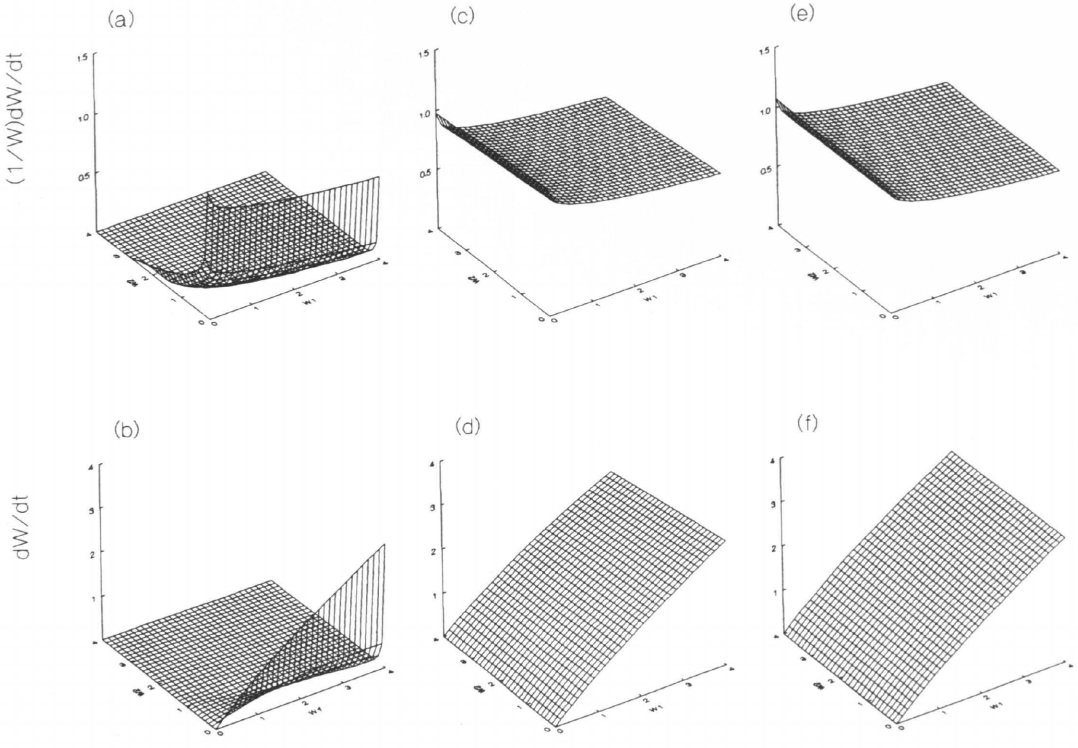

Fig. 6. Per capita (upper row) and population (lower row) growth curves for various instances of equations: $(1/W_i)\, dW_i / dt = r[1 - (W_i / K)^{\theta} - \alpha(W_j / K)^{\psi}]$ and $dW/dt = rW\,[1 - (W_i / K)^{\theta} - a\,(W_j / K)^{\psi}]$. With ψ free to change, and all other parameters fixed ($r_0 = 1.074$, $K = 89.875$, $\theta = 0.342$, $\alpha = 2$). In (a) and (b), $\psi = 0.2$; in (c) and (d), $\psi = 1$; in (e) and (f), $\psi = 5$.

of one individual to the population lowers $(dW/dt)/W$ by an amount r_0/K (Emlen 1984), and in this sense the coefficient ψ_i can be termed as the feedback rate of inter-specific competition, and θ_i as the rate of feedback of intraspecific competition. If $\psi_i = 1$, it is the Gilpin-Ayala model; if both $\psi_i = 1$ and $\theta_i = 1$, the Lotka-Volterra model.

Extending this model to a three or more species plant community gives

$$\frac{dW_i}{W_i dt} = r_{i0}\left[1 - \left(\frac{W_i}{K_i}\right)^{\theta_i} - \sum_{j \neq i} \alpha_{ij}\left(\frac{W_j}{K_i}\right)^{\psi_i}\right] \qquad (12)$$

If we assume that there exists a joint effect of multiple species on the growth rate of species i and this joint effect is multiplicative, then we have

$$\frac{dW_i}{W_i dt} = \qquad (13)$$
$$r_{i0}\left[1 - \left(\frac{W_i}{K_i}\right)^{\theta_i} - \sum_{j \neq i} \alpha_{ij}\left(\frac{W_j}{K_i}\right)^{\psi_i} - \alpha'_{ij}\left(\frac{\prod_{j \neq i} W_j}{K_i}\right)^{\psi'_i}\right]$$

where α'_{ij} is the joint effect coefficient, and ψ'_i the feedback rate of joint effect.

For the effect of added fertilisers on growth dynamics of tree species in density-independent communities, we assume that the effect of added fertiliser on tree species is the same as the effect on arable crops, and thus add a term involving the population expansion in arable crops to the above equation, i.e. using the population densities of arable crops to predict the growth of tree species in fertilised environment (in the specific case of

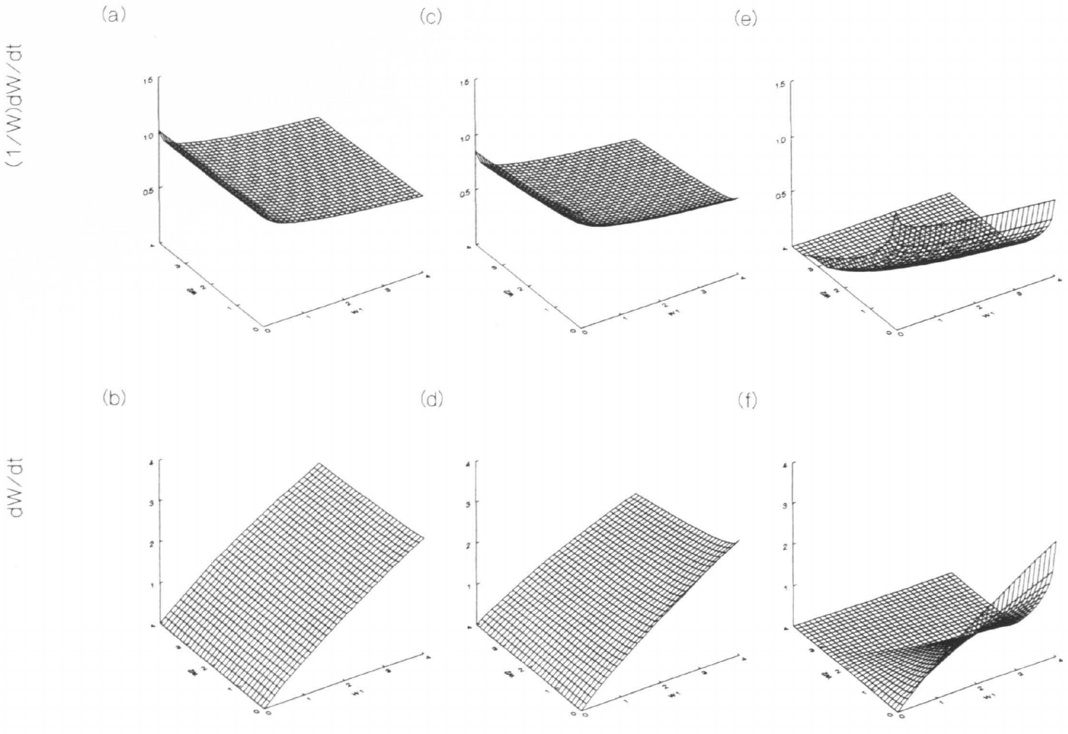

Fig. 7. Per capita (upper row) and population (lower row) growth curves for various instances of equations: $(1/W_i)\, dW_i /dt = r[1^{*} - (W_i / K)^{\theta} - \alpha(W_j /K)^{\psi}]$ and $dW/dt = rW[1 - (W_i / K)^{\theta} - a\,(W_j /K)^{\psi}]$. With α free to change, and all other parameters fixed ($r_0 = 1.074$, $K = 89.875$, $\theta = 0.342$, $\psi = 0.5$). In (a) and (b), $\alpha = 0.2$; in (c) and (d), $\alpha = 1$; in (e) and (f), $\alpha = 5$.

this study, there were different assumptions, see below),

$$\frac{dW_i}{W_i dt} = \qquad (14)$$
$$r_{i0}\left[1 - \left(\frac{W_i}{K_i}\right)^{\theta_i} - \sum_{j \neq i} \alpha_{ij}\left(\frac{W_j}{K_i}\right)^{\psi_i} - \alpha'_{ij}\left(\frac{\prod_{j \neq i} W_j}{K_i}\right)^{\psi'_i}\right]$$
$$+\beta_{ij}\left(\sum_j W_j\right)^{\lambda_i}$$

where β_{ij} refers to the coefficient of management facilitation due to fertilisation, and λ_i is the feedback rate of management facilitation. Fertilisers seem to affect the resource levels in soil and would, in this sense, affect K_i if the asymptotically maximum yield in unfertilised monoculture was taken as K_i, or would not if we suppose that added fertilisers would not influence the density-dependent maximum yield. This can be determined by the observed data. More details about the application of the model are presented in Materials and Methods.

2.3.2 *Implication of Model Coefficient α_{ij} and ψ_i for Species Combination*

Under certain conditions, there are optima for species combination in an intercropping community. Assuming that the growth dynamics in an intercropping community is described by Eq. 11, there are two parameters, ψ_i and α_{ij}, that can be

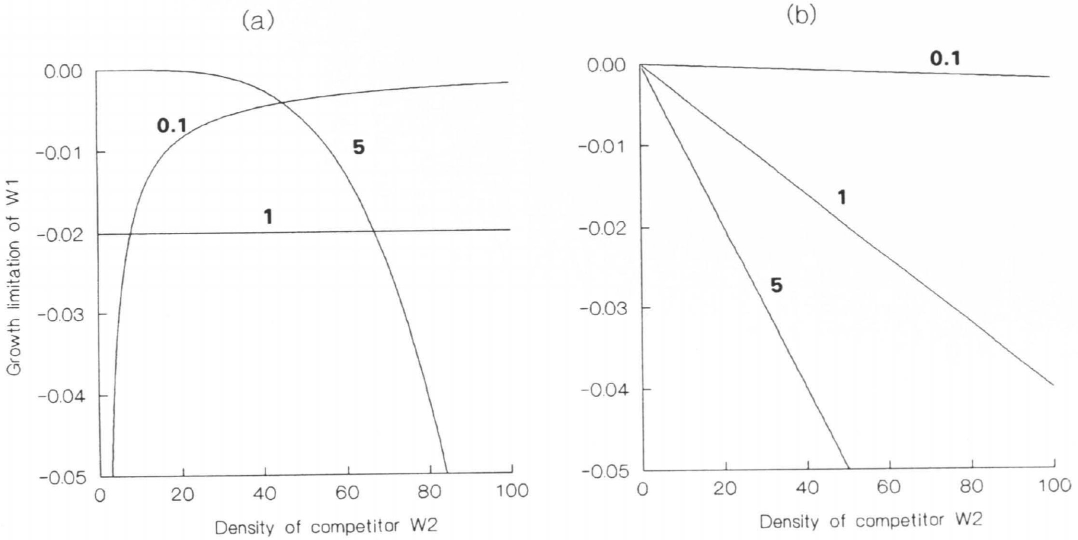

Fig. 8. Relative per capita W_i growth limitation vs density of W_j. In all cases, K is fixed (= 100). (a) Competitive coefficient α is fixed (= 2), ψ = 0.1, 1, and 5; (b) ψ is fixed (= 2), α = 0.1, 1, and 5.

used to determine the species selection for better ecological combination. If ψ_i is free to change and the other parameters are fixed, the species with highest ψ_i (Fig. 6e and 6f) are favoured because higher ψ_i has higher population growth and per capita growth rates (Fig. 6). That is, species W_j that makes species W_i maintain a higher growth rate (or less pressure on the growth of W_i) under competitive pressure from W_j is selectively favoured for the combination of species in intercropping systems.

The competition coefficient α_{ij} is inversely related to ψ_i (see Eq. 11); as can be seen from Fig. 7, the favoured species can be determined by comparing the population growth and per capita growth rates. The highest growth rates (both $(1/W_i)\, dW_i / dt$ and dW_i /dt) of species W_i appear in the lowest α_{ij} (Fig. 7a and 7b), indicating a lower competitive effect from species W_j.

The relative per capita W_i growth limitation (Gilpin et al. 1976) caused by an additional individual of W_j is (see Eq. 11)

$$\frac{\partial}{\partial W_j}\left(\frac{dW_i}{W_i dt}\right)=\frac{\alpha_{ij}\psi_i}{W_j}\left(\frac{W_j}{K_i}\right)^{\psi_i} \tag{15}$$

This per capita growth limitation can be plotted as a function of W_j for different values of ψ_i and α_{ij}. Fig. 8a shows that (when both K_i and α_{ij} are fixed) for $\psi_i = 1$, the Lotka-Volterra equation and the Gilpin model, each individual of W_j has the same effect on the per capita growth rate of W_i, regardless of the density of W_j. For $\psi_i < 1$ (= 0.1), individuals of species j at low densities (e.g. $W_j < 50$) have much greater per capita growth limitation on W_i than that for $\psi_i > 1$ (= 5). At high densities (e.g. $W_j > 50$), this growth limitation can be inversely demonstrated; that is, for $\psi_i > 1$ (= 5), individual of species j have greater per capita growth limitation on W_i than that for $\psi_i < 1$ (= 0.1). Fig. 8b shows that when both K_i and ψ_i are fixed, lower values of competition coefficients α_{ij} have a less per capita growth limitation on W_i than higher values of α_{ij}. The growth limitation is linearly proportional to the increasing densities of W_j.

3 Materials and Methods

3.1 Site Description and Experiments

Agroforestry systems were set up in the Lixiahe wetlands (32°42'–33°96'N and 119°15'–120°51'E) (Fig. 9), Jiangsu Province, China, at an altitude of 1–5 m above sea level (Table 4), where the mean annual rainfall and temperature are around 1000 mm and 14–15 °C respectively.

Experiments with a complete-randomized block design were established at Zhaoguan Forestry Farm in 1984 and run until 1993. Four spacing configurations of *T. ascendens* were applied, with the same overall planting density (1667 trees ha^{-1}). The four spacing configurations were 2 × 3 m, 1.5 × 4 m, 1.2 × 5 m, 1.5 × 2 × 6 m (double-row configuration, 1.5 m = the distance of within-rows, 2 m = the distance of narrow between-rows, and 6 m = the distance of wide between-rows). There were three replicates for each spacing configuration. A control plot of trees without intercropping was randomly chosen in each replicate. The arable crop monoculture was conducted with three replicates side by side with each replicate of four tree spacing configurations. The total area of this trial was 6 ha. Intercropping was conducted in the four tree spacing configurations. Wheat and rape were sown in spring, and after wheat (in June) and rape (in May) were harvested, soybean was sown immediately. These high light-requiring arable crops were intercropped during the first five years, and ryegrass was intercropped in the following two years.

When the tree stands were three years old, five densities of soybean and mung bean (*Vigna radiata* L. Wilczek) were intercropped in the four stands. Both density experiments of soybean and mung bean were designed in complete-randomized blocks (five densities and three replicates). Using bunch seeding, there were three seeds sown in each bunch (Table 5).

Another field study involved the growth of *T. ascendens* and arable crops (wheat and soybean) when both species grew together and when each grew alone in control. *T. ascendens* and arable crops (wheat and soybean) were grown in monoculture; two species (tree+wheat and tree+soy-

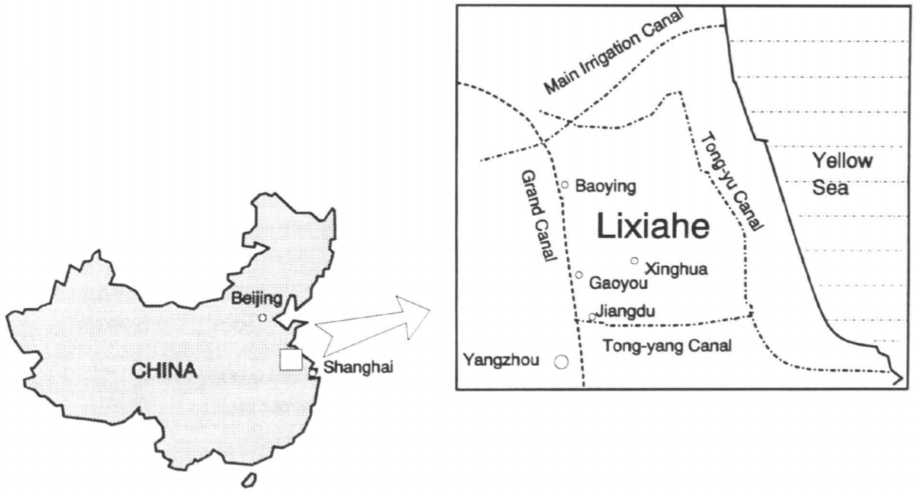

Fig. 9. Location of Lixiahe lowlands, in Jiangsu Province, China.

bean) and three species (tree+wheat+soybean, i.e. two-season intercropping: wheat as the winter intercrop and soybean as the summer intercrop,) were grown together; and three species (tree+ wheat+soybean) were grown together with nitrogen fertilisation. In real intercropping systems, fertilisers are frequently applied to the arable crops for high crop yields under trees. It was assumed that the adding of fertiliser to arable crops could not only increase the yields of crops but also facilitate the tree growth. The effect of added fertilisers can thus be considered as an indirect facilitation effect of wheat or soybean intercropping on tree growth.

T. ascendens was planted in February 1985. Tree density was 1667 trees ha^{-1} with a spacing of 1.5 × 4 m in the intercropping and sole-trees. This experiment was conducted in a complete-randomized block design and each treatment was replicated three times. Intercropping was done under trees during the first five years. Wheat and rape were sown in November and soybean in June. The seeds of arable crops were sown at the same density in the fields under tree stands and in arable crop monoculture. In the fertilisation plots, a fixed amount of nitrogen fertiliser, 750 kg ha^{-1} yr^{-1} (17.5 % of N, thus 131 kg of N ha^{-1} yr^{-1}), was added annually (65.5 kg for wheat and 65.5 kg for soybean). The nitrogen fertiliser was tilled into the soil when wheat or soybean was sown between the tree rows and in crop monoculture. No other measures (e.g. application of pesticides) were taken afterwards.

Table 4. Proportion of the areas of different altitudes above sea level in Lixiahe region (Huang and Huang, unpublished).

Altitude above sea level (m)	Area (km^2)	Proportion (%)
< 1.5	1652	14.2
1.5–2.0	2075	17.8
2.0–2.5	3112	26.7
2.5–3.0	2465	21.1
3.0–3.5	948	8.2
3.5–4.0	554	4.7
4.0–5.0	573	4.9
> 5.0	286	2.4
Total	11665	100

The height, diameter (DBH: stem diameter over bark at 1.3 m) and the crown width and length have measured annually since 1985 till 1993, including crown radius in two directions (across and along rows). A total of twenty-four trees were sampled based on the diameter class for biomass, structural and chemical analyses. Sample trees were carefully felled and stems were cut at intervals of one meter. The fresh weights of leaves, branches, stems, and roots at each layer were measured immediately after cutting in the field, and their dry mass measured after oven-drying (leaves: 105 °C, 24 h; branches, stems and roots: 105 °C; dried to constant weight).

In this forestry experiment farm, we have well studied the relationship between biomass of *T. ascendens* and other components (e.g. DBH, tree height, leaves and roots) (Huang and Huang 1991a, Liu 1990). In the present study, the tree biomass of *T. ascendens* was thus calculated using the fitted regression equations, $DM = 193.87 DBH^{2.178}$ ($R^2 = 0.9935$), where *DM* denotes the total (above- and under-ground) dry mass (g) and *DBH* is the stem diameter (cm) of trees over bark at height 1.3 m (Liu 1990).

Table 5. Sowing densities of soybean and mung bean intercropped with *Taxodium ascendens*.

Crop species	Sowing density (kg ha^{-1})	Spacing (cm)	Area per replicate of tree spacing (ha)			
			Spac I [1]	Spac II	Spac III	Spac IV
Soybean	67.5	25×36.0	0.0018	0.0024	0.0012	0.0036
	75.0	25×32.0	0.0018	0.0024	0.0012	0.0036
	82.5	25×29.5	0.0018	0.0024	0.0012	0.0036
	90.0	25×26.5	0.0018	0.0024	0.0012	0.0036
	97.5	25×25.0	0.0018	0.0024	0.0012	0.0036
Mung bean	30.00	25×36.0	0.0018	0.0024	0.0012	0.0036
	33.75	25×32.0	0.0018	0.0024	0.0012	0.0036
	37.50	25×29.5	0.0018	0.0024	0.0012	0.0036
	41.25	25×26.5	0.0018	0.0024	0.0012	0.0036
	45.00	25×25.0	0.0018	0.0024	0.0012	0.0036

[1] Spac I, Spac II, Spac III and Spac IV refer to tree spacings of 1.5×4 m, 1.2×5 m, 2×3 m and 1.5×2×6 m respectively.

The arable crops, e.g. wheat (*Triticum aestivum*), rape (*Brassica napus*), soybean (*Glycine max*), mung bean (*Vigna radiata*) and ryegrass (*Lolium perenne*) were randomly sampled at the harvesting time (ripe for agricultural harvesting) with five replicates (a total of 15 plots in each spacing, each plot: 1 × 1 m). Their yields and biomasses were measured in the field and in the laboratory, including the grain yields, ears of grain, grains per ear, above-ground and under-ground dry mass. All inputs (costs of seeds, fertilisers, labours etc.) and outputs (yields) of the intercrops were recorded and calculated to determine the threshold of the intercrop production in terms of productive coexistence. The monetary value of intercrop output included grain yields and straw, but for the trees only the timber volume was calculated. Budgets of inputs and outputs in the whole forest farm were annually recorded and calculated, including investment cost, labour, fertiliser, seeds of intercrops, electricity, irrigation, and intercrop yields.

3.2 Soil Analyses

In order to identify the effects of agroforestry management on soil, some factors, e.g. pH, organic matter, carbon, nitrogen, phosphorus, potassium, CEC, Ca, Mg, Al, Fe and Na were analysed. Soil was randomly sampled in the fields of agroforestry systems, tree monocultures, arable crop monocultures, and as a control, in the swamps where the agroforestry experiments were set up in winter of 1984. In this paper, the data sampled and analysed in October of 1993 was used. Every sample spot was vertically sampled in three layers (0–20, 20–40 and 40–60 cm). All soil samples for physical property analyses were carefully cored to avoid structural disturbance. The samples were stored in cloth or plastic-lined sampling bags in the field, and air-dried, ground and sieved for chemical analyses in the laboratory.

Soil pH was determined by a pHS-2 meter with a soil/water solution ratio of 1:2.5 (Academia Sinica 1978). Total N was determined by the Kjeldahl method and soil samples were digested in sulphuric acid along with potassium sulphate (Academia Sinica 1978, Bremner and Mulvaney 1982, Binkley and Vitousek 1989). For water-soluble nitrogen analysis, soil samples were hydrolysed by sodium hydroxide and a mixture of $FeSO_4 7H_2O$ with zinc; ammonia-N was absorbed by boric acid and N was determined by titrating with 0.01 N standard hydrochloric solution (Academia Sinica 1978, Binkley and Vitousek 1989). Available P was extracted by sodium bicarbonate and determined by a spectrophotometer 721 (Academia Sinica 1978, Olson and Sommers 1982). K, Ca, Mg and Na were digested with $HF\text{-}HClO_4$ in a Pt crucible. K and Na were determined by flame photometry, and Ca and Mg were determined by EDTA titrimetry (Academia Sinica 1978, Lanyon and Heald 1982, Knudsen et al. 1982). Si, Fe, Al were dissolved by Na_2CO_3 fusion. Si was determined by gravimetry, Fe by atomic absorption, and Al by titrimetry (Academia Sinica 1978, Barnhisei and Bertsch 1982, Olson et al. 1982, Hallmark et al. 1982). Cation-exchange capacity (CEC) was determined by titrating with standard hydrochloric solution following extraction with the ammonium acetate method and a centrifugal machine (Academia Sinica 1978).

3.3 Determination of Model Parameters

In this study, time, *t* (year), or age of tree stands and yield, *W*, (DW, tons ha^{-1}) were taken as the principal components. Eq. 9 is then

$$\frac{dW}{dt} = M_{tr}(W,t) + F_{tr}(W,t) - C_{tr}(W,t) + S_{tr}(W,t) \qquad (18)$$

where *W* is the yield (DW, tons ha^{-1}) of total as trees plus arable crops in the *T. ascendens*-intercrop system; F_{tr} is the facilitation gain (tons ha^{-1}) of tree species (*T. ascendens*); C_{tr} the competition loss (tons ha^{-1}) of tree species, i.e. the decrease in tree growth caused by the competition effect of arable crops on trees for nutrients and water; and S_{tr} represents the yield (tons ha^{-1}) of complementary use of resources. The two terms are thus equivalent to the overall interaction in Eq. 7. In the present study, the indirect effect of fertilisation N on tree species, as an indirect facilitation (F_{tr}), was the difference between the trees grown in fertilised plots and unfertilised plots at age *i* in the intercropping regime, and the competition loss of arable crops on trees was the difference between the tree growth in monoculture and tree growth in the intercropping regime at age *i* (in unfertilised plots). The overall interaction, facilitation and competition loss can be thus determined by:

$$I_{tr}(W,t) = F_{tr}(W,t) - C_{tr}(W,t) \tag{19}$$

$$F_{tr}(W,t) = \tag{20}$$

$$\left(\frac{dW_{a,trf}}{dt} - \frac{dW_{m,tr}}{dt}\right) + \left(\frac{dW_{m,tr}}{dt} - \frac{dW_{a,tr}}{dt}\right) =$$

$$\frac{dW_{a,trf}}{dt} - \frac{dW_{a,tr}}{dt}$$

$$C_{tr}(W,t) = \frac{dW_{m,tr}}{dt} - \frac{dW_{a,tr}}{dt} \tag{21}$$

where the superscript *m,tr* indicates the tree growth in monoculture, the subscript *a,tr* denotes the tree (unfertilised) growth in agroforestry, and *a,trf* the tree growth in the fertilised plots in agroforestry.

The last term on the right of Eq. 18 stands for the yields of arable crops (wheat and soybean) since we consider the production of arable crops under trees as an index of complementary use of resources, a result of additional use of available resources by growing crops under trees. This was determined by

$$S_{tr}(W,t) = \frac{dW_w}{dt} + \frac{dW_s}{dt} \tag{22}$$

where the subscript *w* denotes the yield of wheat, and *s* the yield of soybean (in agroforestry systems).

The tree growth in monoculture (M_{tr}) was determined by

$$M_{tr}(W,t) = \frac{dW_{m,tr}}{dt} \equiv r_{tr0} W_{m,tr}\left[1 - \left(\frac{W_{m,tr}}{K_{tr}}\right)^{\theta_m}\right] \tag{23}$$

where θ_m denotes the feedback rate of tree growth in tree monoculture.

Obviously, Eq. 18 is relative to Eqs. 12–14. In Eq. 18 the right term, M_{tr}, is determined by Eq. 23, F_{tr} by the difference between Eq. 14 and Eq. 13, C_{tr} by the difference between Eq. 23 and Eq. 12, and the gain of resource sharing under trees, S_{tr}, by the sum between wheat and soybean, i.e. Eq. 22 (also see Table 6).

When confronted with the task of fitting the Lotka-Volterra model to experimental data, most ecologists have obtained *r* and *K* by a standard technique, linear regression. Then given a point estimate for each species' *r* and *K*, a similar regression approach can be used to estimate the competition coefficients (Pascual and Kareiva 1996, Roughgarden 1979). However, one weakness for this approach is that the use of the point estimates of *r* and *K* from pure culture experiments to estimate the α's in the second stage conceals the uncertainty about the initial *r* and *K* parameter estimates (Pascual and Kareiva 1996). In this study the data in tree monoculture was used to estimate the parameter *K* of tree species using the logistic equation, and $(dW/dt)/\ W = r[1 - (W\ /\ K)^{\theta}]$ was used to estimate θ and r_0.

To estimate the indirect facilitation coefficient, β_{ij}, we assume that the amount of fertiliser N that could be shared by trees increases with decreasing growth of arable crops under trees from year to year. For example, wheat grown under the stands of *T. ascendens* absorbed 47.91 kg N ha^{-1} at tree-stand-age four, and 41.13 kg N ha^{-1} at age five (Liu 1990). We also assume that the larger trees would be able to tap more nutrients from soil (Comerford et al. 1980, Pan and Raynal 1995). For example, *T. ascendens* absorbed 160.52 kg N ha^{-1} in an intercropping system when the mean tree diameter (DBH) was 5.1 cm, and 182.9 kg N ha^{-1} when the mean tree diameter (DBH) was 7.54 cm (Liu 1990). Therefore, we have a formula from Eq. 14 for *T. ascendens*

$$\frac{dW_{trf}}{dt} = \frac{dW_{tws}}{dt} + \beta_{trj}\sum_{tr\neq j} W_j^{'} + \gamma_{tr}\left(\frac{W_{trf}}{K_{trf}}\right)^{\lambda_{tr}} \tag{24}$$

where W_{trf} is the tree biomass (DW) (tons/ha) in the fertilised tree+wheat +soybean system, W_{tws} is the tree biomass in the unfertilised tree+wheat +soybean system, β_{trj} and γ_{tr} the facilitation coefficient of fertilised intercropping regime on trees, λ_{tr} the rate of facilitation feedback of fertilised intercropping regime on trees, K_{trf} the final maximum biomass in the stands of *T. ascendens* in the fertilised monoculture, and W_j' is the differences between the maximum yields (K_j) of arable crops (j = wheat and soybean) in fertilised monoculture and those (W_j) in fertilised intercropping regime at age *i* (i.e. $W_j' = K_j - W_j$).

Considering the growth of annual crops (e.g. wheat and soybean) under trees, the difficulty is that the tree species is perennial, while wheat or soybean is annual. The comparison in yield dynamics by years between perennial and annual species using the above model requires a reasonable approach. There are two alternatives. One is that the growth of annual crops each year and the annual growth of tree are taken as one generation. The other is that the annual intercrops are assumed as the 'perennial' crops as tree species. The 'decreasing or increasing rate' of yield of intercrops versus time (year) in monoculture may be ignored (i.e. identical yield from year to year) if we assume that the required resources are fully provided. If wheat grows in an environment with limited available resources, the consecutively annual yield would decrease due to reduced nutrient level in soil with annual harvest. The mean yields of crops in the first year in monoculture could thus be considered as the maximum yield, K_c. In this study, we used the latter alternative. The K_c was calculated using the data of wheat or soybean in monoculture by the logistic equation: $dW_c/dt = r_{c0}W_c(1 - W_c/K_c)$, where W_c is the yield of arable crops and K_c the maximum yields of arable crops. To make the equation forms of interactions of wheat or soybean vs tree species identical to those of tree species vs the arable crops, the competition equation was used in the form:

$$\frac{dW_c}{dt} = r_{c0}W_c\left[1 - \left(\frac{W_c}{K_c}\right)^{\theta_c} - \alpha_{ct}\left(\frac{W_{tr}}{K_c}\right)^{\psi_c}\right] \tag{25}$$

where r_{c0} is the rate of change of crop yields by years, W_c the yields of arable crops, α_{ct} competition coefficient of *T. ascendens* on intercrops, W_{tr} the yield of tree species, K_c the maximum yields of arable crops, θ_c the feedback rate of intraspecific competition of arable crops, and ψ_c the feedback rate of interspecific competition of trees on intercrops. In the fertilised plots, a formula for intercrops (wheat and soybean) was used:

$$\frac{dW_{cf}}{dt} = \frac{dW_c}{dt} + \beta_c W_{tr}^{'} + \gamma_c\left(\frac{W_{cf}}{K_{cf}}\right)^{\lambda_c} \tag{26}$$

where W_{cf} is the biomass yields (tons/ha) of arable crops in the fertilised intercropping plots (tons/ha), β_c the facilitation coefficient of the fertilised intercropping regime on intercrops, W_{tr}' the differences (tons/ha) between the final maximum biomass (K_{tr}) of *T. ascendens* in monoculture and the tree biomass (W_{trf}) in the fertilised intercropping regime at age i (i.e. $W_{tr}' = K_{tr} - W_{trf}$), γ_c is the facilitation coefficient of the fertilised intercropping regime on intercrops, K_{wf} the maximum yield of intercrops in the fertilised monoculture, and λ_c is the rate of facilitation feedback of fertilised intercropping regimes on intercrops.

3.4 Calculation of Tree Canopy and Open-range Index

(1) Asymmetric crown development

The most observable direct plant-plant interaction is the spatial competition in the tree crown, and consequent development of an askew crown, in which the competitive pressure comes from the expanded crown of adjacent plants. In this study we define asymmetric crown development ratio (*ACDR*) as:

$$ACDR = (Cr_r - Cr_p)/[\ 0.5(Cr_r + Cr_p)] \tag{27}$$

where Cr_r is the crown width (m) of between-rows, and Cr_p is that of within-rows. The equation describes the ratio of the difference ($Cr_r - Cr_p$) between crown width of between-rows and that of within-rows to the mean crown width ($0.5(Cr_r + Cr_p)$) of between-rows and within-rows, assuming that if the trees are growing without direct crown competition between plant-plant, the tree crown develops normally, i.e. $Cr_r - Cr_p = 0$.

(2) Between-rows open-ranges and relative between-rows open-ranges

The arable crops are often intercropped in the open range of between-rows of tree stands. In order to

Table 6. Equations used to model the population dynamics and interactions among plant populations in *Taxodium ascendens*-intercrop systems.

Eq. 6.1. The yield dynamics in *T. ascendens*-intercrop systems.

$A(W, t) = M_{tr}(W, t) + F_{tr}(W, t) - C_{tr}(W, t) + S_{tr}(W, t)$

Eq. 6.2. The overall interaction in the *T. ascendens*-intercrop systems where tree species was taken as a principal component.

$I_{tr}(W, t) = F_{tr}(W, t) - C_{tr}(W, t)$

Eq. 6.3. The facilitation gain of tree species, which was caused by the application of fertiliser to the intercrops.

$$F_{tr}(W,t) = \left(\frac{dW_{trf}}{dt} - \frac{dW_{m,tr}}{dt}\right) + \left(\frac{dW_{m,tr}}{dt} - \frac{dW_{tws}}{dt}\right) = \frac{dW_{trf}}{dt} - \frac{dW_{tws}}{dt}$$

Eq. 6.4. The competition loss of *T. ascendens*, which is caused by intercrops.

$$C_{tr}(W,t) = \frac{dW_{m,tr}}{dt} - \frac{dW_{tws}}{dt}$$

Eq. 6.5. The yield of resource sharing under trees.

$$S_{tr}(W,t) = \frac{dW_{wf}}{dt} + \frac{dW_{sf}}{dt}$$

Eq. 6.6. The growth of *T. ascendens* without interaction with intercrops.

$$M_{tr}(W,t) = \frac{dW_{m,tr}}{dt} \equiv r_{tr0} W_{m,tr}\left[1 - \left(\frac{W_{m,tr}}{K_{tr}}\right)^{\theta_m}\right]$$

Eq. 6.7. The interaction model between *T. ascendens* and wheat in the *T. ascendens*+wheat system.

$$\begin{cases} \dfrac{dW_{trw}}{dt} = r_{tr0} W_{trw}\left[1 - \left(\dfrac{W_{trw}}{K_{tr}}\right)^{\theta_{tw}} - \alpha_{trw}\left(\dfrac{W_w}{K_{tr}}\right)^{\psi_{tw}}\right] \\ \dfrac{dW_w}{dt} = r_{w0} W_w\left[1 - \left(\dfrac{W_w}{K_w}\right)^{\theta_w} - \alpha_{wt}\left(\dfrac{W_{trw}}{K_w}\right)^{\psi_{wt}}\right] \end{cases}$$

Eq. 6.8. The interaction model between *T. ascendens* and soybean in the *T. ascendens*+soybean system.

$$\begin{cases} \dfrac{dW_{trs}}{dt} = r_{tr0} W_{trs}\left[1 - \left(\dfrac{W_{trs}}{K_{tr}}\right)^{\theta_{ts}} - \alpha_{trs}\left(\dfrac{W_s}{K_{tr}}\right)^{\psi_{ts}}\right] \\ \dfrac{dW_s}{dt} = r_{s0} W_s\left[1 - \left(\dfrac{W_s}{K_s}\right)^{\theta_s} - \alpha_{st}\left(\dfrac{W_{trs}}{K_s}\right)^{\psi_{st}}\right] \end{cases}$$

Eq. 6.10. The interaction model between *T. ascendens* and wheat as well as soybean in the fertilised *T. ascendens*+wheat+soybean system (two seasonal intercropping).

$$\begin{cases} \dfrac{dW_{trf}}{dt} = \dfrac{dW_{tws}}{dt} + \beta_{tr}(W_w^{'} + W_s^{'}) + \gamma_{tr}\left(\dfrac{W_{trf}}{K_{trf}}\right)^{\lambda_{tr}} \\ \dfrac{dW_{wf}}{dt} = \dfrac{dW_{w2}}{dt} + \beta_w W_{tr}^{'} + \gamma_w\left(\dfrac{W_{wf}}{K_{wf}}\right)^{\lambda_w} \\ \dfrac{dW_{sf}}{dt} = \dfrac{dW_{s2}}{dt} + \beta_s W_{tr}^{'} + \gamma_s\left(\dfrac{W_{sf}}{K_{sf}}\right)^{\lambda_s} \end{cases}$$

Eq. 6.9. The interaction model between *T. ascendens* and wheat as well as soybean in the *T. ascendens*+wheat+soybean system (two seasonal intercropping).

$$\begin{cases} \dfrac{dW_{tws}}{dt} = r_{tr0} W_{tws}\left[1 - \left(\dfrac{W_{tws}}{K_{tr}}\right)^{\theta_{tws}} - \alpha_{tw2}\left(\dfrac{W_{w2}}{K_{tr}}\right)^{\psi_{tw2}} - \alpha_{ts2}\left(\dfrac{W_{s2}}{K_{tr}}\right)^{\psi_{ts2}} - \alpha'_{tws}\left(\dfrac{W_{w2}W_{s2}}{K_{tr}}\right)^{\psi_{tws}}\right] \\ \dfrac{dW_{w2}}{dt} = r_{w0} W_{w2}\left[1 - \left(\dfrac{W_{w2}}{K_w}\right)^{\theta_{w2}} - \alpha_{wt2}\left(\dfrac{W_{tws}}{K_w}\right)^{\psi_{wt2}}\right] \\ \dfrac{dW_{s2}}{dt} = r_{s0} W_{s2}\left[1 - \left(\dfrac{W_{s2}}{K_s}\right)^{\theta_{s2}} - \alpha_{st2}\left(\dfrac{W_{tws}}{K_s}\right)^{\psi_{st2}}\right] \end{cases}$$

$A(W, t)$ (tons/ha): biomass production (DW) in agroforestry.
$C_{tr}(W, t)$ (tons/ha): competition loss of trees.
$F_{tr}(W, t)$ (tons/ha): facilitation gain of trees.
I_{tr} (ton/ha): overall interaction arable crops on tree species.
K_{sf} (ton/ha): maximum yield of soybean in the fertilised monoculture.
K_s (tons/ha): maximum biomass yield of soybean in monoculture.
K_{tr} (tons/ha): final maximum biomass in the stands of *Taxodium ascendens* in monoculture.
K_w (tons/ha): maximum biomass yield of wheat in monoculture.
K_{wf} (ton/ha): maximum yield of wheat in the fertilised monoculture.
$M_{tr}(W, t)$ (tons/ha): tree biomass in tree monoculture (sole-trees).
r_{s0}: initial increase rate of soybean yields.
r_{tr0}: initial growth rate of tree species (*T. ascendens*).
r_{w0}: initial increase rate of wheat yields.
$S_{tr}(W, t)$ (tons/ha): gain of resource sharing under tree stands.
W_s (tons/ha): soybean biomass in the tree+soybean system.
W_{s2} (tons/ha): soybean biomass in the tree+wheat+soybean.
W_{sf} (tons/ha): soybean biomass in the fertilised tree+wheat+soybean.
W_{trf} (tons/ha): tree biomass in the plots where arable crops were fertilised.
W_{trs} (tons/ha): tree biomass in the tree+soybean.
W_{trw} (tons/ha): tree biomass in the tree+wheat.
W_{tws} (tons/ha): tree biomass in the tree+wheat+soybean.
W_w (tons/ha): wheat biomass in the tree+wheat.
W_{w2} (tons/ha): wheat biomass in the tree+wheat+soybean.
W_{wf} (tons/ha): wheat biomass in the fertilised tree+wheat+soybean.
$W_{m,tr}$ (tons/ha): tree biomass in monoculture.
W_s' (tons/ha): differences between the maximum yield (K_{sf}) of soybean in fertilised monoculture and the soybean yields (W_{sf}) in the fertilised intercropping regime at age *i* (i.e. $W_s' = K_{sf} - W_{sf}$).
W_{tr}' (tons/ha): differences between the final maximum biomass (K_{tr}) of *T. ascendens* in monoculture and the tree biomass (W_{trf}) in the fertilised intercropping regime at age *i* (i.e. $W_{tr}' = K_{tr} - W_{trf}$).
W_w' (tons/ha): differences between the maximum yield (K_{wf}) of wheat in fertilised monoculture and the wheat yields (W_{wf}) in the fertilised intercropping regime at age *i* (i.e. $W_w' = K_{wf} - W_{wf}$).
α_{st}: competition coefficient of *T. ascendens* on soybean in the tree+soybean.
α_{st2}: competition coefficient of *T. ascendens* on soybean in the tree+wheat+soybean.
α_{trs}: competition coefficient of soybean on *T. ascendens* in the tree+soybean.
α_{trw}: competition coefficient of wheat on *T. ascendens* in the tree+wheat.
α_{ts2}: competition coefficient of soybean on *T. ascendens* in the tree+wheat+soybean.
α_{tw2}: competition coefficient of wheat on *T. ascendens* in the tree+wheat+soybean.
α_{wt}: competition coefficient of *T. ascendens* on wheat in the tree+wheat.
α_{wt2}: competition coefficient of *T. ascendens* on wheat in the tree+wheat+soybean.
α'_{tws}: joint effect coefficient of wheat and soybean on *T. ascendens* in the tree+wheat+soybean.
β_s: facilitation coefficient of the fertilised intercropping regime on soybean.
β_{tr}: facilitation coefficient of the fertilised intercropping regime on *T. ascendens*.
β_w: facilitation coefficient of the fertilised intercropping regime on wheat.
γ_{tr} : facilitation coefficient of the fertilised intercropping regime on *T. ascendens*.
γ_w : facilitation coefficient of the fertilised intercropping regime on wheat.
γ_s : facilitation coefficient of the fertilised intercropping regime on soybean.
λ_{tr}: rate of facilitation feedback of fertilised intercropping regimes on *T. ascendens*.
λ_w: rate of facilitation feedback of fertilised intercropping regimes on wheat.
λ_s: rate of facilitation feedback of fertilised intercropping regimes on soybean.
θ_m : density-feedback rate of *T. ascendens* in monoculture.
θ_s : feedback rate of soybean in the tree+soybean.
θ_{s2} : feedback rate of soybean in the tree+wheat+soybean.
θ_{ts} : density-feedback rate of *T. ascendens* in the tree+soybean.
θ_{tw} : density-feedback rate of *T. ascendens* in the tree+wheat.
θ_{tws} : density-feedback rate of *T. ascendens* in the tree+wheat+soybean.
θ_w : feedback rate of wheat in the tree+wheat.
θ_{w2} : feedback rate of wheat in the tree+wheat+soybean.
ψ_{st}: rate of specific competition feedback of *T. ascendens* on soybean in the tree+soybean.
ψ_{st2}: rate of specific competition feedback of *T. ascendens* on soybean in the tree+wheat+soybean.
ψ_{ts}: rate of specific competition feedback of soybean on *T. ascendens* in the tree+soybean.
ψ_{ts2}: rate of specific competition feedback of soybean on *T. ascendens* in the tree+wheat+soybean.
ψ_{tw}: rate of specific competition feedback of wheat on *T. ascendens* in the tree+wheat.
ψ_{tw2}: rate of specific competition feedback of wheat on *T. ascendens* in the tree+wheat+soybean.
ψ_{wt}: rate of specific competition feedback of *T. ascendens* on wheat in the tree+wheat.
ψ_{wt2}: rate of specific competition feedback of *T. ascendens* on wheat in the tree+wheat+soybean.
ψ'_{tws}: rate of the joint effect of wheat and soybean on trees in the tree+wheat+soybean.

study the influence of between-rows open-ranges of tree (O_r), we simply define it as:

$$O_r = RA - RCA \tag{28}$$

where RCA is the area (m^2) of projected zone of tree crowns of between-rows on the ground (i.e. the tree crown width (m) of between-rows × per unit length (m) of rows), and RA is the area (m^2) between two rows. The row width is 4 m in tree spacing 1.5 × 4 m, 5 m in spacing 1.2 × 5 m, 3 m in spacing 2 × 3 m, and 6 m in spacing 1.5 × 2 × 6 m.

Relative between-rows open-range (RO_r) is:

$$RO_r = 1 - RCA/RA \tag{29}$$

(3) Within-rows open-ranges and relative within-rows open-ranges

Even though the intercrops are frequently grown in the open range of between-rows of trees (the between-rows of trees refer to the wider space between plant and plant, e.g. 4 m is the distance of between-rows in tree spacing 1.5 × 4 m; the within-rows of trees are the narrower space between plant and plant, e.g. 1.5 m is the distance of within-rows in tree spacing 1.5 × 4 m), the tree canopy of within-rows will affect the light, temperature and wind on the forest ground (Huang et al. 1993). Consequently the intercrops will respond to it. Within-rows open-range of tree stands, O_p, is defined as:

$$O_p = IPA - IPCA \tag{30}$$

where $IPCA$ is the area (m^2) of projected zone of within-rows crowns (i.e. the tree crown width (m) of within-rows × per unit length (m) of the strips of within-rows), and IPA is the areas of within-rows. The distance between two plants in a line is 1.5 m, 1.2 m, 2 m and 1.5 m, respectively, in the spacing 1.5 × 4 m, 1.2 × 5 m, 2 × 3 m and 1.5 × 2 × 6 m (double-row configuration: narrower row is 2 m, wider row is 6 m).

Relative tree within-rows open-range, RO_p, is:

$$RO_p = 1 - IPCA/IPA \tag{31}$$

(4) Canopy open-ranges and relative canopy open-range

The canopy open-range of tree stands, O_c, has a significant effect on intercrop growth (Huang and Huang 1991a), especially before canopy closure. In this study, the canopy open-range of tree stands is defined as the open range in tree stands per unit area, and expressed as:

$$O_c = GA - N_{tr}[(CR_1 + CR_2)/4]^2\pi \tag{32}$$

where the CR_1 is the tree crown width of between-rows, CR_2 is that of the within-rows, N_{tr} is the number of tree individuals per unit, and GA is the ground area per unit.

Relative tree canopy open-range, RO_c, is:

$$RO_c = 1 - N_{tr}[(CR_1 + CR_2)/4]^2\pi/GA \tag{33}$$

(5) Tree crown volume and space-volumed open-range

Tree crown volumes (V) were calculated assuming that the crown was a paraboloid according to the field measurement, as:

$$V = 0.5\pi\ [(R_1 + R_2)/2]^2 L_{cr} \tag{34}$$

where R_1 is the crown radii of row-row, R_2 is the crown radii of plant-plant, and L_{cr} is the crown length.

Space-volumed open-ranges (O_s) in tree stands were calculated as:

$$O_s = GSV - V \tag{35}$$

where GSV is the space volume of forest ground per unit, $GA \times H_s$, (H_s = height of space volume of forest ground). The mean height of trees was used as the height of space of forest ground (H_s).

Relative space-volumed open-range, RO_s, is:

$$RO_s = 1 - V/GSV \tag{36}$$

3.5 Statistics Approaches

Data were analysed by the SYSTAT software package (Wilkinson et al. 1992). Standard analysis of variance (ANOVA) was used to determine the tree growth, canopy development, open-range

Table 7. Parameter sets and statistics for modelling the specific interactions in *Taxodium ascendens*-intercrop systems. Eq. 6.5, 6.7, 6.9 and 6.9 refer to those in Table 6.

Parameter[1]	Unit	Tree monoculture (Eq. 6.6)	Tree+wheat (Eq. 6.7)[2]		Tree+soybean (Eq. 6.8)[2]		Tree+wheat+soybean (Eq. 6.9)[2]			Tree+wheat+soybean with fertilisation (Eq. 6.10)[2]		
			tree	wheat	tree	soybean	tree	wheat	soybean	tree	wheat	soybean
θ_i		0.342	0.334	1.0	0.339	1.0	0.197	1.0	1.0			
K_i	tons/ha	89.785	89.785	10.015	89.785	4.265	89.785	10.015	4.265	89.785	10.36	4.299
r_{io}	tons/ha	1.074	1.074	1.0	1.074	1.0	1.074	1.0	1.0			
α_{trj}			0.042		0.024							
α_{jt}				1.157		0.303		0.736	0.319			
α_{tw2}							0.042					
α_{ts2}							0.024					
α'_{tws}							–0.442					
ψ_{tj}			0.291									
ψ_{jt}				1.954		1.0		1.4	1.0			
ψ_{tw2}							0.291					
ψ_{ts2}					0.298		0.298					
ψ'_{tws}							0.345					
β_i										0.183	0.001	0.001
γ_i										0.4	–0.092	0.014
λ_i										0.068	1.0	1.0
Explained variance[3]		0.98	0.978	0.416	0.982	0.435	0.99	0.348	0.155	0.999	0.963	0.911

[1] Parameters refer to Table 6. Subscript *j* denotes wheat and soybean, *tr* or *t* the trees, and *i* the species (trees, wheat and soybean). The initial values (tons ha^{-1}) for prediction at $t = 0$ were: *T. ascendens* =0.935; wheat = 9.571 in the tree+wheat, 9.61 in the tree+wheat+soybean and 10.36 in the tree+wheat+soybean (fertilisation); soybean = 4.063 in the tree+soybean, 3.977 in the tree+wheat+soybean and 4.299 in the tree+wheat+soybean (fertilisation) (observed mean values)

[2] When tree stand age > 5, wheat and soybean did not continue to be intercropped under the tree stands, thus we have: "If age > 5, then W_w, W_s, W_2, W_{wf}, W_{s2}, W_{sf} = 0" in Eq.6.7, 6.8 and 6.9 during prediction. In Eq.6.10, we also have: "If age > 5, then K_{wf} and K_{sf} = 0"

[3] Explained variance is defined as 1 – Residual/Total (Wilkinson et al. 1992)

differences and the effects of sowing densities of intercrops on the yields under tree stands. POWERSIM (version 2.0, ModellData AS 1993–94), a Complete Software Tool for Dynamic Simulation, was employed for the description of the coexistence gain model of intercropping communities.

Tables 6 and 7 list the equations and parameter values for calculating the growth dynamics and interactive performances of trees and arable crops in *T. ascendens*-intercrop communities. The model used Euler's integration. The cumulative value of level at $t = T + \Delta t$ is based on Level_T and Flow: $Level_{T+\Delta t} = Level_T + \Delta t \times Flow$. At tree-stand-age six and afterwards, the yields of wheat and soybean were set to zero, because there were no intercrops under the trees at that stage.

4 Results

4.1 Canopy Development of *T. ascendens* and Relative Open-range in Different Tree Stands

4.1.1 Asymmetric Crown Development

In the four tree spacing configurations, the asymmetric crown development ratio (*ACDR*) increased with tree-stand-ages (Fig. 10). In the stands of spacing 1.2 × 5 m, the *ACDR* after age six was, nearly all of them, higher than 0, indicating that most of them had asymmetric crown development (Fig. 10b). The most normal development of tree crowns was found in the spacing 2×3 m (Fig. 10c).

Fig. 11 shows the asymmetric crown development in relation to the tree diameter growth. The

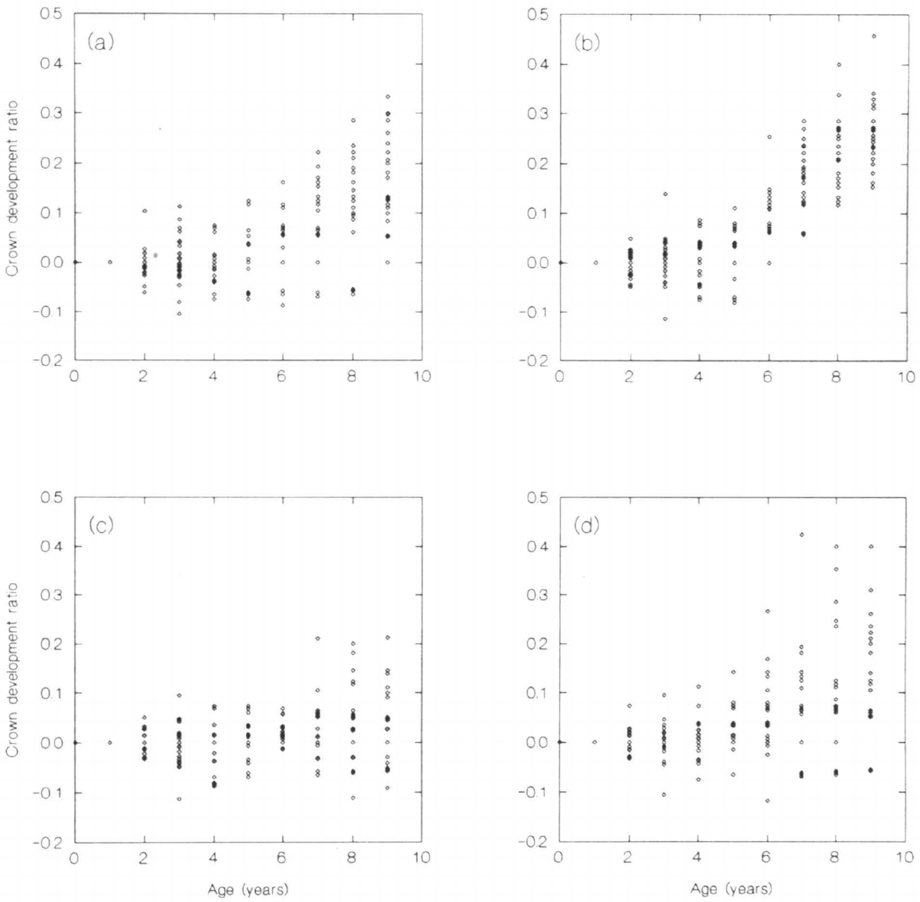

Fig. 10. Asymmetric crown development ratio (*ACDR*) of *T. ascendens* with increasing tree-stand-age in four spacings (a = 1.5 × 4 m, b = 1.2 × 5 m, c = 2 × 3 m, and d = 1.5 × 2 × 6 m).

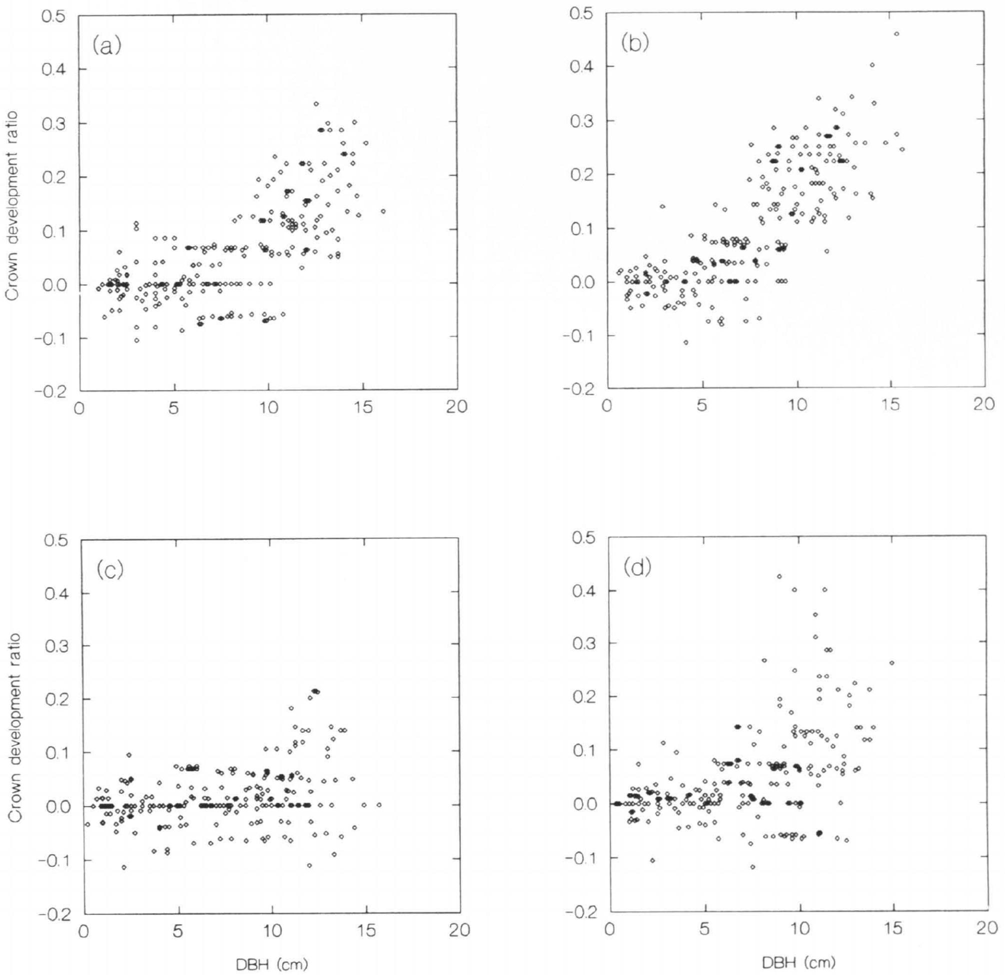

Fig. 11. Relationship between diameter growth and asymmetric crown development of *T. ascendens* in four spacings (a = 1.5 × 4 m, b = 1.2 × 5 m, c = 2 × 3 m, and d = 1.5 × 2 × 6 m).

asymmetric development was most pronounced in spacing 1.2×5 m (Fig. 11b), in which the crown development ratios were consistently above 0 with the tree diameters higher than 10 cm (DBH). In spacing 1.5 × 4 m and 1.5 × 2 × 6 m, the positive values of *ACDR* were observed in the tree diameters above 11 cm and 12.5 cm respectively (Fig. 11a and 11d). Less varying *ACDR* appeared in spacing 2 × 3 m.

4.1.2 Relative Open-range

There were significant differences in the relative between-rows open-ranges (RO_r) between the four tree spacings ($p < 0.001$). The relative between-rows open-ranges in spacing 1.5 × 2 × 6 m were higher than those in the other tree spacings (Fig. 12a). The lowest RO_r was in spacing 2 × 3 m. The RO_r in all four spacings decreased with tree-stand-age.

The results showed distinct differences ($p < 0.001$) in the relative within-rows open-ranges (RO_p) between four spacings, and the RO_p decreased with tree-stand-age (Fig. 12b). The RO_p in tree spacing 2 × 3 m was higher than those in other spacings. The lowest was in spacing 1.2 × 5 m. A negative RO_p means that the canopies of two neighbouring plants were in direct competition, and no within-rows open-range existed between two individual trees. In Fig. 12b, all of the tree spacings (except spacing 2 × 3 m) had a negative RO_p in the nine-year-old tree stands.

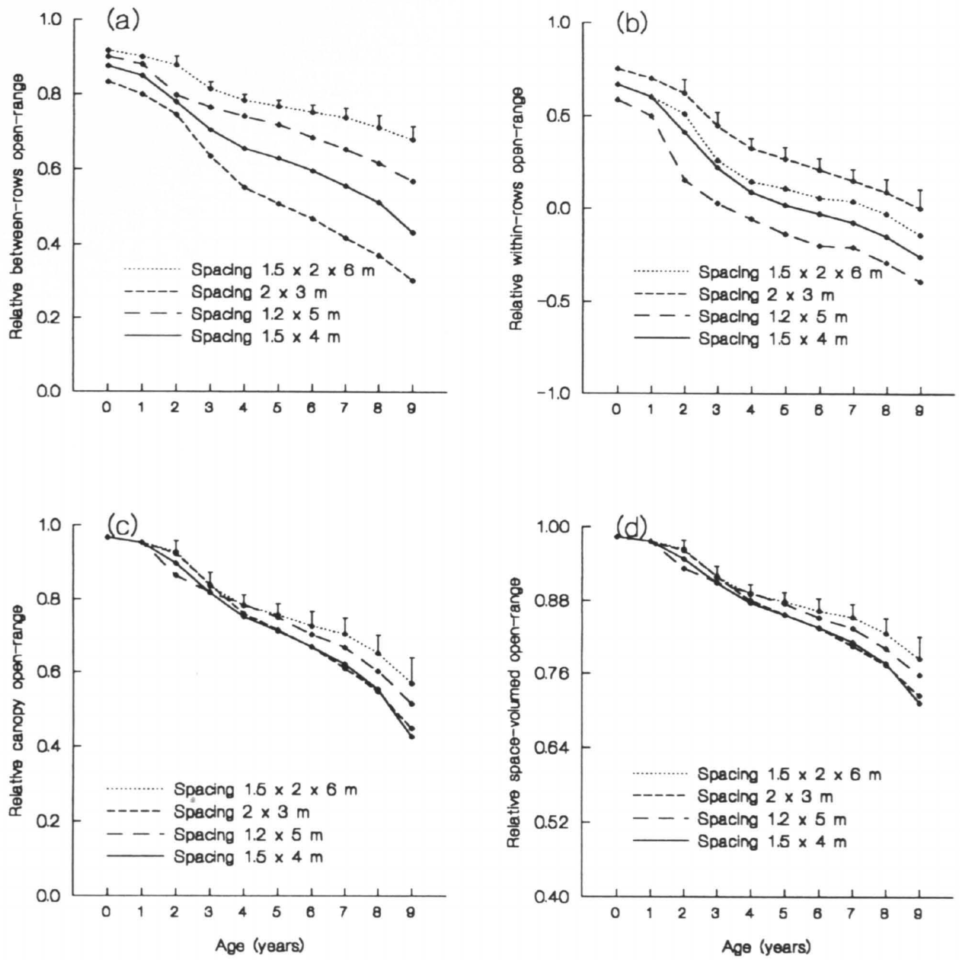

Fig. 12. Relative open-ranges in four spacings of *T. ascendens* (a = relative between-rows open-range, b = relative within-rows open-range, c = relative canopy open-range of tree stands, and d = relative space-volumed open-range of tree stands). To be neatly illustrated in the figure, standard error (S.E.) was presented only for one spacing.

Relative canopy open-ranges (RO_c) did not show significant differences ($p = 0.295$) between four spacings. RO_c varied with increasing tree-stand-age (Fig. 12c).

Relative space-volumed open-ranges (RO_s) in the four spacings did not show any difference ($p = 0.303$), and had a tendency similar to RO_c (Fig. 12d).

Fig. 13 shows the relationship between between-rows open-range and within-rows open-range. In the spacing 2 × 3, the relationship approached the 1 : 1 line (Fig. 13c). The relationships had greater departure from the 1 : 1 line in the tree spacing 1.2 × 5 and spacing 1.5 × 2 × 6 m, showing asymmetric distribution of open-ranges in these spacing configurations.

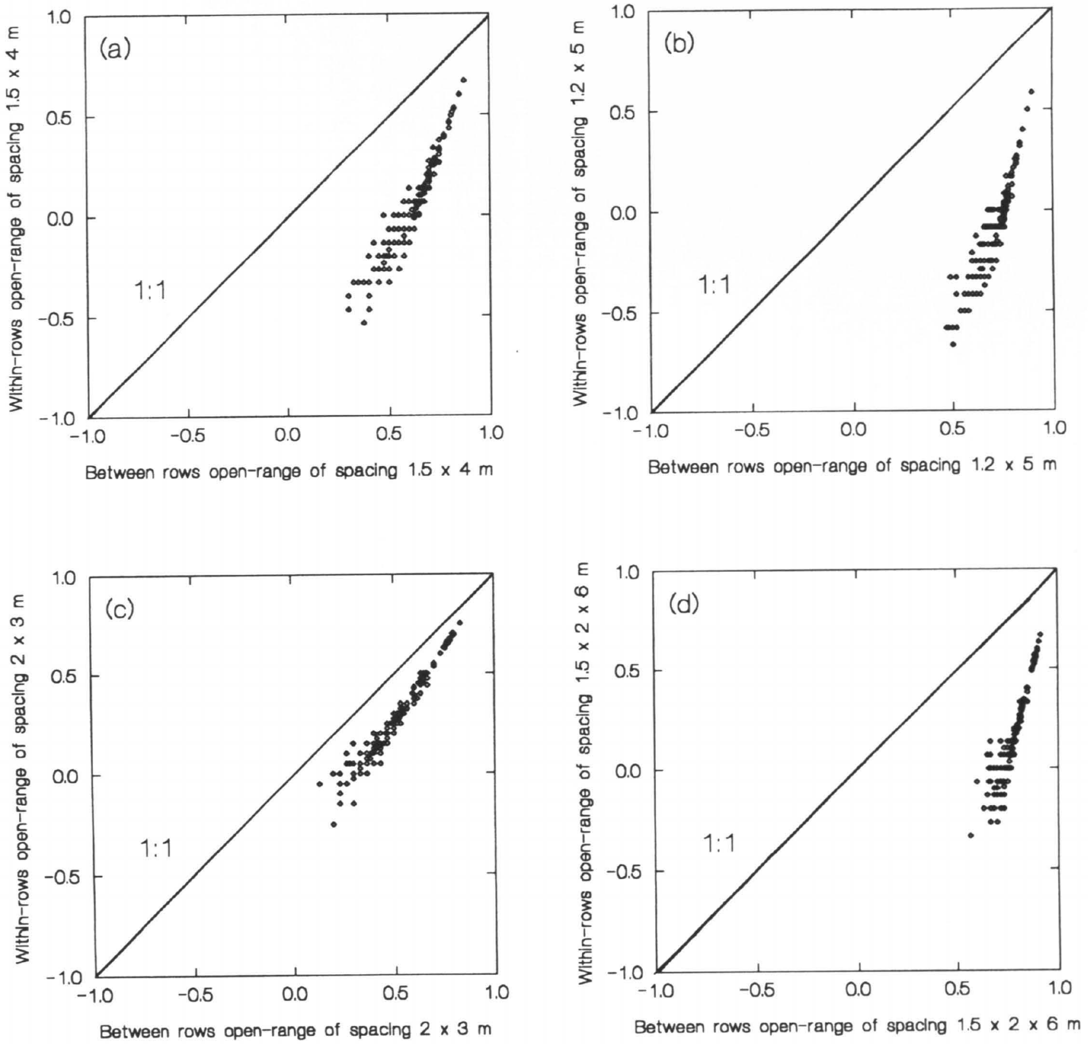

Fig. 13. Relationship between between-rows open-range and within-rows open-range *T. ascendens* in four spacings (a = 1.5 × 4 m, b = 1.2 × 5 m, c = 2 × 3 m, and d = 1.5 × 2 × 6 m).

Under the tree stands of four spacings, wheat yields had positive correlations with between-rows open-ranges (Pearson correlation *R*: 0.685–0.889), within-rows open-ranges (*R*: 0.646–0.83), canopy open-ranges (*R*: 0.716–0.865), and space open-ranges (*R*: 0.715–0.865).

4.2 Growth Comparison of Trees and Arable Crops in Different Intercropping Types

4.2.1 *Effect of Tree Spacing Configurations on the Growth of Trees and Intercrops*

There were no significant differences in tree diameter and height growth (p > 0.05) between tree spacings when tree stands were under the age of eight, but spacing 1.5 × 2 × 6 and spacing 1.2 × 5 m provided wider between-rows open-ranges for intercrops. The height growth was statistically different between tree spacings at the age of nine (p = 0.022).

The results did not show distinct effects of different tree spacings on the growth of intercrops, e.g. wheat, rape, soybean and mung bean (p > 0.05). However, the yields (dry weight) of wheat, rape, soybean and mung bean seemed to be lower in spacing 2 × 3 m than in spacings 1.5 × 4 m, 1.2 × 5 m and 1.5 × 2 × 6 m (Fig. 14). These may have been be caused by the differences in the between-rows open-ranges of tree stands. The spacing 2 × 3 m had the narrowest rows (3 m between the tree rows) among the four configured spacings.

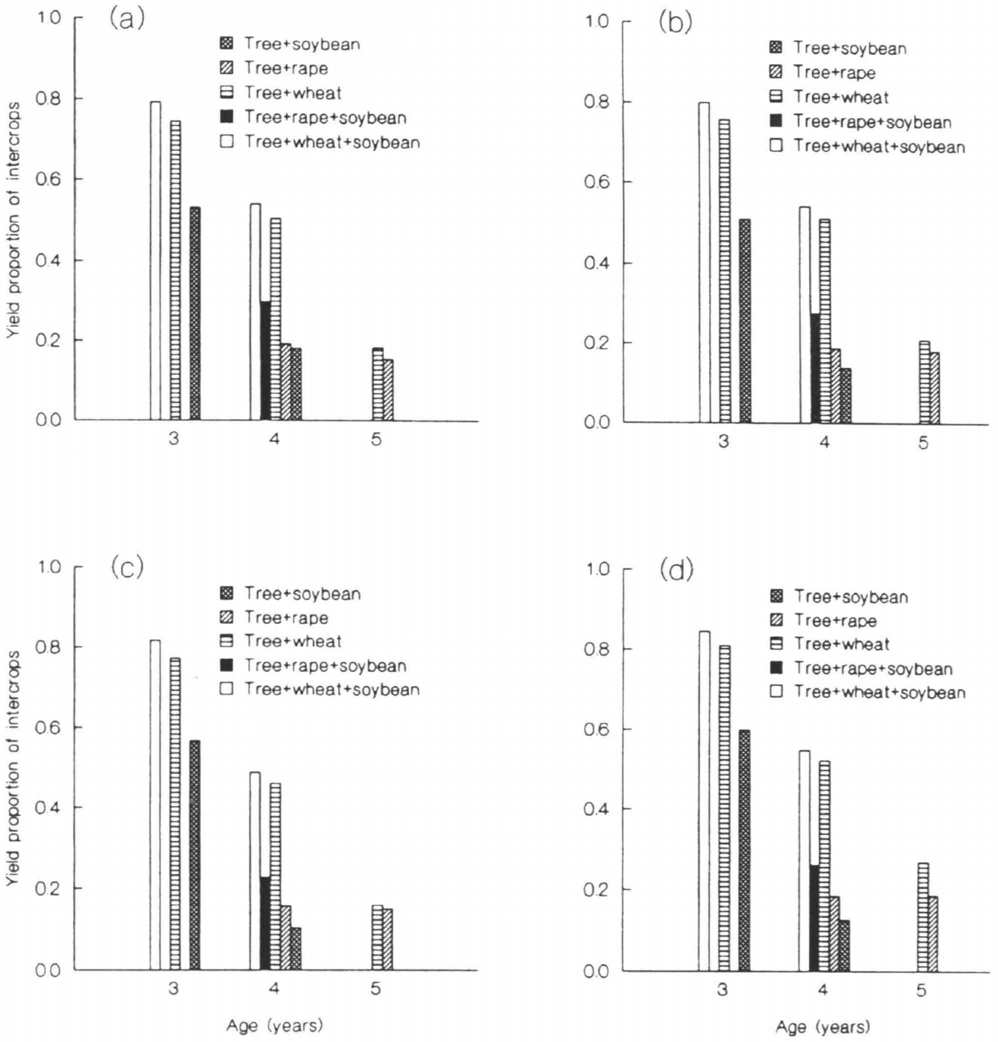

Fig. 14. Grain yields of intercrops in different tree stand spacings. Tree spacing 1, 2, 3 and 4 refer to the spacing s of 1.5 × 4 m, 1.2 × 5 m, 2 × 3 m and 1.5 × 2 × 6 m respectively. Figure (a) is in two-year-old tree stands, (b) in three-year-old stands, (c) in four-year-old stands, and (d) in five-year-old stands. Error bars represent standard errors (S.E.).

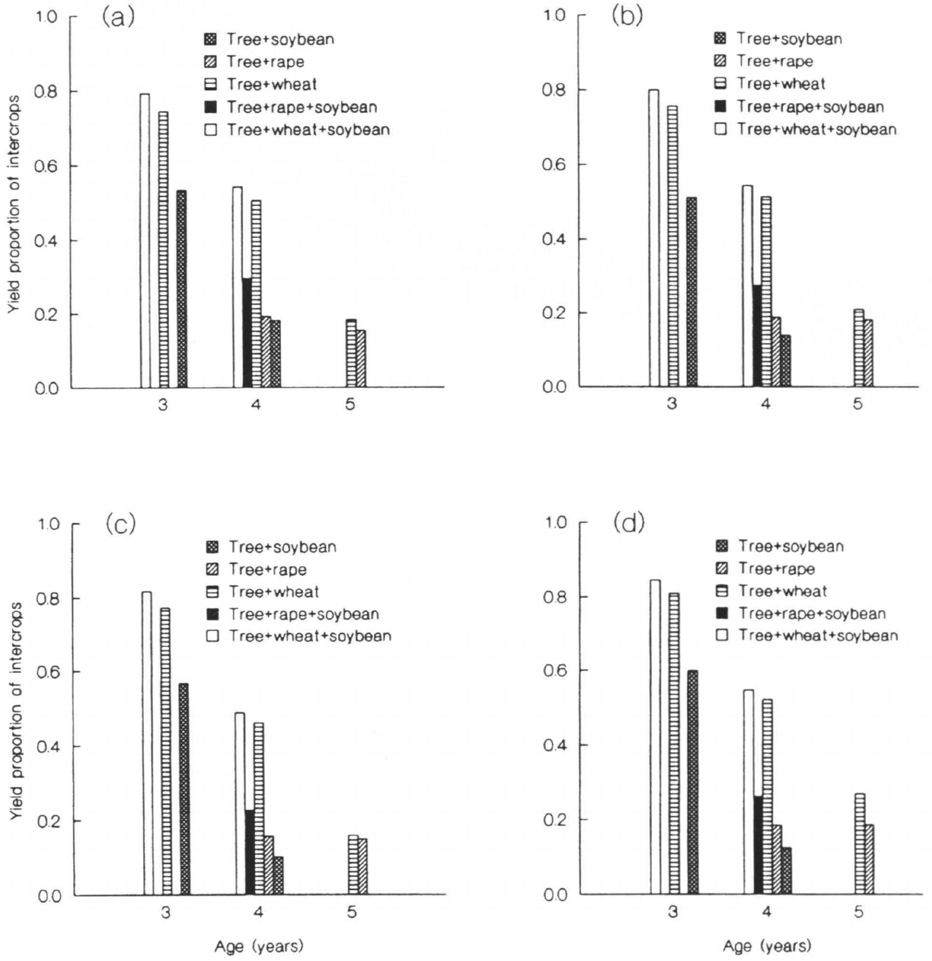

Fig. 15. Proportion of intercrop yields to the total yield of agroforestry in five intercropping types and four tree spacings (a = 1.5 × 4 m, b = 1.2 × 5 m, c = 2 × 3 m, and d = 1.5 × 2 × 6 m).

4.2.2 Yield Proportion of Trees and Intercrops

The mean yield proportion (calculated in dry mass) of intercrops (wheat and soybean) in the four spacing configurations was high at tree-stand-age three, ranging from 0.8 to 0.85 (or 80 % to 85 %) in the tree+wheat+soybean, 0.77 to 0.79 in the tree+wheat (Fig. 15). This suggests that the contribution of intercrops to the total yield of agroforestry is from 77 % to 85 % in the above two intercropping types. In the tree+soybean, the proportion was over 50 %. There is thus great potential in increasing the land productivity in the young stands of *T. ascendens* by intercropping. The yield proportion of the intercrops to the total yield of agroforestry decreased with increasing tree-stand-age. The yield proportion of trees to the total yield of agroforestry ranged from 15 to 23 % in both the tree+wheat+soybean and the tree+wheat, increasing with tree-stand-age.

Fig. 16 shows the total biomass production yields in different *T. ascendens*-intercrop types. The tree+wheat had the maximum total yields at tree-stand-age four in the four tree spacings, whereas in the other combinations the maximum total yields were obtained at different ages.

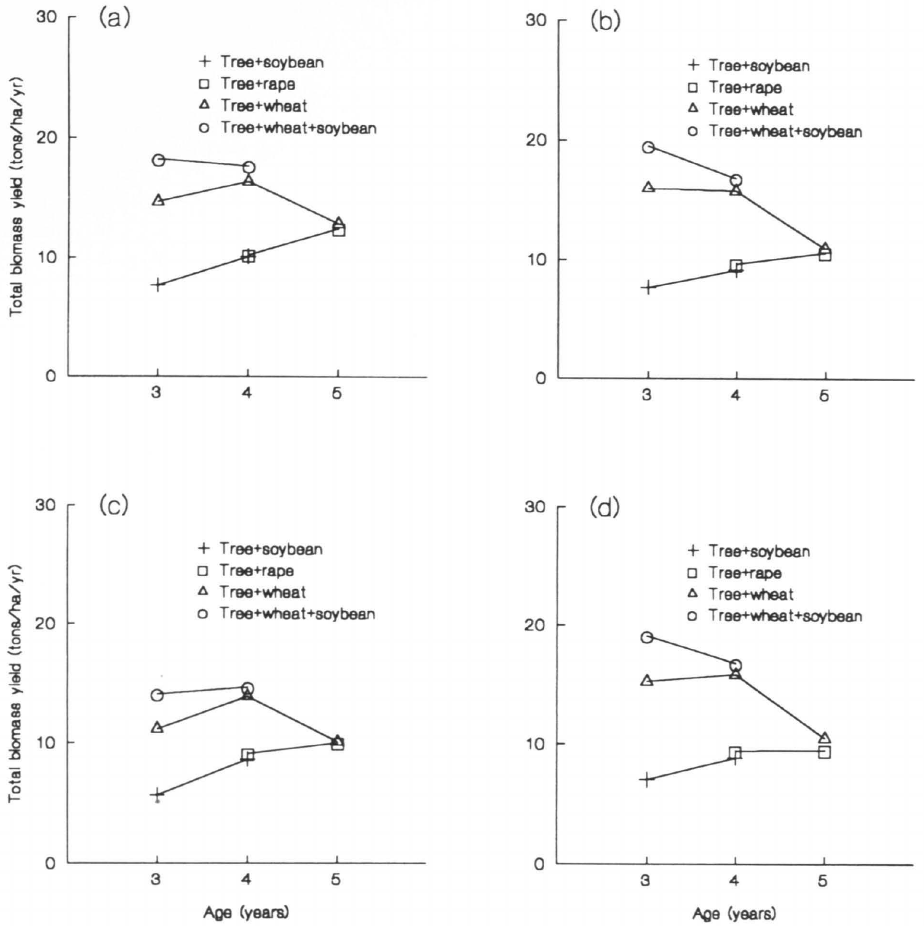

Fig. 16. Total biomass production in different types of agroforestry in four spacings of tree stands (a = 1.5 × 4 m, b = 1.2 × 5 m, c = 2 × 3 m, and d = 1.5 × 2 × 6 m).

4.2.3 Yield Comparison among Sowing Densities of Intercrops

The experiment comparing the sowing density of soybean in the four tree spacings revealed significant differences in grain yields (p = 0.015) between the five sowing densities. Using HSD multiple comparisons, the pairwise comparison probability between the sowing density 6.75 g m^{-2} and 8.25 g m^{-2} was 0.009, showing a significant difference between these two sowing densities. The pairwise comparison probabilities between other sowing densities did not show statistically significant differences (p > 0.05), but the sowing density of 8.25 g m^{-2} gave the highest grain yield (Fig. 17a). There were no significant differences in grain yields (p = 0.477) between the four tree spacings. The sowing density of mung bean did not have any significant differences in the yields neither between the five sowing densities (p = 0.238) and nor between the four tree spacing configurations (p = 0.498).

4.2.4 Effect of the Combination of T. ascendens *with Intercrops on Yields*

The mean yields of wheat, rape, soybean and mung bean varied between 0.34 and 3.8 tons ha^{-1} yr^{-1} in different intercropping types in the four tree spac-

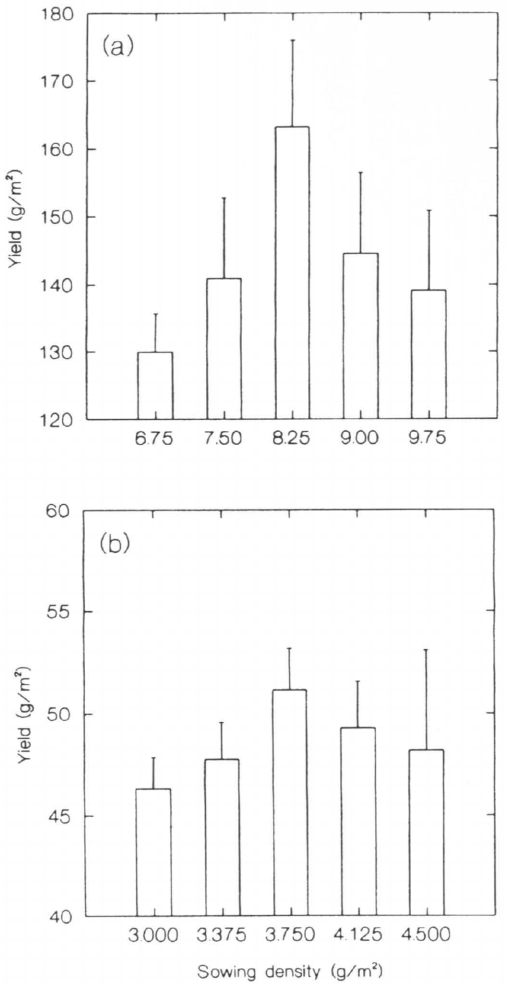

Fig. 17. Yields (and S.E.) of soybean (a) and mung bean (b) in different sowing densities intercropped under the four tree spacing.

ings (Fig. 14). When the tree stands (*T. ascendens*) were five years old, the intercrop yields decreased significantly because of the significant effect of increasing canopy closure. At tree-stand-age six and seven, the yields of intercrops were enhanced by an intercropping of low light-requiring ryegrass (mean fresh weight at age six and seven: 120.53 tons ha^{-1} in spacing 1.5×4 m, 125.25 tons ha^{-1} in spacing 2×3 m, 127.28 tons ha^{-1} in spacing 1.2×5 m, and 126.53 tons ha^{-1} in spacing $1.5 \times 2 \times 6$ m) instead of high light-requiring arable crops (wheat, rape, and soybean).

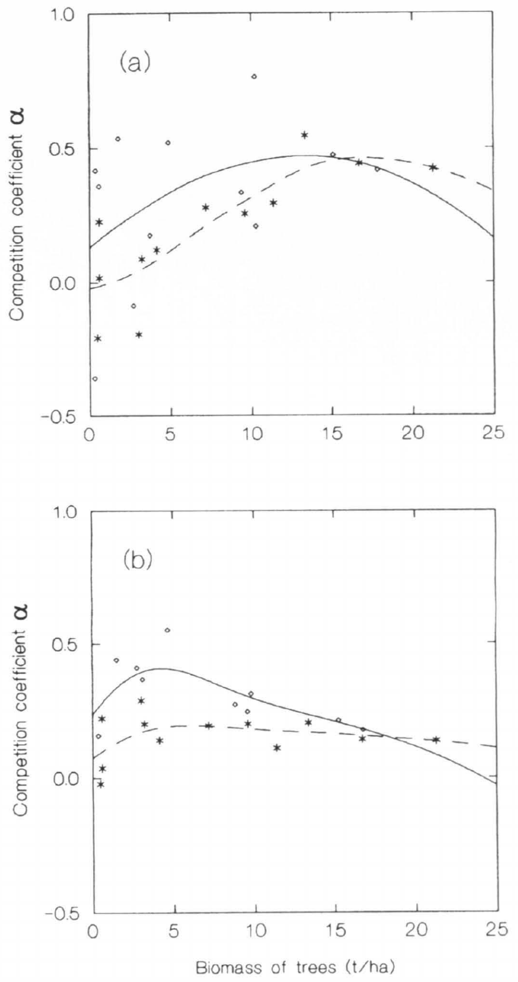

Fig. 18. Competition coefficients α in *T. ascendens*-wheat community (a) and *T. ascendens*-soybean community (b). The solid line (—) indicates the coefficient in the unfertilised treatments; dashed line (- - -) in the fertilised treatment. The lines were smoothed by DWELLS (distance weighted least squares) through a set of points by the least square method. This method produces a true, locally weighted curve running through the points using an algorithm due to Mclain (1974).

The observed results in unfertilised plots demonstrated that the diameter (DBH) and height growth of *T. ascendens* were not significantly influenced ($p > 0.1$) by intercropped wheat and soybean, indicating that intercropping under trees produced extra yields but did not depress the tree growth, and implying that the resource sharing was operative. Therefore intercropping arable crops under trees enables the tapping of the available resources to increase the productivity without significantly interfering with the growth of the principal species. This increases the land-use efficiency in such productive systems.

Fig. 18a shows that increasing biomass of the competitor, *T. ascendens*, increased the values of competition coefficient (competitive effect of trees on wheat) in the *T. ascendens*+wheat community. But this pattern was not monotonic : at a high density of tree biomass the slope decreased with biomass density. Similar patterns were observed in the *T. ascendens*+soybean community (Fig. 18b). When the biomass density of *T. ascendens* was above five tons ha^{-1} the slope of change in the competition coefficient tended to decrease or to remain constant with increasing biomass of competitor.

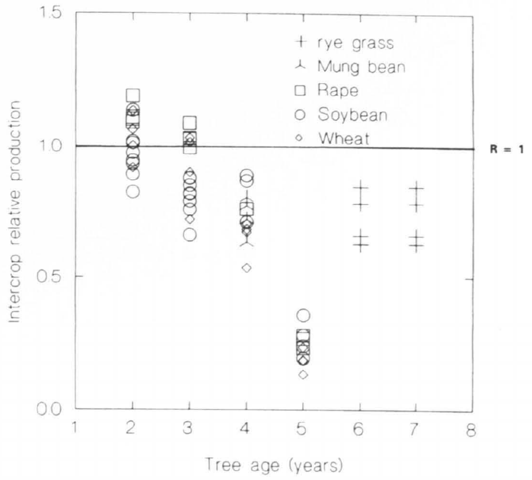

Fig. 19. Relative production of different crops in intercropping systems. *R* denotes the crop relative production.

4.3 Relative Production and Productive Coexistence

The relative yields (R) of wheat, soybean, rape, mung bean and ryegrass were reduced when the tree stands were four years of age or older ($R < 1.0$) (Fig. 19). The relative yields of wheat, soybean and rape were significantly reduced under the five-year-old stands. The relative yields of intercrops rose when the ryegrass was intercropped under the six- and seven-year-old stands, suggesting that the relative production and land equivalent ratio could be probably increased by substituting the high light-demanding crops with the shade-tolerant ones.

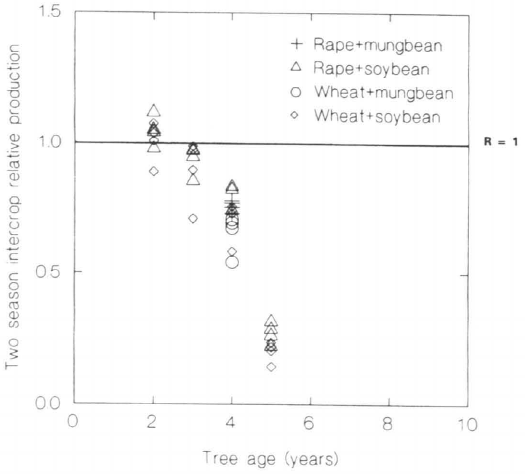

Fig. 20. Relative production of two-season-crops in intercropping systems. *R* denotes the arable crop relative production.

In the two-season intercropping regime, the relative yields of wheat+soybean, wheat+mung bean, rape+soybean and rape+mung bean was below 1.0 when the age of tree stands was three years or more, and those of wheat+soybean and rape+soybean reduced below 0.4 (Fig. 20) under the five-year-old stands, showing a strong negative interaction.

All the land equivalent ratios of various intercropping types were higher than 1.0 (Fig. 21). This suggests that the managed agroforestry systems were advantageous, as compared to monocultures, even though most intercrops were depressed by tree species.

The facilitations or competitions between *T. ascendens* and arable crops appeared in quadrant II (–,+), III (–,–) and IV (+,–) (Fig. 22). There was very little evidence to identify whether the trees and arable crops were facilitated in unfertilised plots because these values were only just on the boundary of quadrant I (+,+), II (–,+) and IV (+,–). However, the observed results showed that *T. ascendens* was facilitated by fertilised intercropping in the fertilised plots.

The realised productive coexistence (RPC) in three intercropping types, i.e. the *T. ascendens*+wheat, *T. ascendens*+soybean and *T. ascendens*+rape, indicates that the shaded area of RPC in quadrant I (+,+), II (–,+) and IV (+,–) was larger in the *T. ascendens*+rape than in the *T. ascendens*+wheat and the *T. ascendens*+soybean, implying that rape may have a higher ecological combining ability with *T. ascendens* in agroforestry systems as compared to wheat and soybean (Fig. 22 and 22).

4.4 Model Parameter Estimation and Analyses

A model was developed to describe the interactions and the growth dynamics of trees and intercrops in the *T. ascendens*-intercrop communities.

In the case of logistic equation $(dW/dt) / W = r_0[1 - (W/K)^\theta]$, θ equals 1.0, setting a linear relationship. This is equivalent to the assumption that either the growth rate drops linearly with W or the death rate rises with W, or both. Fig. 23a (using the data in tree monoculture) is intuitively clear: the relationship between the observed per capita growth rate $(dW/dt) / W$ and the population density W (biomass) of *T. ascendens* is not linearly proportional, and a linear logistic model ($\theta = 1$) departs from the observation (Fig. 23a and 23b: dotted line (- - -)). Adding the exponent, θ, a close fit to the observed data was obtained (see Fig. 23a), and about 98 % ($R^2 = 0.98$; Table 7) of the variance in the data set can be explained by the equation. However, a significant linear relationship can be shown between the observed per capita growth rate and the population size of *T. ascendens* using linear regression analysis (F = 33.732, $p < 0.005$: reject the hypothesis that the slop of the line is zero), but a lower proportion of variance was explained by the linear relation ($R^2 = 0.771$). This suggests that the addition of θ could make the model more accurate to fit the growth dynamics of *T. ascendens*.

Table 7 shows that many ψ_is departed from 1.0, suggesting that competitive effects are not linearly proportional between *T. ascendens* and wheat or soybean (also see Table 8 and Fig. 18).

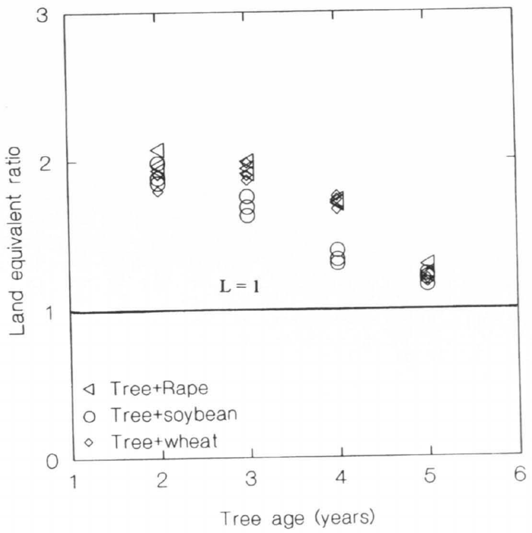

Fig. 21. Land equivalent ratios (L) in different intercropping types.

In testing the linear model with biological data, an exact fit is not expected, since there is simply too much unavoidable heterogeneity. The important question is whether a slightly more complicated model yields significantly more accurate results. When the models were compared using the explained variance for the whole model, differences between the LV model and the model developed in the present study or GA model were significantly observed (Table 8). When the models were ranked according to the proportion of explained variance, the new model was about as good as the GA model, but much better than the LV model.

If the models are justified according to the agreement with observed data, the model developed in the present study was better than the others. The results demonstrated that the new model fitted to the observed data quite well in describing the performance of tree growth in all of four management types (Fig. 24), while the LV model departed significantly from the observed data in the *T. ascendens*+wheat system, the *T. ascendens*+soybean and the *T. ascendens*+wheat+soybean system (Fig. 24b, 24c, and 24d), and the GA model departed from it in the *T. ascendens*+soybean system (Fig. 24c). When *T. ascendens* was grown in monoculture, the performance of the three models was identical. The new model was better in describing the wheat and soybean growth than the LV model and the GA model in all of four intercropping types (Fig. 25a–d), especially in describing soybean (Fig. 25c and 25d), suggesting that the new model was more accurate.

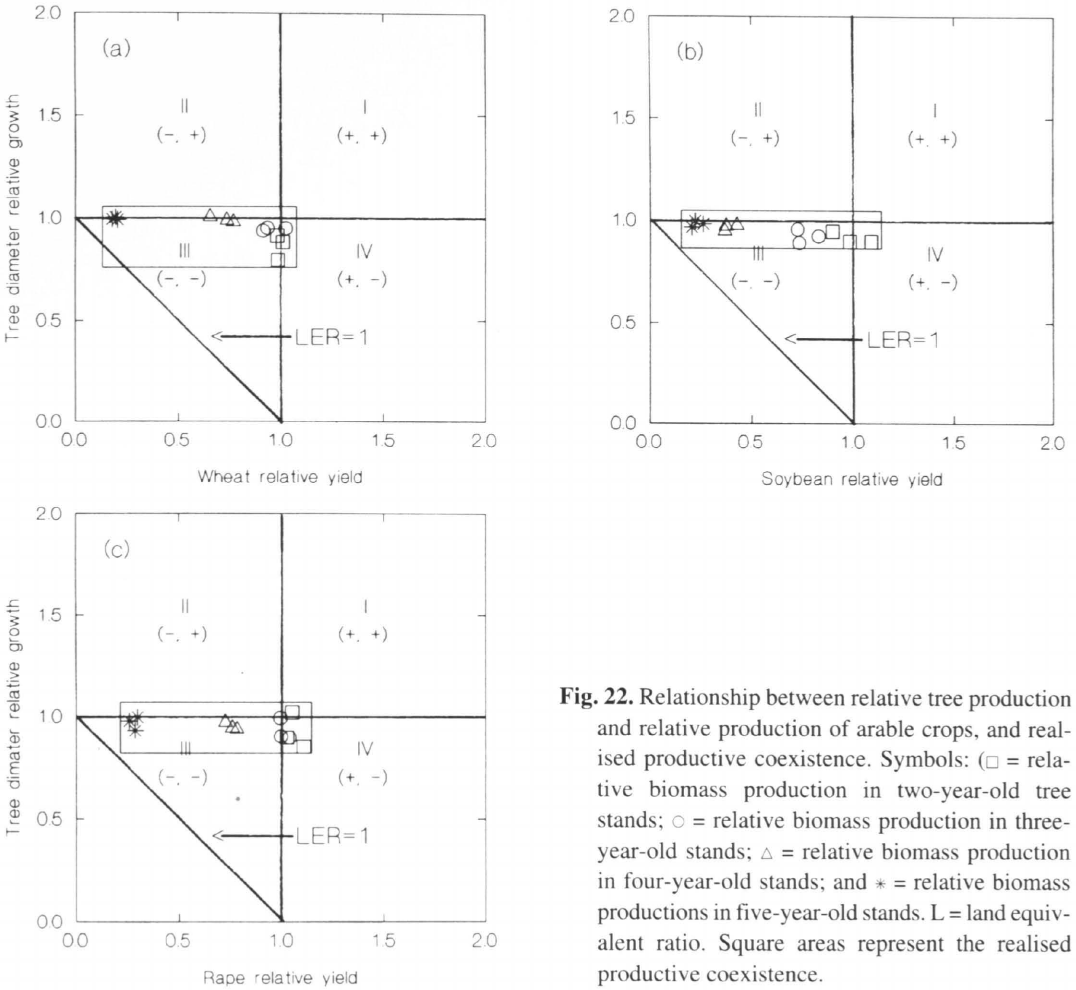

Fig. 22. Relationship between relative tree production and relative production of arable crops, and realised productive coexistence. Symbols: (□ = relative biomass production in two-year-old tree stands; ○ = relative biomass production in three-year-old stands; △ = relative biomass production in four-year-old stands; and ∗ = relative biomass productions in five-year-old stands. L = land equivalent ratio. Square areas represent the realised productive coexistence.

4.5 Comparison Between the Model and Observed Data

4.5.1 Growth Dynamics

The model developed in the present study was used to describe the interspecific interactions and the biomass dynamics in *T. ascendens*-intercrop systems. Comparing the observed with calculated biomass of *T. ascendens*, a close agreement between model and data was generally observed (Fig. 24a–d). The cumulative biomass of trees versus time (age) exhibits definite trends, i.e. the cumulative biomass increased with age in the intercropping communities over the nine-year period (Fig. 24a–d). However, some over-estimations

Table 8. Parameter sets and statistics of three models of specific interactions in *Taxodium ascendens*-intercrop systems.

Parameter	Unit	Tree monoculture	Tree+wheat		Tree+soybean		Tree+wheat+soybean		
			tree	wheat	tree	soybean	tree	wheat	soybean
New model									
θ_i		0.342	0.334	–0.786	0.339	–0.471	0.197	–0.786	–0.419
			(1.0)[2]		(1.0)		(1.0)	(1.0)	
K_i	tons/ha	89.785	89.785	10.015	89.785	4.265	89.785	10.015	4.265
r_{io}	tons/ha	1.074	1.074	1.0	1.074	1.0	1.074	1.0	1.0
α_{trj}			0.042		0.024				
α_{jt}				–0.023		0.121		–0.023	0.029
				(1.157)		(0.5)		(0.736)	(0.575)
α_{tw2}							0.042		
α_{ts2}							0.024		
α'_{tws}							–0.442		
ψ_{tj}			0.291						
ψ_{jt}				0.132		–0.003		0.132	–3.29
				(1.954)		(0.462)		(1.4)	(0.327)
ψ_{tw2}							0.291		
ψ_{ts2}					0.298		0.298		
ψ'_{tws}							0.345		
Explained variance[1]		0.98	0.978	0.975	0.982	0.995	0.99	0.975	0.956
				(0.416)		(0.899)		(0.348)	(0.754)
LV model									
K_i	tons/ha	89.785	89.785	10.015	89.785	4.265	89.785	10.015	4.265
r_{io}	tons/ha	0.672	1.074	1.0	1.074	1.0	1.074	1.0	1.0
α_{trj}			5.985		15.121				
α_{jt}				0.92		0.303		0.852	0.319
α_{tj2}							5.985		
α_{jt2}							15.121		
α'_{tws}							–4.498		
Explained variance		0.926	0.657	0.223	0.911	0.435	0.985	0.135	0.155
GA model									
θ_i		0.342	0.335	–0.789	0.07	–0.471	0.147	–0.781	–0.598
K_i	tons/ha	89.785	89.785	10.015	89.785	4.265	89.785	10.015	4.265
r_{io}	tons/ha	1.074	1.074	1.0	1.074	1.0	1.074	1.0	1.0
α_{trj}			0.042		–14.38				
α_{jt}				–0.021		0.005		–0.009	–0.051
α_{tj2}							–2.728		
α_{jt2}							–7.565		
α'_{tws}							0.368		
Explained variance		0.98	0.979	0.969	0.995	0.939	0.991	0.974	0.882

[1] Explained variance is defined as 1 – Residual/Total

[2] Values in parentheses are based on the estimates where the exponent was fitted at $\theta = 1.0$, because of the assumption of no asymmetrical intraspecific interaction in annual plants by years

or under-estimations were observed.

The calculated and observed annual yields of intercrops were in close agreement (Fig. 25). The calculated yields of soybean seem to fit better to the observed data than those of wheat. This may be due to wheat experiencing not only the competition effect of trees, but also the greater climate uncertainty during the deciduous time of trees.

When wheat and soybean were grown under trees, there were no significant decreases in biomass over the first two years in the tree+soybean community and over the first three years in the tree+wheat system (the trends were clearly observed in the estimated curves and observed data) (Fig. 25), suggesting that there were no considerable competition effects of trees on intercrops. This is due to the small tree stature that allows enough light to penetrate to the ground to provide for crop growth. In the present experimental area wheat grows over a period from November to the beginning of July, and *T. ascendens* is deciduous from the end of October to mid-April. This type of agroforestry has been termed a sequential system (Sanchez 1995). Obviously in this intercropping community the competition is not evident simply because the light and nutrient demands for growth occur at different time for each component, resulting in a less competitive loss of wheat yields compared to that of soybean.

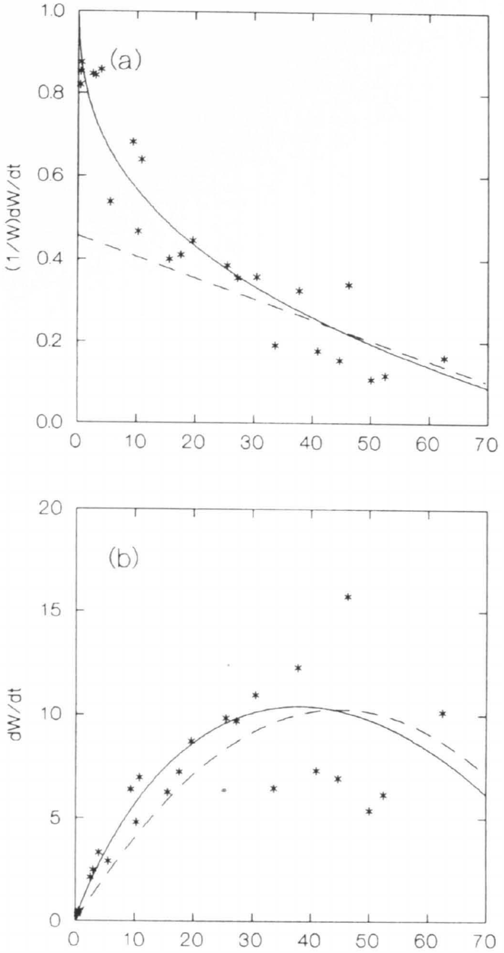

Fig. 23. Comparison of relative growth rate and growth rate between observed data and estimated curves using different values of coefficients in equation $(1/W)\,dW/dt = r[1 - (W/K)^{\theta}]$ and $dW/dt = rW[1 - (W/K)^{\theta}]$ compared with the Lotka-Volterra model. W = tree biomass. The symbol * denotes the observed values. (a) Solid line (—): $\theta = 0.342$, $r = 1.074$ and $K = 89.785$; dashed line (—): $\theta = 1$ (the Lotka-Volterra model), $r = 0.457$ and $K = 89.785$. (b) Solid line (—): $\theta = 0.342$, $r = 1.074$ and $K = 89.785$; dashed line (—): $\theta = 1$, $r = 0.457$ and $K = 89.785$.

Total annual biomass (i.e. in the model annual biomass increment of trees in monoculture + annual competition loss of trees + annual facilitation gain of trees + annual wheat yield under trees + annual soybean yields under trees) in the *T. ascendens*-intercrop system was slightly overestimated during the first year, and underestimated from the second year onwards (Fig. 26a). Calculated accumulative total yields had a very close fit to the observed yields (Fig. 26b), implying that this model is able to represent precisely the dynamics of total yields in *T. ascendens*-intercrop systems.

The calculated coexistence gain in the fertilised *T. ascendens*+wheat+soybean system was about the same in the first three years, and then decreased (Fig. 26c). The reason for the decrease in coexistence gain was the competitive effect of trees on wheat and soybean, which resulted in significant yield reduction of intercrops (wheat and soybean).

4.5.2 *Interactive Performance*

To illustrate the magnitude of interactions among populations of trees, wheat and soybean, the interaction model developed in the present study was used to calculate the facilitation gain and overall interaction (Fig. 27). Application of fertiliser N to wheat or soybean, as an indirect facilitation on tree growth, increased the annual biomass of tree stands (Fig. 27a). The overall interaction (indirect facilitation gain of trees-competition loss of trees) demonstrated definite positive values (Fig. 27b), showing that wheat and soybean intercroppings with application of N will improve tree growth. The overall interaction here

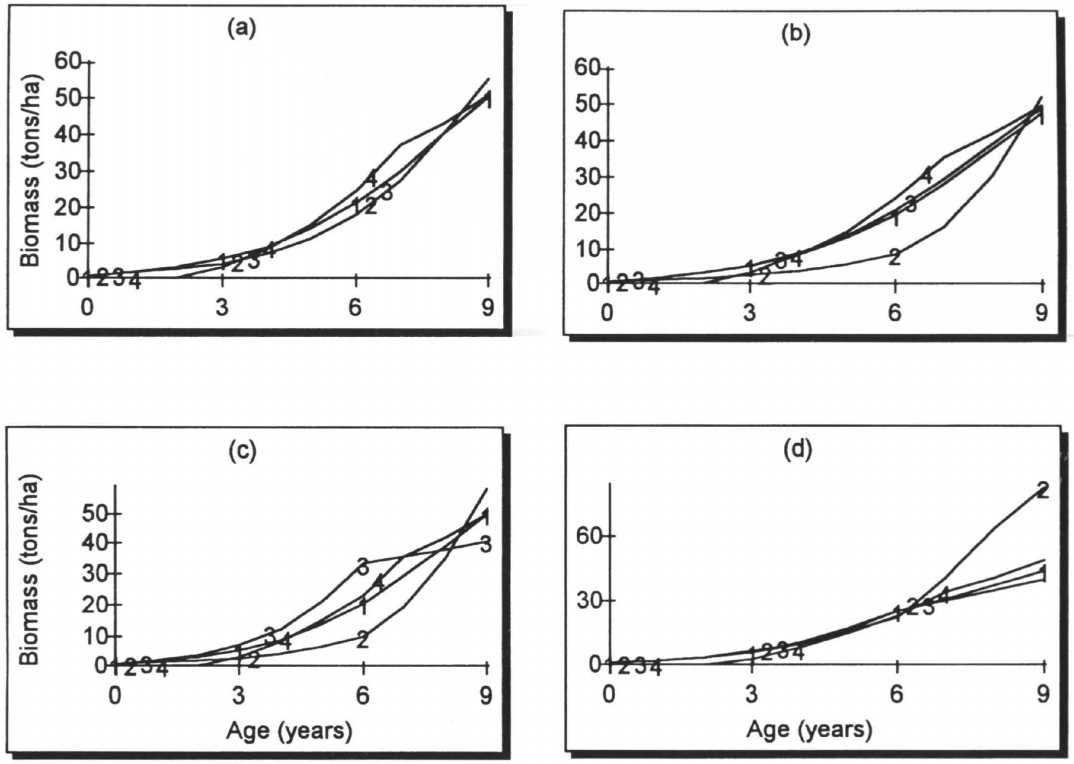

Fig. 24. Comparison of the model developed in the present study (1), the Lotka-Volterra (LV) model (2), and the Gilpin-Ayala (GA) model (3) in calculating the cumulative biomass of *T. ascendens*-intercrop systems against observation (4). Figure a = tree (*T. ascendens*) in monoculture; b = tree in *T. ascendens*+wheat; c = tree in *T. ascendens*+soybean; and d = tree in *T. ascendens*+wheat+soybean system.

refers to the effect of wheat and soybean on trees, because the tree species was managed as the principal component in the timber plantation while wheat and soybean were used to increase the land-use efficiency by sharing the available resources under trees.

Fig. 28 demonstrates the interactions of one species in relation to densities of another species. Indirect facilitation gain of *T. ascendens* decreased with increasing intercrop density (Fig. 28a). Competition losses of wheat and soybean showed definite increases versus densities of tree biomass (Fig. 28b and 28c). The competition loss of wheat increased slightly at low biomass density (less than four tons ha^{-1}) of *T. ascendens* (Fig. 28b).

Annual soybean biomass decreased distinctly along with increasing biomass density of trees (Fig. 29a). No significant decrease in wheat yield was reported by the model at low biomass density (lower than three tons ha^{-1}) of trees (Fig. 29b). At higher biomass density of trees, wheat biomass decreased with increasing mass density of trees. The primary reasons for the different patterns of decrease in the yields of wheat and soybean perhaps are that wheat suffers less competition pressure than soybean under tree stands.

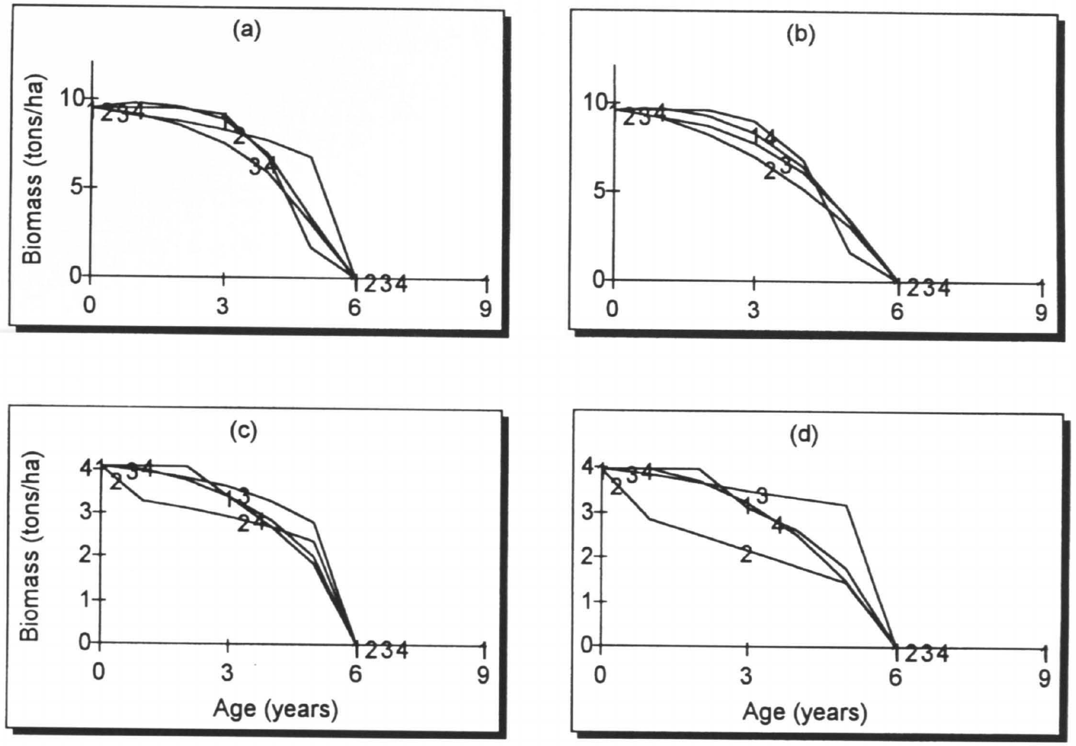

Fig. 25. Comparison of the model developed in the present study (1), the Lotka-Volterra (LV) model (2), and the Gilpin-Ayala (GA) model (3) in calculating the annual biomass of arable crops in *T. ascendens*-intercrop systems against observation (4). Figure a = wheat in *T. ascendens*+wheat; b = wheat in *T. ascendens*+wheat+soybean; c = soybean in *T. ascendens*+soybean; d = soybean in *T. ascendens*+wheat+soybean system.

4.6 Effects of Agroforestry Management on Soils

4.6.1 Chemical Properties

The pH declined significantly in the soil (0–60 cm) after nine years of agroforestry management (Fig. 30a$_1$ and 30a$_2$), and differed significantly between these and waste field ($p < 0.01$).

At the depths of 0–20 cm and 20–40 cm, the amounts of soil organic carbon were higher in agroforestry systems than in the fields without agroforestry management (Fig. 30b$_1$ and 30b$_2$). Total nitrogen and water soluble nitrogen in agroforestry systems were also higher than those in waste fields ($p < 0.1$), especially at depths of 0–40 cm (Fig. 30c$_1$, 30c$_2$, 30d$_1$ and 30d$_2$). There was little difference in the amount of available phosphorus ($p = 0.637$; Fig. 30e$_1$ and 30e$_2$), while the available potassium contents in agroforestry systems were lower than in the field without agroforestry management ($p < 0.1$) (Fig. 30f$_1$ and 30f$_2$). The contents of sodium and silicon did not differ significantly ($p > 0.1$), but were lower at the depths of 0–20 cm and 20–40 cm in agroforestry systems than in the waste field, while were about the same at the 40–60 cm layer in both fields (Fig. 30g$_1$, 30g$_2$, 30h$_1$ and 30h$_2$).

4.6.2 Nutrient distribution

There were significant differences in the distribution of organic carbon, total nitrogen, water-solu-

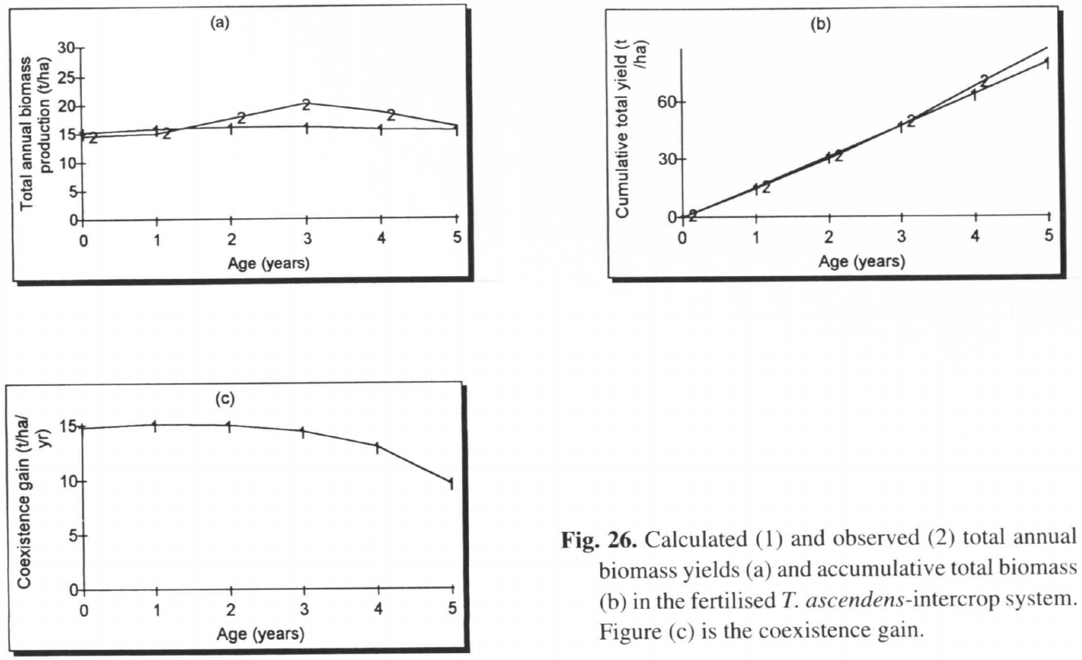

Fig. 26. Calculated (1) and observed (2) total annual biomass yields (a) and accumulative total biomass (b) in the fertilised *T. ascendens*-intercrop system. Figure (c) is the coexistence gain.

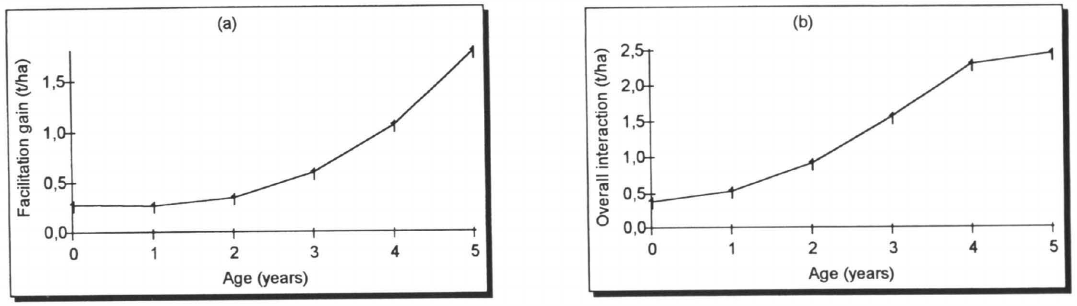

Fig. 27. Interactive performance of *T. ascendens* , intercropped with wheat and soybean. Figure (a) demonstrates the facilitation gain of *T. ascendens*; and (b) the overall interaction.

ble nitrogen, sodium and silicon contents at the soil depths from 0 to 60 cm ($p < 0.01$). The pH rose with increasing soil depth (0–60 cm) in the agroforestry systems (Fig. $30a_1$). The organic carbon and total nitrogen levels fell as the soil depth rose (Fig. $30b_1$ and $30c_1$). The contents of sodium and silicon were lower at the depths of 0–20 cm and 20–40 cm than at the 40–60 cm layer in the soil with agroforestry management (Fig. $30g_1$ and $30h_1$).

There was significant difference in the distribution of pH ($p < 0.05$) and of available phosphorus content ($p < 0.01$) between two tree rows (width: 6 m). The pH of soil in the middle of tree between-rows was higher and the available phosphorus content was lower than those under the tree crowns. The other nutrient contents, e.g. total nitrogen, water soluble nitrogen, CEC, Mg, Si, Al and Na, were about similar within 6-metre wide field ($p > 0.95$).

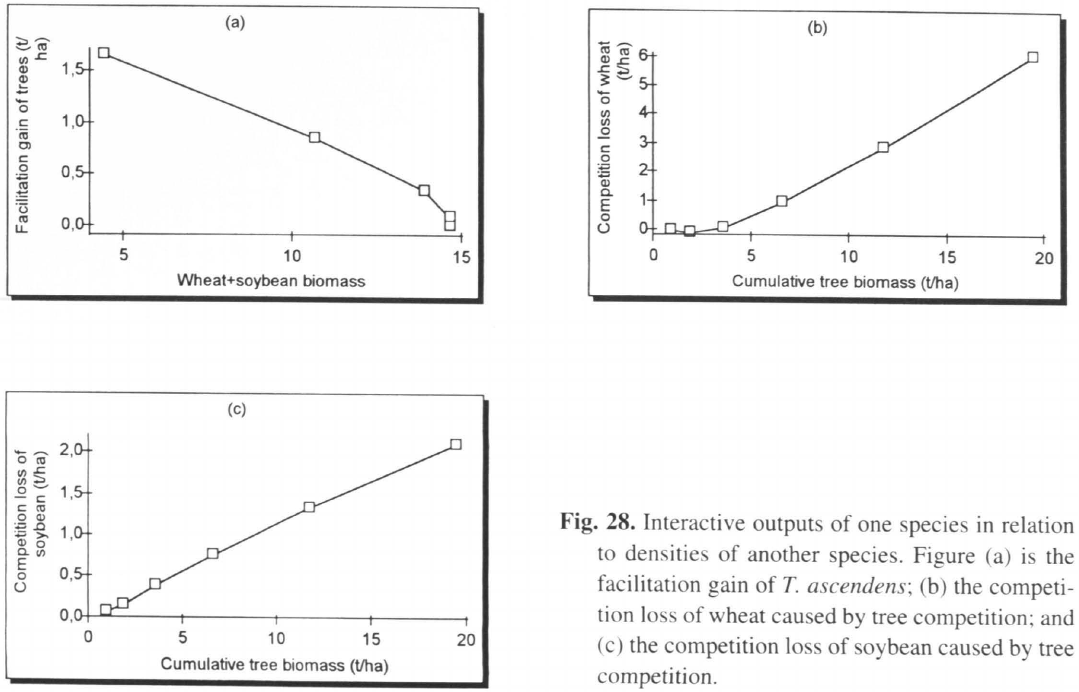

Fig. 28. Interactive outputs of one species in relation to densities of another species. Figure (a) is the facilitation gain of *T. ascendens*; (b) the competition loss of wheat caused by tree competition; and (c) the competition loss of soybean caused by tree competition.

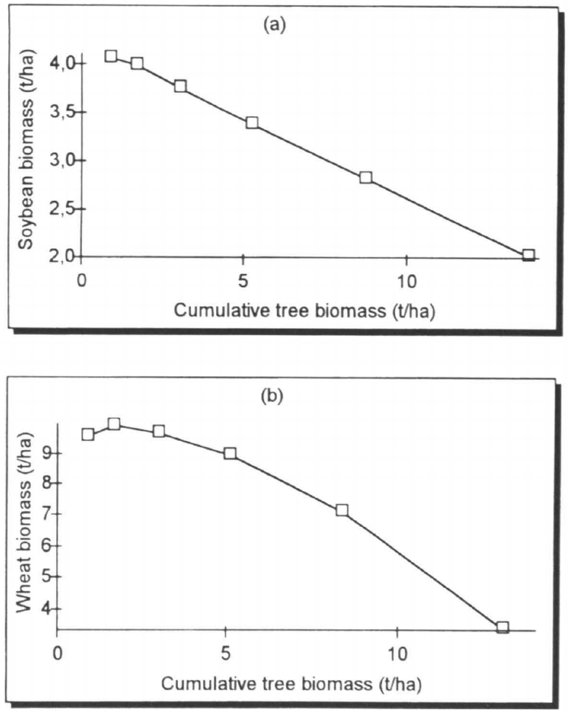

Fig. 29. Annual arable crop yields in relation to *T. ascendens* population density. (a = soybean; b = wheat).

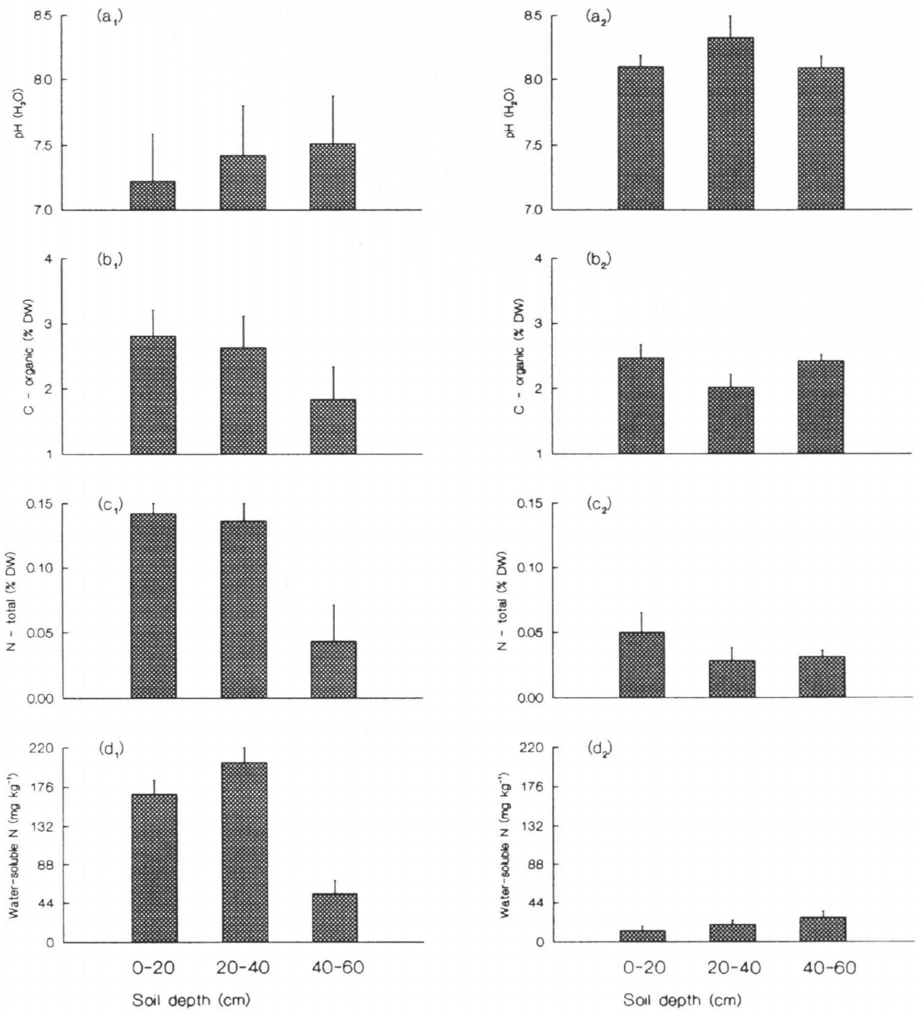

Fig. 30a. Soil chemical properties of the forest floor after nine years of agroforestry management (a_1, ..., d_1) and waste fields without agroforestry management (a_2, ..., d_2).

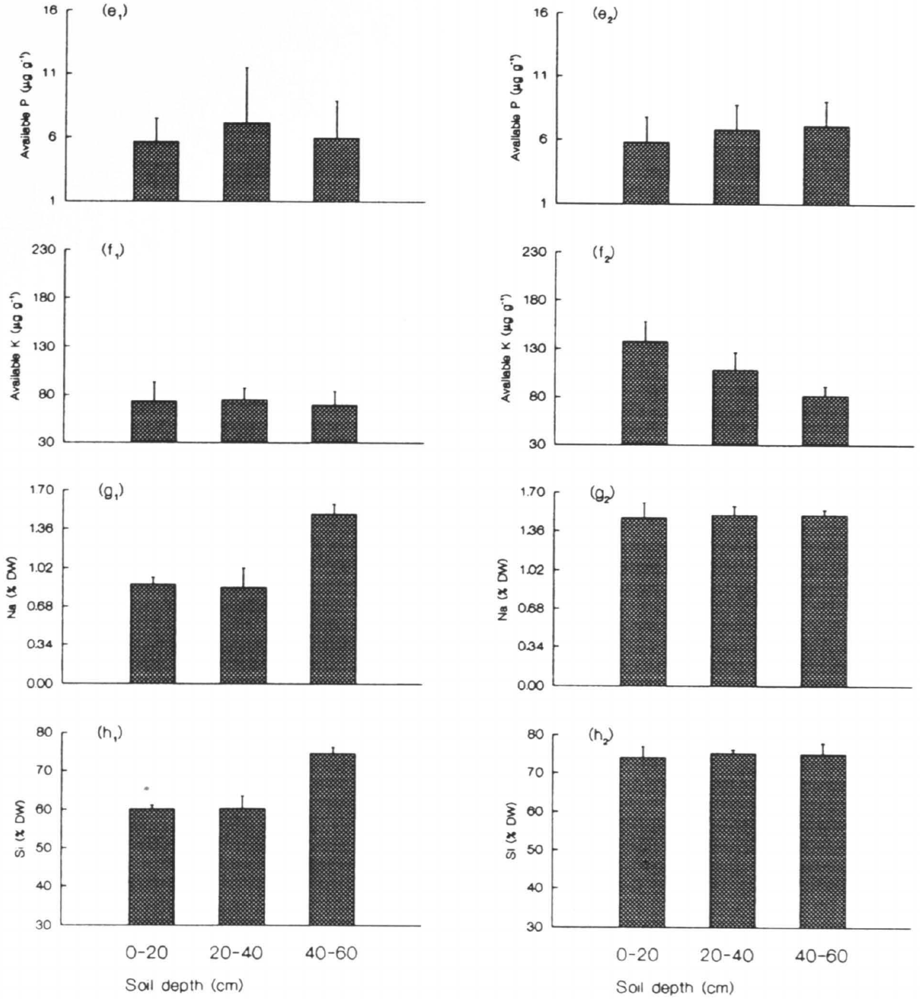

Fig. 30b. Soil chemical properties of the forest floor after nine years of agroforestry management (e_1, ..., h_1) and waste fields without agroforestry management (e_2, ..., h_2).

5 Discussion

5.1 Effect of Open-ranges on Arable Crops

The results of the present study demonstrated the effect of the open-ranges in tree stands on the high light-requiring arable crops. Among the environmental factors likely to be influenced by the open-ranges (termed gaps in natural forests) are: light, including both the total amount received and the relative importance of diffuse and direct beam radiation; and soil properties, including moisture, temperature and nutrient concentrations (Runkle et al. 1995). Important variables also include open-range size, position, and height (Runkle et al. 1995, Canham et al. 1990).

In the present study, the open-ranges in tree stands clearly affected the yields of high light-requiring arable crops, especially when the size of the open-ranges reduced below a critical level. These include between-rows open-range, within-rows open-range, canopy open-range and space-volumed open-range in tree stands. The impact of the within-rows open-range mainly results from the decrease in the penetration of the side-light (reaching the between-rows ground), which is intercepted by the within-rows canopy, especially when no within-rows open-range exists between adjacent plants.

The space-volumed open-range in tree stands was calculated to incorporate also the open-range height which will influence light, temperature, humidity and soil factors (Runkle et al. 1995, Canham et al. 1990). Therefore the space-volumed open-range represents the real effect of the open space in the tree stands on the environment and intercrop growth. Thus, it is worth considering in attempts to determine the optimum management of species composition in agroforestry systems.

The effect of open-ranges on the understorey is directly relative to the light environment (Kohyama 1993, Bradshaw and Spies 1992). An investigation to assess the effects of *Leucaena leucocephala* on the productivity of maize, cowpea and sweet potato in Sierra Leone detected reduced yields of maize and sweet potato in the rows immediately adjacent to the trees (Karim et al. 1991). In Nigeria intercropping *Leucaena leucocephala* with maize indicated that above-ground competition for light was more important than below-ground competition (Kang et al. 1981). In another study, examining the resource-use ability of multipurpose trees in an intercropping system, the crop yield was found to be depressed by competition with trees for light (Srinivasan et al. 1990).

In the present study, the following assumptions were made: during the first three years, the reduction of light caused by the canopy does not reach a level that will significantly decrease the growth of the high light-requiring crops; thereafter, open-ranges are distinctly relative to the growth of these crops because the reduced light is less than that required for the growth of intercrops. This critical value of light or open-ranges can be assumed to determine whether or not these high light-requiring arable crops will continue to be intercropped. In practice, the measurement of the open-ranges seems to be easier than direct light measurement, and the values of open-ranges are easier to calculate and use in management.

Agroforestry ecosystems can be extremely dynamic, with available resources and environmental conditions changing over time (Buck 1986). Management can affect the allocation of these resources and the biomass production by controlling inter- and intra-species competition (Huang and Huang 1991, Huang et al. 1993). In our experiments, the yields of wheat, rape and soybean during the first three years varied only slightly in different spacings and for different tree stand ages, indicating very little competition by the trees. This suggests that the four stand spacings of *T. ascendens* may provide sufficient light for the growth of understorey arable crops, without much competition with these crops for light. When tree stands were four years old, the total biomass yield of the

tree+wheat system reached its highest level. If the goal of agroforestry management is the production of maximum biomass, this critical stage is obviously the optimal period for regulating the species composition.

The aim of agroforestry is to maximize positive and minimize negative interactions (Young 1989a). The goal of plant management in agroforestry is to alter crops in the horizontal, vertical, and time dimensions such that they share the different resource pools in a way that minimizes mutual interference and maximizes resource sharing (Buck 1986, Huang and Wang 1992). In plant arrangement, open-ranges in tree stands will have a significant effect on the intercrop growth and species coexistence, because open-ranges increase the environmental heterogeneity (Runkle et al. 1995, Busing 1995). Plant growth requires continuous and balanced access to light, water, and nutrients. In agroforestry systems, the access of understorey intercrops to these factors – especially to light – is influenced by open-ranges. These environmental variables vary with open-range size, position within the open-range, and height of the open-range (Canham et al. 1990).

5.2 Competition Between Trees and Arable Crops

Some current theories concerning population and community ecology make predictions as to how the intensity of competition will change in different environments, e.g. along gradients in resource availability (Grime 1979, Tilman 1982, 1988, Keddy 1989, Grace 1995). Previous studies have found that competitive intensity increases (Wilson and keddy 1986) or does not vary (Wilson and Shay 1990, Wilson and Tilman 1993) with soil fertility. Miller (1996) observed that fertiliser treatments in a competition experiment using *Brassica rapa* and *Raphanus sativus* had a significant effect on the intensity of interspecific but not on intraspecific competition, and both of the results depended on the range of soil fertiliser and on the density of competitors: at a lower level of fertilisation, competition tended to decrease with nutrient addition, but not monotonically.

Unfortunately, most of these studies are based on annual plants, and less on tree species and annual crops. Moreover few results are available for comparison on the rate change of competitive intensity in consecutive generations or with increasing ages of plant species in the communities involving perennials. The results of the present study did not show significant differences in the curve of competition coefficients (*T. ascendens* on wheat and soybean) with increasing cumulative biomass of trees between the two nutrient levels (i.e. unfertilised and fertilised). It is also apparent that the inter-specific interaction between trees and intercrops is not linearly proportional. This evidence is important for identifying the interactive performance and for developing an accurate prediction model in perennial-annual communities.

5.3 Model Analyses

In general, to decide on the adequacy of a model, several criteria have frequently been considered (Gilpin and Ayala 1973): (1) simplicity, i.e. the model contains the minimum number of parameters that are necessary to account for the observed results; (2) accuracy, i.e. the explained variance should be as close to 1.0 as possible and the shape of estimated performance should agree well with observation; (3) reality, i.e. all of the parameters of the model could have biological interpretation; and (4) generality. In the present study, the model was developed with five parameters, one more than the GA model, and two more than the LV model. The model can explain a high proportion of variance of experimental data and is able to estimat the biomass dynamics well fitted to the observations. Lately, the present model has also been validated using independent data, and it gave a good prediction of interactions among species in agroforestry systems (Huang 1998). The parameters in the model, even though they sometimes do not necessarily have biological significance, somehow have a biological interpretation. According to the above criteria, the present model seems to be acceptable in describing the interactions of species in *T. ascendens*-intercrop systems.

Ong (1995) proposed a tree-crop interaction equation for quantifying the crop and tree component effects: overall interaction = fertility effect –

competition effect (Sanchez 1995). A positive overall interaction means net complementary effect, and a negative value indicates net competition. In the fertilised treatments of the present study, the results were similar to Ong's work (1995), except that he used arable crops as the principal components and trees were only used as a mulch resource to improve soil fertility (Sanchez 1995). No crop overall interaction was calculated in the present study.

When adding an individual of a second species, we can expect the rate of growth of the first species to be reduced. It is uncertain that the rate of growth of the first species is linearly proportional to the density of the second species. Confronted with large population or many species involved in a complex system, most previous workers assume that it is roughly proportional. Then using this assumption, many coefficients are estimated for describing or simulating a complex system in an uncertain environment. Obviously, these coefficients conceal the uncertainty of intraspecific and interspecific interaction. If these coefficients are used to estimate the coefficients of other equations (e.g. a master model with several submodels), this proportion relationship will be further augmented, and an accurate model will be difficult to be formulated.

In the present model, θ_i and ψ are respectively the feedback rate of intraspecific competition and that of interspecific competition at which the feedback effects change. It can be expected, if the intraspecific or interspecific competition is linearly proportional, that θ_i and ψ will tend to become zero; if it is asymmetric, θ_i and ψ will depart from zero. These two flexible parameters with the power-law appear to increase the range of accurate representation in the interactions of plant communities. Thus the present model may be a useful alternative for describing the intraspecific and interspecific interactions even in an uncertain complex ecosystem, just adding two more feedback coefficients to the LV model or one more feedback coefficient of interspecific competition to the GA model. However, it is not certain that this model has the same interaction process as found in other complex systems, even though this model is expected to have perhaps a greater generality and to be also more precise and realistic. Further theoretical and experimental work is needed.

5.4 Productive Coexistence

In the present work, when the trees were young (the first three years), they did not depress crop yields. A higher land equivalent ratio (L) was thus obtained together with high yields of trees and rape. After the tree stands were three-years-old, the trees exerted a negative influence on the arable crops; although L remained higher than 1.0, the yield of the crop component was lower than that in monoculture.

Rape seemed to have a higher ecological combining ability with *T. ascendens* than wheat or soybean. A possible reason for this is that the competition of trees with rape for light is less distinct than that of trees with wheat or soybean. The leaves of *T. ascendens* appear around 10–20 April, and rape is ripe for harvesting around 15–25 May, while wheat is ripe for harvesting around 10–20 June. Soybean is sown after rape or wheat is harvested, and there is competition with trees for light during the whole growth period of soybean.

In the present study, the facilitation of intercrops by tree species was not identified in the unfertilised treatment, but this does not mean that trees do not have any positive effects on intercrops. Even though the tree species may have a positive effect on the environment, the intercrops frequently show a decline in production because the effect of tree competition on intercrops is often stronger than the effect of trees on the environmental improvement. For instance, in April, May and June, when dry weather and wind are dominant in the experimental area, it is possible that the tree stands can protect the intercrop growth. The air humidity in four-year-old stands of *T. ascendens* increases by 0.7–4 percentage points as compared to the open fields (Huang and Huang 1991a). In five rows of tree belts (tree height: 8.5 m; canopy closure 0.8–0.9) the wind velocity has been measured as 1.14 m s^{-1}, when it was 2.3 m s^{-1} in the open field (Gao 1987). Damage to rape or wheat by the wind could be reduced by tree stands. Well designed experiments are therefore required to separate facilitation from competition.

5.5 Resource Sharing

The production of an understorey arable crop is conditioned by the modification of the understorey light environment by the overstorey crop (Vandermeer 1989, Newman 1986). The light environment in the understorey has considerable influence on the resource sharing in tree stands. In the experiment of tree spacing, it was observed that the understorey light environment can be regulated by widening the distance between rows of tree stands to increase the light between rows (Huang and Wang 1992, Huang et al. 1993). There are at least two ways to increase the resource sharing under tree stands. One is the switch from intercropping of high light-requiring crops to the intercropping of low light-requiring crops, and another is the regulation of the tree stand composition. For sharing of nutrients and water, the characteristics of tree and arable crop species (e.g., structures of the crown and root systems, the level of nutrient requirement), are of great importance. To maintain the maximum yield or profit of agroforestry, a control of the canopy composition of tree stands is needed. The critical canopy closure for maximum yield can be taken as the index for optimal control. For instance, the total yield of agroforestry in this study peaked when the tree stands were four years old. The canopy closure of tree stands at this time could be considered as the critical stage for optimal control of tree stands.

5.6 Application of Fertilisers to the Intercrops as an Indirect Facilitation for Tree Growth

Recent studies have emphasised the role of positive feedbacks in the dynamics of plant communities (Pugnaire and Haase 1996, Hobbie 1992, Wilson and Agnew 1992), and reported the primary roles of facilitation among plants, especially in the ability of plant species to improve their environment by enhancing nutrient availability or resource capture (Bertness and Shumway 1993, Callaway 1994). Vandermeer (1989) discussed the environments modified to produce facilitation in intercropping ecology, and important factors included N, water (e.g. relative yield totals as a function of irrigation), P, K, and protection from pests, as well as weed control as indirect facilitation. This suggests that facilitation, i.e. positive interaction between species, is more important than previously recognised in the dynamics of plant communities (Bertness and Shumway 1993).

In intercropping or alley cropping systems of agroforestry, when arable crops (e.g. wheat, rape and soybean) were grown under trees, application of nutrients to these crops (quite common in practice) facilitated the tree growth. This indirect facilitation is important in productive regimes. Indirect facilitation is assumed to occur through trees sharing the fertilisers with arable crops. The increased growth of *T. ascendens* was observed in fertilisation N (131.25 kg N ha^{-1} yr^{-1} for arable crop intercropping under trees), indicating that application of N to the intercrops will facilitate tree growth.

Most facilitation occurring in agroforestry is a result of the effect of intercrops on the environment and the positive response of tree species to it. Tree species could also have a positive effect on the environment, for instance, by protecting a crop from storm damage or herbivores, and by providing the crop with nitrogen (e.g. legume species) (Vandermeer 1989). To facilitate tree growth by intercrops or to facilitate the arable crop growth by trees, the positive modification of environmental factors should be considered. The best-documented approach is the combination of legume species (Nair 1985, Raintree 1990, Young 1989c). Others include the decrease in soil erosion and the reduction in pest attack (Young 1989c, Perrin 1977, Kass 1978, Nickel 1973). In the experiments of current study, the increase in the facilitation of tree growth in agroforestry mainly results from the improvement of physical and chemical properties of the soil, e.g. soil porosity, water retention, pH and organic material (Huang and Huang 1991).

5.7 Possibility of Agroforestry Management for Soil Improvement

One of the most important hypotheses concerning agroforestry is based on the capacity of the tree root systems to trap such nutrients in the soil solution that would otherwise be lost by leaching and to recycle them through litter to the soil surface (Young 1989a). In this study, the contents of organic carbon, total nitrogen, and water-soluble nitrogen were higher in the topsoils (0–40 cm) of agroforestry systems, while those of phosphorus and potassium were lower than those without agroforestry management. The increase of organic carbon, total nitrogen and water-soluble nitrogen may result from the litter of trees and arable crops, from nitrogen fixing of intercropped soybean or from ryegrass. The reduction of other nutrients except P may be caused by the removal of harvested arable crops and by leaching from forest floors. Thus, in this experiment, the primary benefits of agroforestry management on soil were the increased levels of organic carbon and nitrogen as well as the reduction of pH.

The decrease of high pH due to agroforestry management was a surprising result. In strongly acidic soils, one hypothesis is that recycling of bases in tree litter can help to reduce soil acidity or check acidification (Young 1989a). In the present studies, agroforestry management resulted in reduced pH in swamp soils with inherently high pH (pH >7.5), as compared to the uncultivated lands where weeds grew poorly. Similar results have been found by Liu (1990) and Huang (unpublished), the later observation was from a tree-fish-arable crop system. This may have resulted from integrated measures (e.g. tilling and other buffering effects by intercropping) and leaching. The reduction of excessively high pH values will obviously increase the survival rate and growth of *T. ascendens* and other crops, as indicated by the fact that seedling leaves of *T. ascendens* become yellow when the pH is above 7 and may die when the pH is above 9 (Huang 1978). This is also of interest to local farmers since soil improvement using agroforestry techniques leads to better agricultural production.

The pH rose as soil depth increased. This suggests that the effect of agroforestry management on pH primarily happens in the top soil layer. The pH of soil in the middle of tree between-rows was slightly higher than that under the tree crowns.

In practice, the distribution of soil nutrients will provide some information to improve the fertilisation in agroforestry. It was now observed, for instance, that the content of available potassium in the soil of middle of between-rows was lower than in the soil under the tree canopy.

Compared to tree or arable crop monocultures, agroforestry systems returned more nutrients back to the soil. When the tree stands of *T. ascendens* were five years old, the amounts of N, P and K returned to the soil as litter from a system combining trees with arable crops were 89.6, 5.3 and 32.8 kg ha^{-1} annually, while those in the monoculture of *T. ascendens* were 66.2, 3.2 and 12.1 kg ha^{-1} respectively (Liu 1990).

In general, the results in the present study suggest that a yield advantage can be achieved in a well designed agroforestry system. Facilitation and complementary use of resources are the primary contribution to the overyielding of species combination. Model development for describing coexistence gain and population interactions was one of main tasks in this study. Both theoretical consideration and actual results suggest that the present models are able to represent the intraspecific and interspecific competition and to estimat the outcome of competition more accurately than the LV model or GA model, especially in a complex ecosystem with an uncertainty of competitive patterns. There is a potential for the present models to be applied also to other complex ecosystems, but further experiments are needed to test the validation of these models in such situations.

6 Conclusions

According to the outcome of the present study, it is possible to conclude as follows:

(1) A theoretical framework for productive coexistence of populations in agroforestry systems was further developed. The criteria of productive coexistence as used in the present work provide an approach for investigating the interaction patterns and ecological combining ability among different species or populations.

(2) A theoretical framework for coexistence gain and interaction of populations was developed so as to describe the advantage and dynamic development of species combination in *T. ascendens*-intercrop systems. This was also one of the main objectives in the present work. The coexistence gain as defined by the present study suggests that a deliberately designed agroforestry system exploits the positive interaction and contributes to sharing of the available resources. The theoretical framework was further formulated as a mathematical model. The model of population interaction was compared with the previous Gilpin-Ayala and Lotka-Volterra models. The new model can well describe the interaction of populations in *T. ascendens*-intercrop systems, and it can take both the GA model and the LV model as special cases; this provides flexibility for describing the different patterns of intra- and inter-specific interactions. However, this model needs to be further studied and tested. Coefficients ψ and α in the model could possibly be used in species selection for better ecological combination in multi-species production systems.

(3) The results of the present study show that managed *T. ascendens*-intercrop systems are advantageous as compared to monocultures of trees or arable crops. All land equivalent ratios of various intercropping types were above 1.0, even though the relative yield of intercrops was below unity. The growth of *T. ascendens* was not significantly influenced by intercropped wheat or soybean, indicating that intercropping under trees produced extra yields but did not depress the tree growth, and implying that the resource sharing was operative.

(4) The contribution of the intercrop yields to the total biomass yield of agroforestry was from 50 % to 85 % in three-year-old stands, suggesting a high potential to increase land productivity by intercropping regimes; however, this contribution was reduced as the tree stands grew older. The high initial LERs of agroforestry systems found in the present study may simply have occurred because of lack of interspecific effects at the early stages of tree stand development.

(5) Canopy open-ranges were correlated with the yields of intercrops. When tree stands became five years old, the relative yields of rape, soybean and wheat decreased significantly as a result of decrease in the open-ranges.

(6) Tree diameter, height growth and tree biomass production were facilitated by fertilizing in intercropping regimes. The increase in resource sharing efficiency under tree stands was enhanced by the replacement of high-light-requiring crops (wheat, rape or soybean) by low-light-requiring ryegrass (*Lolium perenne*).

(7) A somewhat unexpected result was a decrease in the (originally high) pH of the soil after nine years of agroforestry management. This is of significance for improving the agricultural production in the swamp soil with high pH. The levels of organic carbon, total nitrogen and water-soluble nitrogen in the top soil were higher in agroforestry systems than in the field without agroforestry management, suggesting possible improvement of the soil nutrient balance by agroforestry regimes.

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Publication Schedule Acta Forestalia Fennica is published intermittently, 3 to 6 numbers per year.

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ISBN 951-40-1603-3
ISSN 0001-5636

9 789514 016035

Cover: Jarmo Koivunen