Mycorrhiza (1996) 6:409–415

ORIGINAL PAPER

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Localized alteration in lateral root development in roots colonized by an arbuscular mycorrhizal fungus

Accepted: 29 August 1996

Abstract The morphological responses of root systems to localized colonization by endophytes is not well understood. We examined the responses of lateral roots to the arbuscular mycorrhizal (AM) fungus *Gigaspora margarita* Becker & Hall inoculated locally into the soil. Peanut (*Arachis hypogaea* L.) and pigeon pea (*Cajanus cajan* (L.) Millsp.) were examined. Root boxes filled with nutrient-poor soil in were inoculated in one half with the fungus and in the other half with a sterilized inoculum. Responses were apparent after 30 days but not after 20 days. Overall, lateral root development was more advanced in inoculated soil. This was clearly observed for 2nd- and 3rd-order lateral roots, but less clear for 1st-order lateral roots in both species, although percentage of colonized root length was higher in 1st-order lateral roots. Whilst in peanut the responses were clearly evident at the level of lateral roots initiated on more proximal parts of the tap root axis, they occurred on more distal parts in pigeon pea. We conclude that plants under nutrient-poor conditions give priority to mycorrhizal roots when partitioning assimilation products within the root system. Thus, AM formation may induce local morphological alteration of root systems.

Key words *Arachis hypogaea* L. · arbuscular mycorrhizas · *Cajanus cajan* (L.) Millsp. · *Gigaspora margarita* Becker & Hall · Split-root system

Introduction

The morphology of root systems is the primary determinant of functions such as soil exploration and exploitation, water and nutrient absorption, and anchorage. However, root system morphology is often altered by environmental factors, especially physical (Galamay et al. 1992; Iijima et al. 1991; Kono et al. 1987a; Pardales et al. 1991), chemical (Drew 1975; Pardales et al. 1992) and biotic (Cooper and Grandison 1987) soil conditions. It is thus important to examine the morphological responses of the root system when evaluating root function under a given soil environmental condition.

As pointed out by Atkinson et al. (1994), it had been assumed previously that arbuscular mycorrhiza (AM) formation did not influence root system morphology, but recent studies demonstrated effects of AM formation on a range of morphological parameters. For example, topological analysis by Fitter (1985) revealed that an AM root system had more lateral roots of higher branching order than a non-AM root system in *Trifolium pratense*. Using the same methodology, Schellenbaum et al. (1991) found a similar trend in *Vitis vinifera*, while Hetrick et al. (1988) showed that AM formation promoted root elongation growth rather than branching in *Andropogen gerardii*. Both Price et al. (1989) and Berta et al. (1995) reported that AM formation decreased the specific root length of host plants. Berta et al. (1990) suggested that alteration in root morphology following AM colonization was linked to a decrease in meristematic activity of root apices in *Allium porrum*, although they found no such anatomical changes in *Prunus cerasifera* (Berta et al. 1995). Thus evidence is accumulating that AM formation can alter root system morphology but that the patterns of alteration vary between host species.

Several mechanisms have been envisaged for the alteration of root systems following AM colonization (Berta et al. 1993). AM formation can increase nutrient absorption, especially of elements with low mobility in soil such as phosphorus (P), and some studies have reported changes in phytohormone balance in association with AM formation (Allen et al. 1980; Allen et al. 1982; Dannenberg et al. 1992; Drüge and Schönbeck 1992). Such changes in nutritional and hormonal status can influence root system morphology directly.

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Morphological analyses of AM root systems have been based on comparisons between AM and non-AM plants. However, the growth of AM and non-AM plants differs in most cases and alterations in root system morphology are confounded by effects due to plant size (Berta et al. 1995). Although some investigations compared inoculated and uninoculated plants of similar size (Hooker et al. 1992; Yano et al. 1996b), such plants may still differ physiologically because of nutritional and hormonal effects of AM.

This present investigation attempted to determine whether AM formation can affect root system morphology independently of effects on the size and physiological status of the shoot. We examined the direct effects of AM formation on root system morphology using a split-root system in which a portion of the roots was inoculated with *Gigaspora margarita* Becker & Hall. If AM formation directly affects root system morphology, such an inoculation of AM fungi should induce distinct localized root development. Responses of the two legumes peanut (*Arachis hypogaea* L.) and pigeon pea (*Cajanus cajan* (L.) Millsp.) were compared.

Materials and methods

A nutrient-poor soil (artificially aggregated subsoil of Andosol) in which only trace levels of Truog-P were detected was used without sterilization. Root boxes (20 cm long, 25 cm high, 2 cm wide) were divided vertically into two equal compartments by a plate. The soil in one compartment (+AM) was thoroughly mixed with 10 g of fungal inoculum (Cerakinkong, Central Glass Co. Ltd., Japan) containing approximately 1000 spores of *Gigaspora margarita* Becker & Hall, while the soil in the other compartment (–AM) was mixed with the same amount of steam-sterilized inoculum. After filling each compartment, the dividing plate was gently removed. A preliminary experiment confirmed that the steam-sterilized inoculum did not affect root development.

A pregerminated seed of peanut (CV. Chibahandachi) or pigeon pea (Snow Brand Seed. Co. Ltd., Japan) was planted on the interface between the two soil treatments in each root box. Plants were cultured in a glasshouse and watered by submerging the entire root box in a water bath for 30 min at 10-day intervals. Root systems were sampled at 20 and 30 days after planting by the pinboard method of Kono et al. (1987b); this allows sampling with minimum disturbance of the intact root system. Sampled root systems were preserved in folmalin 1:acetic acid 1:70% ethyl alcohol 18 by volume. Four replicate root boxes were prepared for each species and sampling time.

The tap root axis growing almost along the border between the two soil compartments (see Fig. 1) was divided into four sections in which branching lateral roots remained intact, at 0–5 cm, 5–10 cm, 10–15 cm and 15–20 cm from the tap root base. Lateral roots that developed on the +AM and –AM sides were collected separately by considering the tap root as a base line. Thus, eight groups of lateral roots were obtained for each root system. For each group of lateral roots, the number of roots was counted for each branching order. The lengths of individual 1st-order lateral roots were directly measured using a ruler, and the total length of all lateral roots within each group was measured by the image analysis method of Tanaka et al. (1995). The length of (2nd + 3rd)-order lateral roots was obtained by subtracting the 1st-order laterals from the total length of lateral roots.

Each root sample was cleared with 10% KOH and stained with trypan blue (Phillips and Hayman 1970) in lactoglycerol. Stained root samples were randomly collected from each group and percentage of colonized root length estimated by the grid line intersection method (Giovanetti and Mosse 1980). Data were statistically analyzed by the paired-sample *t*–test between lateral roots in the inoculated and uninoculated soil zones.

Results

In 20-day-old root systems no differences in lateral root development were apparent between +AM and –AM soil zones for either plant species (Fig. 1a,b). By 30 days, however, differences were observed between the two soil zones for both species, the contrast being greater for peanut than for pigeon pea (Fig. 1c,d).

In 20-day-old root systems, no significant differences were detected ($P = 0.05$) in root number or total root length for either legume. However, the percentage colonized root length was significantly higher in +AM than in –AM for each branching order of lateral roots as well as for total lateral roots in peanut. Likewise, colonization of pigeon pea lateral roots was higher in the +AM soil zone, but not significant yet (Table 1).

Lateral root number and length in 30-day-old root systems of both legumes were generally higher in the +AM than in the –AM zone, although responses and/or significance level differed among lateral roots of different branching orders. In peanut, the number of 2nd-order lateral roots was significantly higher in +AM than in –AM, although the number of 1st-order lateral roots was almost the same. The number of 3rd-order lateral roots appeared to be higher in +AM than in –AM soil zone but the difference was not significant. The lengths of lateral roots of any branching order in 30-day-old root systems of peanut were all significantly higher in +AM than in –AM soil zones. The difference in root length between the two soil zones was higher for the (2nd + 3rd)-order than for 1st-order lateral roots.

In pigeon pea, the number of lateral roots was significantly higher in +AM than in –AM soil zones for both 2nd- and 3rd-order lateral roots of 30-day-old root systems. However, as in peanut, the number of 1st-order lateral root was almost the same between the two soil zones, but the total number of lateral roots of different branching orders was relatively higher in +AM than in –AM. The mean values of lateral root length in +AM always appeared to exceed those in –AM soil zones, but the differences were not significant.

The branching density of 1st-order lateral roots, calculated as the number of 2nd-order lateral roots per unit axial length of 1st-order roots, appeared to be higher in +AM than in –AM soil zones but the differences were not significant in either legume. In 30-day-old root systems, the percentage colonized root length was significantly higher in +AM (approximately 20–30%) than in –AM soil zones (less than 10%) for each order of lateral roots in both plant species. Since differences in lateral root development between +AM and –AM soil zones were particularly evident in 30-day-old

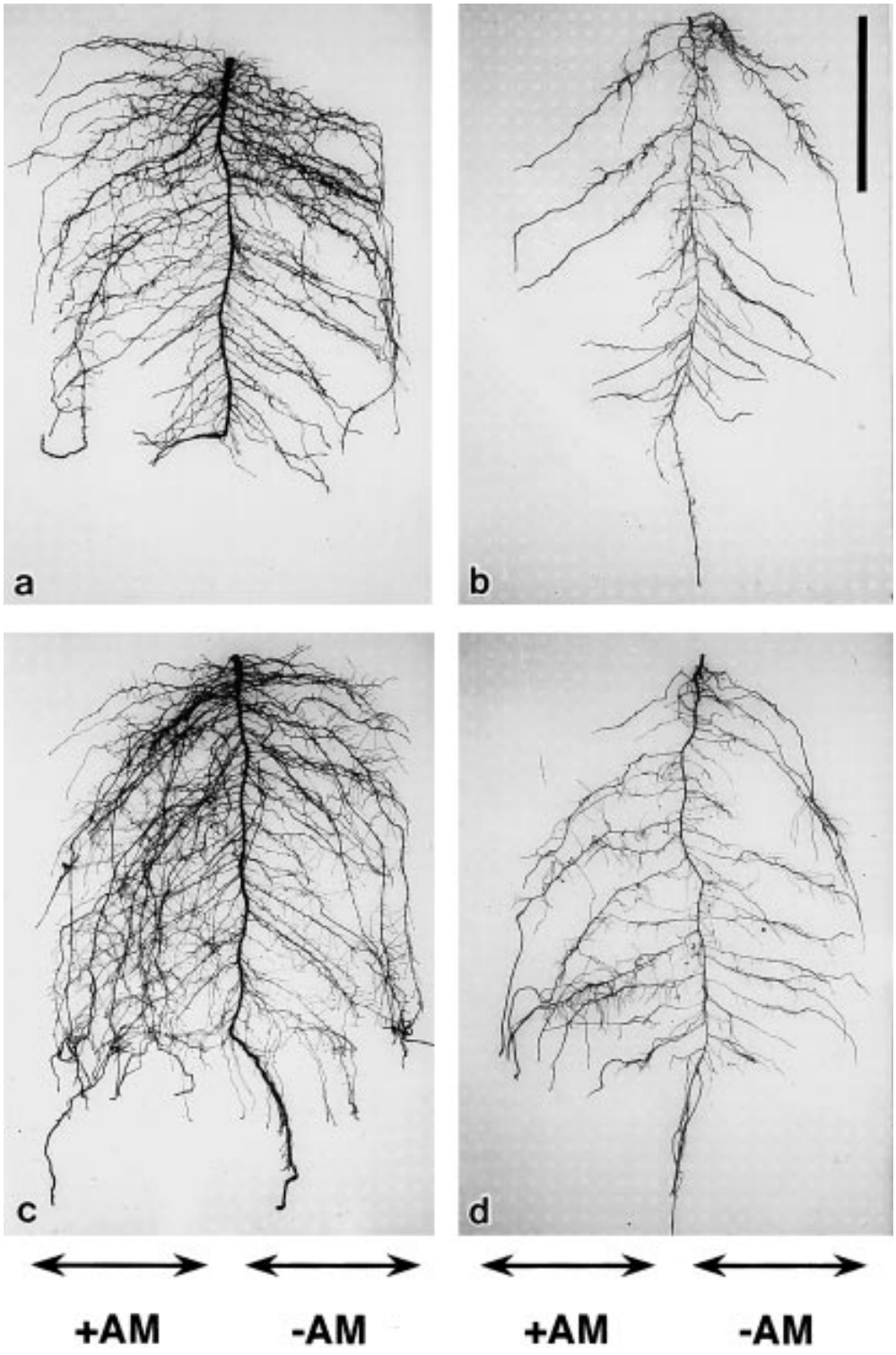

Fig. 1a–d Appearance of root systems in root boxes in which the left half was inoculated with non-sterilized inoculum of*Gigaspora margarita* (*+AM*) and the right half with a sterilized inoculum (*–AM*) **a, b** 20-day-old peanut and pigeon pea; **c, d** 30-day-old peanut and pigeon pea, respectively; bar 10 cm

root systems of both legumes, more detailed analyses were made on these root systems.

Lateral root number was greatest in peanut in the most proximal section of the tap root axis, and decreased acropetally (Fig. 2). However, the pattern of decrease was different between +AM and –AM soil zones, especially in sections 3 and 4 of the tap root. Significant differences between the two zones were only detected for 2nd-order lateral roots in section 1 of the tap root axis. In contrast, in pigeon pea, lateral root number tended to increase acropetally from the most proximal section towards section 4, especially in the +AM soil zone, and a significant difference between the soil zones was found in section 4 for the total number of all lateral roots.

The distribution patterns of lateral root length along

Table 1 Number, length, branching density and percentage of colonized root length of lateral roots (LR) of 20- and 30-day-old peanut and pigeon pea inoculated with non-sterilized (+AM) and sterilized (−AM) inocula of *Gigaspora margarita*

Plant		Soil zones	Root number per soil zone				Root length in soil zone (m)			Branching density of 1st LR[a]	Colonized root length (%)		
			1st LR	2nd LR	3rd LR	All LR	1st LR	2nd + 3 rd LR	All LR		1st LR	2nd + 3rd LR	All LR
20 days	Peanut	+AM	68	408	0	477	3.93	2.21	6.14	101	28.0	21.3	26.0
		−AM	64	362	0	426	3.74	1.62	5.36	04	7.0	8.3	7.5
		P	0.220	0.472		0.445	0.602	0.123	0.237	0.262	0.008*		
	Pigeon pea	+AM	52	127	0	179	1.81	0.53	2.34	65	11.2	3.2	9.5
		−AM	52	132	0	184	1.91	0.56	2.48	69	1.0	0.4	0.9
		P	0.667	0.935		0.939	0.755	0.932	0.854	0.879	0.057	0.139	
30 days	Peanut	+AM	74	1285	262	1621	5.86	11.86	17.72	219	26.3	19.2	21.5
		−AM	72	923	91	1085	4.92	6.46	11.38	190	7.1	3.7	5.3
		P	0.668		0.166	0.054				0.164			
	Pigeon pea	+AM	57	307	20	384	2.51	2.73	5.25	116	27.5	21.5	25.2
		−AM	53	244	2	298	2.25	1.59	3.84	104	2.0	1.2	1.6
		P	0.525			0.141	0.304	0.055	0.070	0.228	0.006*		0.003*

* Significant differences at $P = 0.05$ and 0.01, respectively, between +AM and −AM
[a] The number of 2nd LR per metre of 1st LR

the tap roots of both legumes (Fig. 3) were similar to those for root number. In peanut, the lengths of (2nd + 3rd)-order lateral roots and the total length of all lateral roots were significantly higher in +AM than in –AM zones in sections 1 and 2 of the tap root axis, while the length of 1st-order lateral roots was not different. In pigeon pea, on the other hand, promoted root elongation in +AM compared with –AM zones was only found for the total length of (2nd + 3rd)-order and all lateral roots in section 4.

In both plants, the percentage colonized root length was always higher in +AM than in –AM soil zones, and greater for 1st-order than for (2nd + 3rd)-order lateral roots at any section of the tap root axis (Fig. 4). In peanut, AM colonization of 1st-order lateral roots was highest at section 3, while that for (2nd + 3rd)-order lateral roots did not show such a peak. On the other hand, in pigeon pea, the colonization of 1st-order lateral roots did not show any strong peak, while that of (2nd + 3rd)-order lateral roots peaked at section 2.

Discussion

Several studies have shown that AM colonization can influence root system morphology of host plants (Berta et al. 1990, 1995; Fitter 1985; Hetrick et al. 1988; Hooker et al. 1992; Price et al. 1989; Schellenbaum et al. 1991; Yano et al. 1996b). All these studies, however, examined the effect of AM by comparing separate plants inoculated or uninoculated with AM fungi, and did not distinguish between direct effects of AM formation and combined effects due to changes in plant size or physiology.

To overcome this problem, we compared roots within a vertically-split single root system, half of which was inoculated with an AM fungus and half uninoculated. Marked increases in lateral root development were found in 30-day-old peanut and pigeon pea in response to localized AM formation by *Gigaspora margarita*, independent of changes in shoot size or physiological status. However, it should be noted that minor colonization of roots in the –AM soil zone was observed. Such colonization may have been due to passage of fungal hyphae from the +AM to the –AM soil zones and/or to the indigenous soil fungi of the unsterilized soil used. Moreover, we cannot exclude growth depression of lateral roots in the –AM soil zone as a response to promotion of those in +AM soil zone.

The absence of changes in root system morphology in 20-day-old root systems of both species, despite increases in percentage colonized root length parallel observations that AM fungal colonization preceded morphological alteration of roots in *Allium porrum* (Berta et al. 1990), *Vitis vinifera* (Schellenbaum et al. 1992) and *Prunus cerasifera* (Berta et al. 1995). In these studies, significant enhancement of shoot growth in AM plants accompanied changes in root system morpholo-

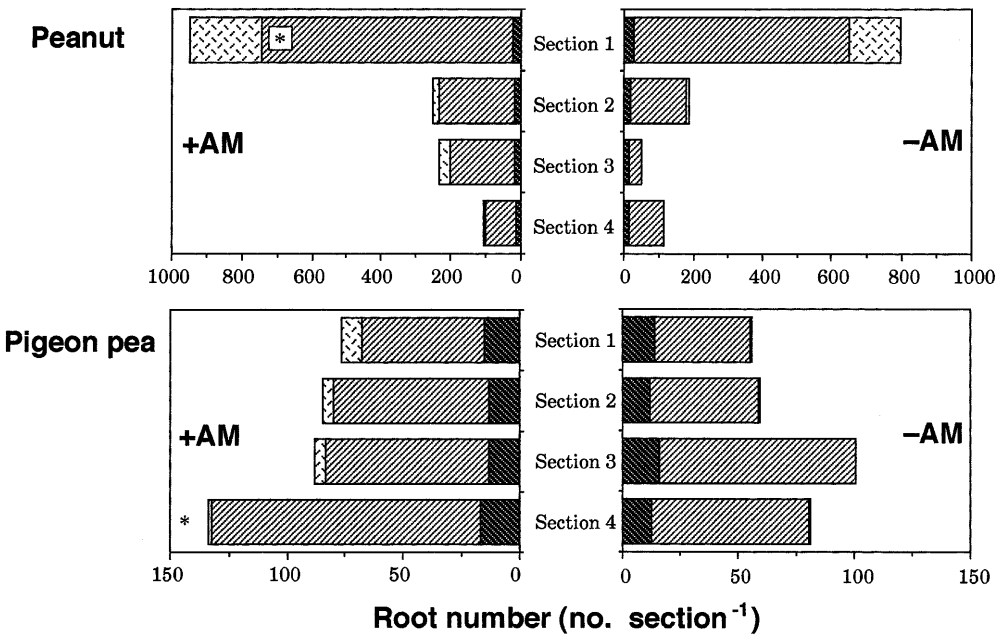

Fig. 2 Distribution of lateral roots along the tap root in terms of the number in 30-day-old peanut and pigeon pea. *+AM* and *–AM* represent lateral roots in soil zones inoculates with non-sterilized and sterilized inocula of *G. margarita*, respectively. Lateral roots were classified into different branching orders (▩) 1st, (▨) 2nd, (⊡) 3rd, and initiating sections along each tap root axis: section 1 = 0–5 cm, section 2 = 5–10 cm, section 3 = 10–15 cm, section 4 = 15–20 cm from the tap root base. * indicates a significant difference at $P = 0.05$ between +AM and –AM within each section

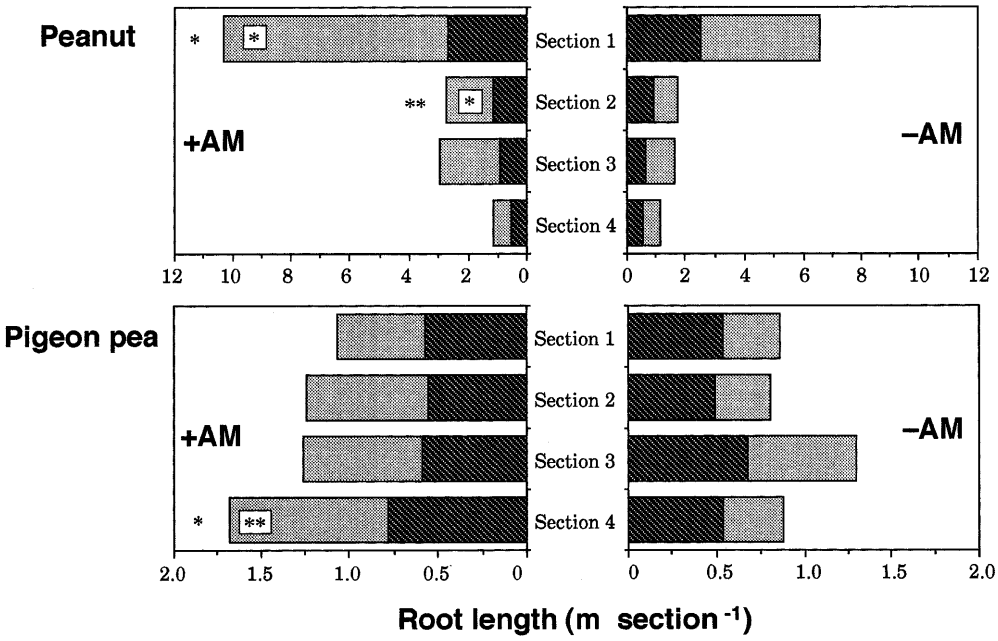

Fig. 3 Distribution of lateral roots along the tap root in terms of length in 30-day-old peanut and pigeonpea. *+AM* and *–AM* represent lateral roots in soil zones inoculated with non-sterilized and sterilized inocula of *G. margarita*, respectively. Lateral roots were classified into different branching orders (▩) 1st, (▧) (2nd + 3rd), and initiating sections along each tap root axis as in Fig. 2 * and ** indicate significant differences at $P = 0.05$ and 0.01, respectively, between +AM and –AM within each section

gy, whereas our results suggest that an altered root system morphology succeeding AM colonization can occur without such shoot changes.

Whilst the major responses were seen in 2nd- and 3rd-order lateral roots the percentage of colonized root length was highest in 1st-order lateral roots. This may be explained by the fact that lateral roots originate in the pericycle of the mother root (Esau 1977), and their initiation may be strongly influenced by the previous environment of the mother root. The similar number of 1st-order lateral roots in the two soil zones in both legumes is also probably due to elongation of the tap (mother) root along the border of the two soil zones and consequent exposure to the inoculum.

AM colonization is greatly affected by root aging. Hepper (1985) and Amijee et al. (1993) showed that apical root parts were more susceptible to colonization than more basal root parts. Moreover, we have reported elsewhere that the pattern of AM colonization along a root axis is affected by individual root aging with an inherent progress in time (Yano et al. 1996a). Thus the age of individual roots must be considered when evaluating morphological responses of root systems to AM colonization. In the present study, each tap root axis was divided into four sections and AM and non-AM lateral roots initiating from each section were compared to minimize effects of the age range of the roots. In terms of number and length of laterals, in

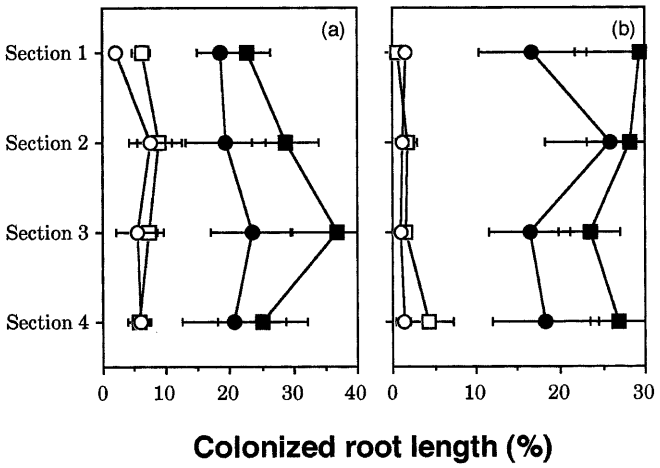

Fig. 4 Distribution of the percentage of colonized root length on lateral roots along the tap root in 30-day-old peanut (**a**) and pigeon pea (**b**). (■) and (●) indicate 1st- and (2nd + 3rd)-order lateral roots grown in soil zones inoculated with non-sterilized inocula of *G. margarita* (□) and (○) indicate 1st- and (2nd + 3rd)-order lateral roots grown in soil zones inoculated with sterilized inocula. Lateral roots were further classified into initiating sections along each tap root axis as in Fig. 2

peanut the response to AM was pronounced in relatively old roots initiating from the more proximal part of the tap root axis, while in pigeon pea the maximum response occured in younger lateral roots initiated from the more distal part of the tap root axis. However, there was no clear relationship between the percentage of colonized root length and the lateral root responses in terms of number or length along the tap root.

Baylis (1975) hypothesized that root hair length and root diameter determines dependency of plants on mycorrhizas for acquisition of mineral nutrients, i.e. fine roots and longer root hairs produce less mycorrhizal dependency than a coarser root system with shorter root hairs. Some reports partially support this hypothesis (Manjunath and Habte 1991; St. John 1980). In the present study, the peanut root system was apparently coarser than that of pigeon pea. Furthermore, root hairs develop in two ways in peanut, either in a rosette radially from the point of lateral root emergence on the mother root or along the root axis usually behind the root tip (Meisner and Karnok 1991). We observed that root hair emergence was almost restricted to the former type, leading us to suspect that mycorrhizal dependency may be greater in peanut than in pigeon pea. Although we could not evaluate mycorrhizal dependency of each species in terms of dry matter increase since we employed a split-root method, our results show clear interspecific difference in responsiveness to the AM colonization, i.e. peanut developed lateral roots more vigorously in +AM soil than pigeon pea.

The differences in morphological response of the root systems were undoubtedly due to different partitioning of photosynthate and the derivative assimilates between AM and non-AM roots within the root system. However, the direct mechanisms inducing the different partitioning in the root systems are not clear. One possible mechanism is an increase in nutrient absorption by AM roots. AM formation frequently enhances P absorption, which could result in changes of root system morphology; however, the soil used in this study contained almost no available P. Another possible mechanism is that changes in hormonal balance due to AM formation caused a different sink activity for translocates from the shoot between the two halves of the root system. Whatever the case, our experimental system will be useful to investigate the physiological background for the morphological responses of root systems to AM formation.

The soil volume exploited by an AM root system is determined not only by the external hyphae of AM fungi but also by the roots themselves. In spite of this, most studies have attributed mycorrhizal benefits in nutrient uptake solely to the increase in soil volume exploited by the development of external hyphae. This might be true if AM formation caused no alteration or even a reduction in root system size. However, the present results clearly show that the number and length of lateral roots were promoted in both legumes by AM colonization under nutrient-poor soil conditions. This increased root volume is also important for the obligate AM fungi since it enables increased soil colonization. Therefore, the development of a root system, as an organ for nutrient uptake and for microorganism proliferation, strongly determines AM functioning as a whole. In this respect, Kothari et al. (1990) emphasized that more attention should be paid to root morphology in order to understand the effects of mycorrhizal fungi on mineral nutrient uptake and water relations in plants. We propose that quantitative, structural and functional aspects of root systems forming mycorrhizas also need to be analysed in addition to the fungal component in order to fully comprehend the mechanism of the symbiotic benefits.

Acknowledgement We are grateful to the Chiba Prefectural Agricultural Experiment Station in Japan for supplying peanut seeds.

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