

Coconut-based homegardens: mechanisms of complementarity in sharing of growth resources among homegarden trees in the South Andaman Islands of India

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Abstract: Complementarity among tree species in sharing the growth resources is a key to the sustainability in crop productivity. However, information on how the species separate their niches above- as well as below the ground and develop complementarity in sharing the growth resources is poorly known for the homegardens of humid tropics. This study reports aboveground growth resource (sunlight) sharing, and pattern of fine root biomass distribution, and uptake of N, P and K by the coconut tree (main crop) and its intercrops (clove and nutmeg trees) in a coconut-clove and a coconut-nutmeg plantation in the South Andaman Islands of India. The main crop and its intercrops have the same geometry in the plantation as they have in homegardens of the islands. The study included three tree species (coconut, clove and nutmeg), and five distances (0.75, 1.50, 2.65, 3.80 and 4.55 m) from the coconut towards its intercrops. The coconut intercepted 30-32 % sunlight above the canopy of its intercrops. The intercrops, in turn, restricted their root distribution up to 2.65 m from their trunk. The coconut, however, extended its roots quite close to its intercrops. In addition to its own niche, the coconut mined nutrients from underneath of its intercrops, but the intercrops utilized the nutrients only from their niches. These observations suggest that trees in homegardens separate their niches horizontally below the ground and, thereby, develop complementarity in the growth resource sharing. Above the ground, the main crop, however, intercepts light and imposes partial shade on its shade-loving intercrops. This information has bearing for managing above- and below-ground growth resource sharing in agroforestry systems.

Resumen: La complementariedad entre especies de árboles en la distribución de los recursos de crecimiento es clave para la sostenibilidad de la productividad de los cultivos. Sin embargo, la información sobre cómo las especies separan sus nichos arriba y debajo de la tierra y desarrollan la complementariedad al compartir recursos de crecimiento es poco conocido para los huertos familiares de la zona tropical húmeda. Este estudio reporta el reparto de recursos para el crecimiento aéreo (luz solar), así como el patrón de distribución de biomasa de las raíces finas, y la absorción de N, P y K, por el cocotero (cultivo principal) y sus cultivos asociados (árboles de clavo y de nuez moscada) en una plantación de cocoteros y clavo, y de cocoteros con nuez moscada, en las Islas Andamán del Sur, India. El cultivo principal y sus cultivos asociados tienen la misma geometría en la plantación y en los huertos familiares de las islas. El estudio incluyó tres especies de árboles (cocotero, clavo de olor y nuez moscada), y cinco distancias (0.75, 1.50, 2.65, 3.80 y 4.55 m) entre el cocotero y sus cultivos asociados. El cocotero interceptó 30-32 %

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de la luz solar arriba de las copas de los cultivos asociados. Los cultivos asociados, a su vez, limitaron la distribución de sus raíces hasta una distancia de 2.65 m desde su tronco. El cocotero, sin embargo, extendió sus raíces hasta llegar bastante cerca de sus cultivos asociados. Además de su propio espacio, el cocotero extrajo nutrientes por debajo de sus cultivos asociados, pero estos últimos sólo utilizaron los nutrientes de sus propios espacios. Estas observaciones sugieren que los árboles en los huertos familiares separan sus nichos horizontalmente debajo del suelo y, de esta manera, desarrollan la complementariedad en la distribución de los recursos de crecimiento. Por encima de la superficie del suelo, el cultivo principal, sin embargo, intercepta luz y crea una sombra parcial sobre sus cultivos asociados que son esciófitos. Esta información tiene implicaciones importantes para el manejo del reparto de recursos de crecimiento por encima y por debajo del suelo en los sistemas agroforestales.

Resumo: A complementaridade entre as espécies de árvores na partilha dos recursos de que depende o crescimento, é fundamental para a sustentabilidade da produtividade das culturas. No entanto, a informação sobre como as espécies separam os seus nichos, acima e abaixo do solo, para desenvolver a complementaridade na partilha dos recursos que determinam o crescimento é pouco conhecida para os quintais de casa nos trópicos húmidos. Este estudo dá nota dos recursos de crescimento acima do solo (luz solar) e partilha e padrão de distribuição da biomassa das raízes finas e absorção de N, P e K pelo coqueiro (cultura principal) e das culturas consociadas (árvores de cravo e noz-moscada) numa plantação de coqueiro - cravo e noutra de coqueiro - noz-moscada, no Sul das Ilhas Andaman da Índia. A cultura principal, e as suas consociadas, obedeceram à mesma geometria na plantação, como têm nos quintais de casa das ilhas. O estudo incluiu três espécies de árvores (coqueiro, cravo e noz-moscada) e cinco distâncias (0,75, 1,50, 2,65, 3,80 e 4,55 m) contadas a partir do coqueiro para as suas consociadas. O coqueiro interceptou 30-32 % da luz solar acima da copa das suas consociadas. Estas, por sua vez, restringiram a sua distribuição radicular até 2,65 m de seu tronco. O coqueiro, no entanto, estendeu suas raízes até bem perto das espécies consociadas. Além de seu próprio nicho, o coqueiro minou os nutrientes mesmo debaixo das espécies consociadas, se bem que estes tenham utilizados nutrientes apenas nos seus próprios nichos. Estas observações sugerem que as árvores nos quintais de casa separam seus nichos horizontalmente abaixo do solo e, assim, desenvolvem a complementaridade na partilha de recursos necessários ao crescimento. Acima do solo, a cultura principal, no entanto, intercepta a luz e impõe o sombreamento parcial nas espécies heliófilas consociadas. Esta informação tem influência para a gestão da partilha de recursos para o crescimento, acima e abaixo do solo, em sistemas agroflorestais.

Key words: Complementary relations, growth resources, niche separation, nutrient uptake, root distribution.

Introduction

Two types of interactions, i.e. competitive and complementary, are found in natural ecosystems and agroecosystems (Callaway 1998), which shape community structure, plant diversity and system's functions (Bruno *et al.* 2003; Callaway 1995; Pugnaire *et al.* 1996). Competitive interaction in ecosystems (Wedin & Tilman 1993) and agroecosystems (Pandey *et al.* 1999) is well documented. Mechanism of complementary interaction, however, is not much understood so far. Some studies

(Bertness & Callaway 1994; Callaway 1998) argue that complementary interaction is facilitative, either facultative or obligatory, and occurs generally in harsh physical environments. This suggests that habitat amelioration by neighbours is a common denominator of positive interactions (Bertness & Callaway 1994; Callaway & Walker 1997). Other studies report that complementary interaction is mutualistic (Boucher *et al.* 1982). Irrespective of whether facultative or mutualistic, it is now well established that complementary interaction is evolutionary (Bertness & Callaway

1994). But, it is still inconclusive how two species exist together in ecosystems and agroecosystems (Bertness & Callaway 1994).

Homegardens are a prominent land use system (Maroyi 2013; Saikia & Khan 2013; Saikia *et al.* 2012). Homegardens cover 63 % of the arable land in the Andaman and Nicobar Islands of India (Basic Statistics 2001) where plant species of different life forms and heights, i.e. coconut and arecanut palms, clove and nutmeg tree spices, mango, banana, guava fruit trees, and other agroforestry trees grow together and form a multi-storey structure similar to that found in Southeast Asia (Millate-E-Mustafa *et al.* 1996; Pandey *et al.* 2007). From the ground layer to upper stories, the gradient of light and humidity determines different niches that species exploit according to their own requirements (Fernandes & Nair 1986). Niche separation in the homegarden likely occurs due to complementary relations among the plant species for their growth resource sharing, which results in sustainable yield (Jensen 1993; Pandey *et al.* 2007; Soemarwoto 1987). Sustainability in the yields may also be attributed to the compatibility in the homegarden trees for below-ground growth resource utilization (Jensen 1993; Pandey *et al.* 2000; Rhoades 1997). Overstorey trees in the homegarden generally extend their roots quite close to the trunk of their understorey plants, but understorey plants restrict their roots to a limited distance from their trunk (Pandey & Venkatesh 2007). It is still not known how they separate their niches below the ground for utilization of growth resources, particularly nutrients.

We hypothesize that an overstorey tree in a homegarden agroecosystem intercepts light and, thereby, provides partial shade to its understorey tree crops (a facilitation effect), while the understorey tree crops, in return, exploit nutrients only from a limited space below the ground and, simultaneously, tolerate the presence of the overstorey tree. The overstorey tree, however, mines nutrients from its niche as well as from the niches of its understorey crops (intercrops). These facilitation, exploitation and tolerance mechanisms together allow the tree crops to coexist and exploit growth resources complementarily in the homegarden.

Homegardens include typically many species, life forms and involve several organic matter / nutrient input and output processes. Therefore, it is difficult to separate the species-specific interactions. Hence, to simplify species-specific interactions in the complex homegarden agroecosystem,

the present study was carried out in a coconut (*Cocos nucifera* L.), clove (*Eugenia caryophyllata* Thunb) and a coconut-nutmeg (*Myristica fragrans* Houtt. Nees) plantation, having similar tree crop geometry as found in the homegardens. The objectives of the study were to examine: (1) above-ground growth resource (sunlight) sharing, and (2) patterns of fine root biomass distribution (below-ground niche separation), and uptake of N, P and K by the coconut tree (main crop) and its intercrops (i.e. clove and nutmeg trees) at different distances between two tree crops (coconut-clove and coconut-nutmeg) in the plantation. The ultimate objective of the study, however, was to understand the mechanism of complementary interactions among the tree crops in the homegardens of the Andaman Islands of India.

Materials and methods

Study area

The study was conducted in a coconut-clove and a coconut-nutmeg plantation, both twenty-year old, at a research farm of Central Agricultural Research Institute (CARI) at Sipighat, South Andaman Island, India located at 10° 30'-13° 42' N and 92° 14'-94° 14' E and 315 m asl. Soils of the site are dystric fluvisols and the parent material is sandstone. The soils are well drained, sandy-loam, slightly acidic in reaction and moderate to poor in nutrients (Pandey *et al.* 2009). The Islands experience a true maritime climate throughout the year with a little variation in temperature from 23 to 30 °C; humidity varies from 71 to 85 %. December is the coolest month and May is the warmest month. Ten-year data (1997-2006) reveal that average annual precipitation is 3000 mm distributed over 8-9 months from May to January with 86 % occurring between May to November (≥ 400 mm month⁻¹) (wet season). Three months, from February to April, are relatively dry (< 100 mm month⁻¹) (dry season) (Pandey *et al.* 2007). Native vegetation is tropical rainforest dominated by *Dipterocarpus* species.

The coconut-clove and coconut-nutmeg plantations, each about 7 ha, were established in 1983 at the research farm of CARI. Coconut trees (main crop) were planted at a spacing of 7.5 x 7.5 m and spice trees like clove and nutmeg were planted in a quincunx manner (one spice tree in the centre of four coconut trees planted at the corners of a square) as intercrops in the plantation. Fertilizer (N:P:K - 2:1.3:1) 200 g tree⁻¹ and farmyard manure (FYM) 2 kg tree⁻¹ were applied to the trees in an

Table 1. Dimensions of coconut and its intercrops, and light intensity availability to the tree crops in a coconut-clove and a coconut - nutmeg plantation at the South Andaman Islands of India.

Tree	Height (m)	CBH (cm)	Canopy cover (m ²)	*Light intensity (Lux)
Coconut	12.0±0.03	44.9±1.41	98.7±1.09	4865±408
Nutmeg	6.9±0.55	39.6±0.92	48.3±0.72	3294±187
Clove	8.1±0.12	16.14±0.20	42.3±1.91	3387±195

*Intensity of light over coconut is the value recorded in open. Coconut is the top storey, hence light intensity present in open is assumed to be present over the coconut. CBH = circumference at breast height. Coconut (N = 24), Nutmeg (N = 3), Clove (N = 3). Height, CBH and canopy cover of all trees are presented on per tree basis.

area of 50 cm diameter around each tree for four years in the beginning until the trees started bearing. Thereafter, leaves fallen on the ground floor were put around the respective tree every month to simulate soil fertility management that homegardeners (farmers) do in their homegardens. Leaves of coconut were cut into pieces before they were placed. Weeding was performed in the plantation once a year in October.

Experimental design and laboratory analyses

Associations of coconut-clove and coconut-nutmeg (quincunx in planting), similar in shape and size, replicated three times, was selected randomly in the plantation for sampling. In a preliminary study, a maximum of 90 % fine roots were found to be located in the soil to a depth of 20 cm (Pandey & Venkatesh 2007). In each association a line transect was laid randomly from a coconut tree to its intercrop at monthly interval. Total 12 transects (3 transects from a coconut to its intercrop x 4 coconut trees in the quincunx planting) were laid in an association over a year. A monolith (15 x 15 x 20 cm) was excavated along a transect at 0.75, 1.50, 2.65, 3.80 and 4.55 m distance from the coconut tree towards the intercrop. Thus, total 360 monoliths (12 transects x 5 distances x 2 coconut-intercrop associations x 3 replicates) were excavated from the plantation. The monoliths were washed with a fine jet of water using successive 2-mm and 0.5-mm mesh screens. Fine root (< 2 mm diameter) biomass (FRB) and coarse root (2 mm - 1 cm diameter) biomass were

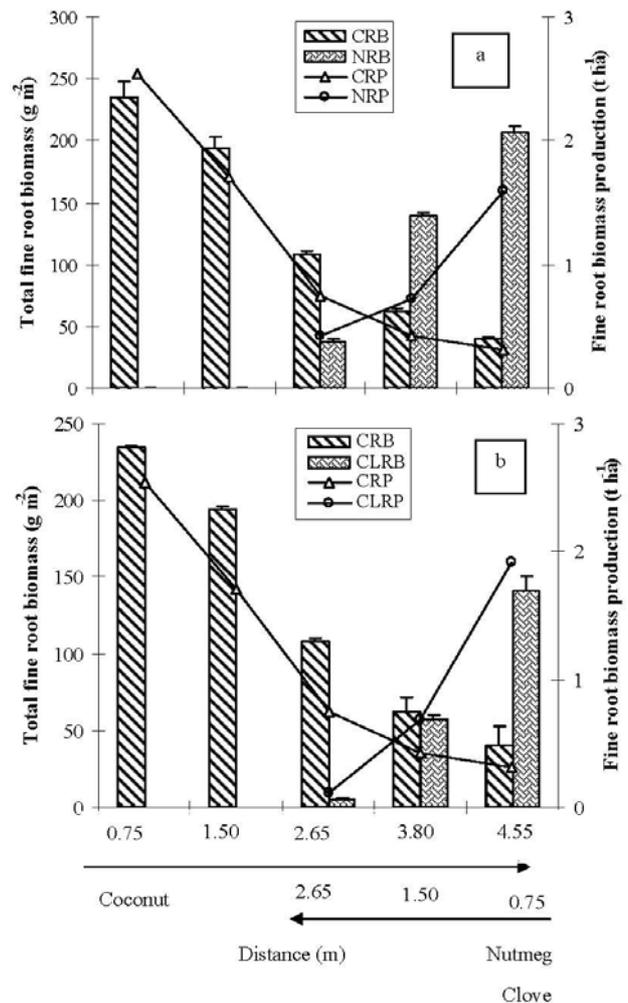


Fig. 1. Fine root biomass production (RP) and total fine root (live + dead) biomass (RB) of (a) coconut (CRP and CRB) and nutmeg (NRP and NRB), and (b) coconut (CRP and CRB) and clove (CLRP and CLRB) at different distances between coconut-nutmeg and coconut-clove trees in a coconut-clove and a coconut-nutmeg plantation at the South Andaman Islands of India.

separated for each species. The fine as well as coarse roots differed among species in colour and texture. FRB was further separated into live and dead root biomass. The live and dead fine root biomass, and coarse root biomass were dried separately at 60 °C in an oven to a constant weight. Fine root biomass production (FRBP) at each distance was calculated as the sum of increments in live root biomass between two successive months and the amount of dead root biomass, which exceeded the amount of decline in the live root biomass during the same period (Singh & Singh 1991). Oven-dried live and dead fine root

Table 2. Summary of analysis of variance (ANOVA) result (*F* value) for live fine root biomass, dead fine root biomass, total fine root biomass, fine root biomass production (FRBP), concentration of N, P, K in the root biomass and uptake of N, P, K by different species at different distances from the studied trees species in a coconut-clove and a coconut - nutmeg plantation at the South Andaman Islands of India.

Source	df	Fine root biomass (g m ⁻²)			FRBP (t ha ⁻¹)	Concentration in fine root biomass (%)			Uptake (kg ha ⁻¹ yr ⁻¹)		
		Live	Dead	Total		N	P	K	N	P	K
Species (S)	2	2308***	1816***	2324***	104***	39***	2473***	522***	49***	113***	198***
Distance (D)	2	3840***	3336***	3873***	414***	70***	155***	32***	349***	300***	535***
Month (M)	11	38***	398***	15***	-	-	-	-	-	-	-
S x D	4	100***	39***	65***	4*	51***	209***	44***	5**	15***	26***
S x M	22	31***	135***	23***	-	-	-	-	-	-	-
D x M	22	7***	75***	5***	-	-	-	-	-	-	-
S x D x M	44	8***	37***	8***	-	-	-	-	-	-	-

****P* < 0.0001, ***P* < 0.01, **P* < 0.05

- Not applicable (see experimental design).

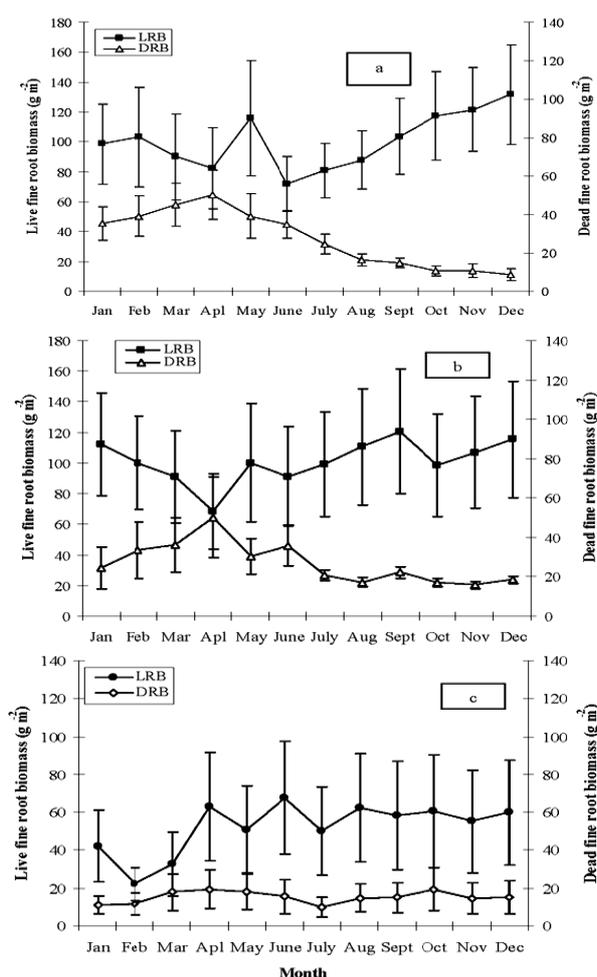


Fig. 2. Seasonal variation in live (LRB) and dead (DRB) fine root biomass of (a) coconut (b) nutmeg and (c) clove in a coconut-clove and a coconut - nutmeg plantation at the South Andaman Islands of India.

biomass samples were pooled across the months, and ground to powder. The powdered samples were analyzed for nitrogen content by micro-kjeldahl method using Kel Plus auto N analyzer, P by colorimetric method and K content by flame photometer. Nitrogen, P and K uptakes at different distances by the studied tree crops in both associations were calculated as FRBP x concentrations of N, P and K in the FRB (Singh & Singh 1991). Intensity of light over the trees was measured by a Lux meter using a ladder. Light intensity in open was treated as the amount of light available over the coconut trees (Pandey *et al.* 2011). Height of the trees was measured using a long stick and a measuring tape.

Statistical analyses

The data were subjected to two-way ANOVA using SPSS statistical package to test for the significance of variation in root biomass (live, dead and total fine root biomass), fine root biomass production and N, P, K concentrations in fine roots, and the uptake of these nutrients by the studied trees. Treatment for the root biomass was: species 3, month 12 and distance 3. Treatment for the remaining parameters was: species 3 and distance 3 (2.65, 3.80 and 4.55 m where root biomass of both main-crop and intercrop was present). One-way ANOVA was performed to test for the significance of variation in root biomass and other studied parameters of coconut due to three distances (0.75, 1.50 and 2.65 m). Number of replicates was three (replicates of coconut-intercrop associations) for both two-way and one-way ANOVA. Means of the

parameters were compared using least significant difference ($P < 0.05$).

Results

Dimension of trees and physical environment

Height, averaged across numbers, of the intercrops was 33 to 42 % lower than the main crop (Table 1). Coconut intercepted 32 and 30 % light above the nutmeg and clove canopies, respectively. Variation in the intercepted light, though not significant, occurred likely due to movement of leaves, which regulated sun rays to travel through spaces among leaflets and leaves to the intercrops.

Fine root biomass distribution

Total fine root biomass (live and dead) varied significantly ($P < 0.0001$) among the species, distance from the tree trunk and months (Table 2). The fine root biomass, averaged across the months and distances, was the highest (127.9 g m^{-2}) in coconut and the lowest (40.7 g m^{-2}) in clove (Fig. 1a, b). In both coconuts and intercrops, fine root biomass was higher closer to their trunks and declined with distance. The fine root biomass of both intercrops, i.e. nutmeg and clove was found up to the middle distance (2.65 m) towards coconut in the coconut-nutmeg and coconut-clove associations. But, the fine root biomass of coconut extended quite close to the trunk (4.55 m) of its intercrops i.e. nutmeg and clove in the associations (Fig. 1a, b). The fine root biomass was 17-20 % of the total root biomass (coarse + fine). Coarse root biomass is not discussed further assuming that coarse roots do not take part in the uptake of nutrients.

Seasonal dynamics in fine root biomass

Live and dead fine root biomass varied significantly ($P < 0.001$) with species and months (Table 2). Live fine root biomass of coconut increased quickly in May, but declined sharply in June. It increased further from July and peaked in December (Fig. 2a, b, c). A decline in live fine root biomass was observed from January to April. On the other hand, the dead fine root biomass declined from May to December. Pattern of seasonal variation in live and dead fine root biomass of nutmeg was similar to that of the coconut tree, but live fine root biomass of clove increased sharply from February to April and, thereafter, declined

gradually with little fluctuations until February. Dead fine root biomass varied across the months with small troughs and peaks. Pattern of seasonal variation in live and dead root biomass in all species was similar at all distances.

Fine root biomass production, and concentrations and uptake of nutrients in the biomass

Fine root biomass production varied significantly ($P < 0.001$) due to the species and distances (Table 2). Fine root biomass production, at all distances was the highest in coconut and the lowest in clove. In both coconut-nutmeg and coconut-clove associations, fine root biomass production in all species was higher closer to the trunk and declined with distance (Fig. 1a, b). Concentration of N, P, and K in fine roots varied significantly ($P < 0.001$) with distance in all species (Table 2). Generally it was higher closer to the trunk and declined with the distance in all species (Fig. 3 a, b). Concentrations of N, P and K in the fine root biomass of nutmeg and clove at all distances within their niches were greater than in the coconut roots found there. Uptake of N, P and K by all species was greater closer to the trunk and declined with the distance. Uptake of N, P and K by the intercrops was up to the middle point (2.65 m) towards their main tree crop, but the main tree crop mined the nutrients quite close (4.55 m) to the trunk of its intercrops (Fig. 4a, b). Uptake of N, P and K by the coconut from the niches of the intercrops, however, was lower than that of the intercrops.

Discussion

The studied coconut-clove and coconut-nutmeg plantations were more than 20-yr-old. Pandey & Singh (2009) reported that coconut-clove and coconut-nutmeg tree crop associations survived for a long time and provided sustainable, though low yields in the homegardens. This indicated that clove and nutmeg intercrops were compatible with coconut trees and co-existed as intercrops. Reduction in the intensity of light over the intercrops indicated that coconut intercepted light and, thereby, facilitated a conducive environment for the intercrops. Clove and nutmeg trees are known to prefer partial shade (Thankamani *et al.* 1994). This facilitative mechanism of aboveground growth resource (partial light) use in the coconut-spice tree associations has been reported among

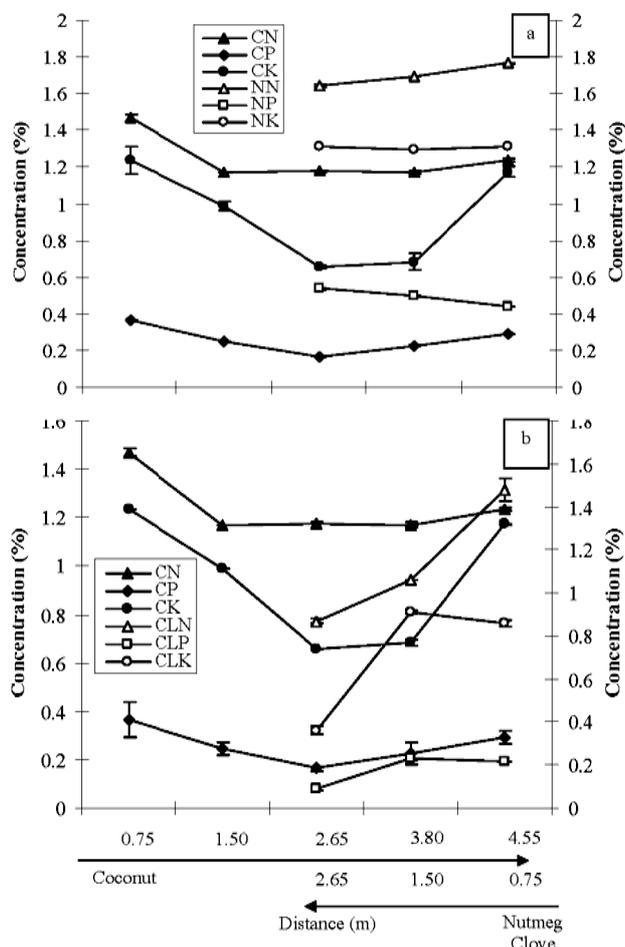


Fig. 3. Concentrations of nitrogen (N), phosphorus (P) and potassium (K) in the root biomass of (a) coconut (CN, CP and CK) and nutmeg (NN, NP and NK), and (b) coconut (CN, CP and CK) and clove (CLN, CLP and CLK) at different distances between coconut-nutmeg and coconut-clove trees in a coconut-clove and a coconut - nutmeg plantation at the South Andaman Islands of India.

species in ecosystems in deserts (Arriaga *et al.* 1993), savanna and woodland (Guevara *et al.* 1992), mediterranean shrub-land (Fuentes *et al.* 1984), salt marshes (Bertness & Hacker 1994), grasslands (Greenlee & Callaway 1996), successional forests (Bertness & Callaway 1994), *Paulownia*- (Zhaohua *et al.* 1986) and *Grevillea*- (Huxley *et al.* 1994) based agroforestry systems. In successional forests young and small understory plants survive under overstorey crops complementarily (Bertness & Callaway 1994). Plants have been found to have positive effects on each other by accumulation of nutrients, provision of

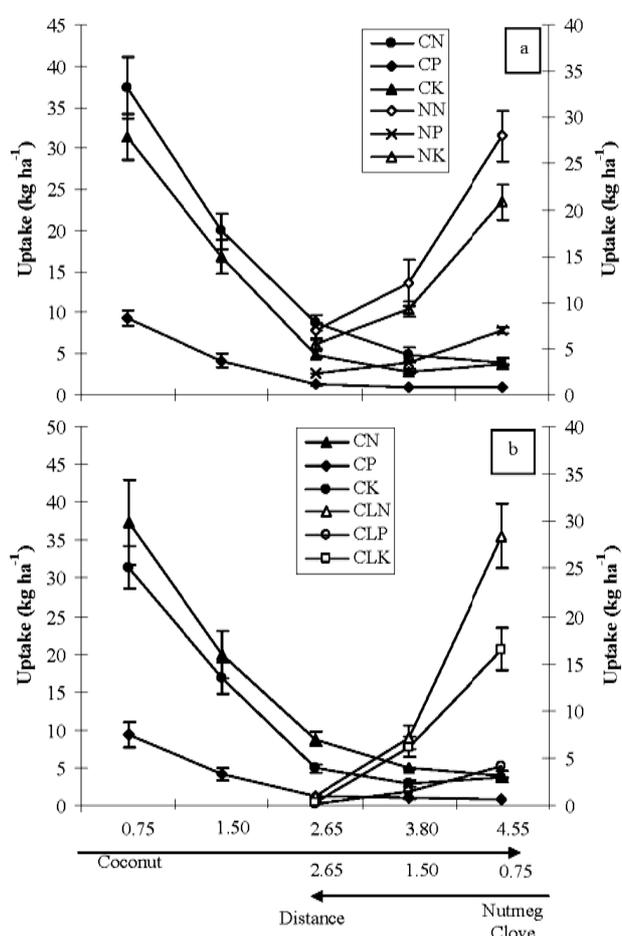


Fig. 4. Uptake of nitrogen (N), phosphorus (P) and potassium (K) by the (a) coconut (CN, CP and CK) and nutmeg (NN, NP and NK), and (b) coconut (CN, CP and CK) and clove (CLN, CLP and CLK) at different distances between coconut-nutmeg and coconut-clove trees in a coconut-clove and a coconut-nutmeg plantation at the South Andaman Islands of India.

shade, and amelioration of disturbances or protection from herbivores by some species, which enhance the performance of neighbouring species (Bertness & Callaway 1994).

Occurrence of fine root biomass of coconut under the intercrops suggested that in the coconut-clove and coconut-nutmeg associations coconut trees extended their fine roots horizontally quite close to the trunk of their intercrops. Wiersum (1982) reported that roots of coconut trees were located in upper depth of soils and were distributed extensively on the floor of homegardens in Indonesia. On the contrary, the fine roots of the intercrops

were brittle and weak and were confined to a certain distance from their trunks as also observed by Wiersum (1982). This horizontal separation of belowground niches of the tree species seemed evolutionary, which occurred probably to meet their nutrients and other growth resource requirements below the ground. Homegardens in Indian subcontinent have been developed since time immemorial (Kumar & Nair 2004). Farmers generally grow coconut trees in the premises of their houses in a wider spacing and spice trees as intercrops under the coconut trees. This probably forced the trees to carve out their niches in a complementary manner over the time for growth resource acquisition. But, the mechanism of interaction below the ground in our study was found different from that of the above ground. We found that the intercrops derived benefit (partial shade) from coconut trees above the ground, but tolerated its presence, in return, in their niches below the ground. This suggests that complementarity in nutrient sharing below the ground is tolerated unlike the facilitative mechanism above the ground. Connell & Slatyer (1977) were of the view that facilitative and tolerance mechanisms of complementary interaction might occur within the same plant community. Nelliatt *et al.* (1974) suggested that horizontally separated root systems could be the basis for complementarities in coconut-cocoa-pineapple multistorey agroforestry systems in Indonesia. Contrary to horizontal niche separation below the ground for nutrient acquisition in our homegardens, vertical niche separation has been reported to occur in *Paulownia*-based agroforestry system in China. *Paulownia* tree has the majority of its fine roots located at 40-100 cm depth, whereas its intercrops, namely wheat, maize and groundnut, above the tree root zone (Zhaohua *et al.* 1986). This vertical niche separation probably makes the *Paulownia*-based agroforestry system complementary. Also, in *Grevillea*-based agroforestry system of Kenya, vertical niche separation occurs below the ground (Huxley *et al.* 1994).

Uptake of N, P and K by the coconut from beneath the clove and nutmeg trees suggested that shelter / co-existence of the intercrops under the main crop (coconut) in the homegardens was not rent-free. Complementarity in the homegarden seemed to have developed in such a way that the intercrops would have to share their belowground growth resources with the main crop. In our study, coconut, being evergreen, flowered and produced fruits every month, and probably possessed a big-

size sink for nutrients above the ground (leaves). Like the coconut, nutmeg was also evergreen and flowered and produced fruits every month, but not as vigorously as the coconut. Clove, being semi-evergreen, flowered and produced fruits seasonally once a year. Comparatively, bigger sink size of coconut was also evident from the greater total uptake of N, P and K across the distances than the intercrops. This clearly suggested that the nutrient uptake potential and size of sink for nutrients in leaves could be the evolutionary forces, which led to the niche separation among the studied tree species in such a way that understorey plants not only tolerated the presence of roots of the main crop but also had to pay lunch bills, though partial, of the over-storey tree. van Noordwijk *et al.* (1996) were of the view that uptake of water and nutrients were often directly proportional to the aboveground demand, i.e. the size of the leaf and the strength of the aboveground sink for nutrients (van Noordwijk *et al.* 1996). Wiersum (1982) speculated that a shallow but extensive root system of coconut in the upper depth of soils in a mixed stand probably helped it to exploit belowground growth resources to the greatest extent.

A similar pattern of fine root distribution of the studied-species in both associations, and uptake of N, P and K by the coconut from the niches of its intercrops suggested that complementarity in the homegarden was not species-specific. Field observation suggested that in addition to the clove and nutmeg, several other trees like fruit trees, agroforestry trees, etc. co-existed with coconut and performed well in the homegardens (Pandey *et al.* 2007). This further corroborated that complementary interaction in the homegarden was not species-specific. Studies related to species-specificity in complementary interactions in homegardens are lacking. However, Callaway & D'Antonio (1991), and Callaway (1992) have found that survival of *Quercus agrifolia* seedlings was much higher under some shrub species than others although it has not been found to be the case for other species. In different ecosystems, distribution and abundance of many species have been found favourably altered by the presence of others (Callaway 1997). Callaway (1998), Kellman & Kading (1992) found that larger plants were more likely to benefit from facilitative associations than smaller plants. Some other studies, however, reported opposite results where younger or smaller plants depended on facilitative partnerships more than older or larger plants

(Archer *et al.* 1988; Callaway & Davis 1993; Callaway *et al.* 1996).

We conclude that coconut tree intercepts sunlight and provides partial shade to its shade-loving intercrops, i.e. clove and nutmeg in coconut-clove and coconut-nutmeg association, respectively, above the ground. Below the ground, the coconut tree extends its roots quite close to the trunk of its intercrops, but the intercrops extend their roots only up to a certain distance within the radius of their canopies. Thus, the main crop and its intercrops separate their niches horizontally. Clove and nutmeg exploit nutrients from their own niches, while coconut exploits nutrients from the niches of their intercrops in addition to its own niche. These observations suggest the occurrence of facilitative mechanism by the main crop to its intercrops above the ground, but exploitative mechanism below the ground. Further, the tolerance by the intercrops (presence of roots of the main crop in the niches of intercrops) make the coconut-clove and coconut-nutmeg associations complementary in the plantation and, therefore, in the homegardens.

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