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Distribution of ^{32}P between Roots and Tops of White Clover: Effect of Mycorrhizal Fungi and Placement Distance from the Roots

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ABSTRACT

In a greenhouse experiment, the effects of *Glomus intraradices* and indigenous mycorrhizal isolates from soils under plow and no-till treatments on the uptake of ^{32}P placed at 1, 2.5 and 4 cm from the roots of white clover (*Trifolium repens*) in 23, 37 or 46 days after planting were compared.Spores of the indigenous fungi were mostly a mixture of *Glomus mossea, G. clarum, G. caledonium* and *G. claroideum* . The colonization of the roots with regard to hyphae, vesicle or arbuscules was significantly different among fungi. Uptake of ^{32}P from different distances from the roots was strongly dependent on the mycorrhizal isolate used and the plant-symbiont age. Indigenous fungi were more effective in translocating ^{32}P from short distances compared with *G. intraradices* as measured in the plants. At the age of 46 days, for example, fungi from no-till and plowed plots transported 8-10 times more ^{32}P to the plants as compared with *G. intraradices*, when^{32}P was placed at 1-cm distance from the roots. These differences, however, disappeared when ^{32}P was placed at 2.5 or 4 cm from the roots. As the plant-symbiont grew older, relatively more ^{32}P was translocated to the tops and the differences between fungi in this respect became more pronounced. In 21-, 37- and 46-day-old plants, for example, and when ^{32}P was placed 1 cm from the root surface, 18, 21 and 56%, respectively, of the absorbed ^{32}P was translocated to the tops in plants inoculated with fungi from plowed fields. Progressively lesser amounts of total absorbed ^{32}P were translocated to the tops as ^{32}P was placed farther away from the roots. For example in 46 days after planting 51, 30 and 11% of total absorbed ^{32}P was translocated to the tops when ^{32}P was placed at 1, 2.5 and 4 cm from the roots, respectively, white clovers being inoculated with fungi from no-till soil. It is concluded that the native mycorrhizal fungi , after a long period of different tillage practices, may have different effects on the partitioning of absorbed phosphorus within white clover.

Keywords: *Glomus* spp, ^{32}P transport , VAM, *Trifolium repens* (white clover).

INTRODUCTION

Studies on the uptake of mineral nutrients by mycorrhizal plants have been mostly concentrated on the effect of fungi on the flow of nutrients to the roots, kinetics of uptake and nutrient metabolism within the fungal hyphae. Soil tillage affects mycorrhizal activity,thus the nutrient uptake by plants (McGonigle *et al*., 1990a; Hamel *et al.,* 1996; McGonigle and Miller 1996, Kabir *et al*., 1997). As an example, no-till cultivation of maize increased the concentration of P in the leaves by 12% during early stages of plant growth (Miller *et al*., 1995). It has been proposed that reduced soil tillage maintains the integrity of the hyphal network in soil and thereby increases the colonization of subsequent crop roots and thus increases the nutrient uptake by the plants (Stirbley, 1987; Fairchild and Miller, 1990; McGonigle *et al*., 1990a; Jasper *et al*., 1992; Miller

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and McGonigle, 1992). Another possibility is that soil tillage intensity might alter the diversity of the indigenous mycorrhizal population (Schenck *et al.,* 1982) which might in turn alter their P-uptake capabilities and P metabolism within the host plants.

The activity of AM fungi is strongly affected by soil factors such as pH, temperature, P content, and organic matter (Smith and Read, 1997). Reduced soil tillage ,decreases soil temperature (Fortin, 1993),alters organic matter (Schoenau and Campbell, 1996) and soil pH (Wells, 1984). Phosphorus applied to untilled soils tends to accumulate in the upper soil layers (Franzluebbers and Hons, 1996), a condition which could also affect the activity of mycorrhizal fungi. For example, high soil P may decrease (Nelsen *et al.*, 1981; Graham *et al.*, 1982; Hicks and Loynachan, 1987; Braunberger *et al.*, 1991) or increase (Bolan *et al.,*1984) root colonization by mycorrhizal fungi or decrease hyphal growth in soil (Demiranda and Harris, 1994) or hyphal branching in *vitro* (Nagahashi *et al*., 1996).

Little is known about the possible role of mycorrhizae in the partitioning of the absorbed mineral nutrients to the plant tops (Smith and Read,1997). There are indications, however, that mycorrhizal symbiosis may affect the shoot/root partitioning of Cs (Horrill and Clint, 1994), Sr (Entry *et al.,* 1994), and Cu and Zn (Weissenhorn *et al.*, 1995) in the plants. This study investigated the effect of different soil tillage practices on the capability of indigenous mycorrhizal fungi for the uptake and partitioning of P in white clover. *Glomus intraradices* was used for comparison.

MATERIALS AND METHODS

Soil samples were taken from long-term experimental plots that had been under different tillage intensities since 1987 in location Langwiese at the Tänikon Experiment Station (46°30´ N; 8°50´E) in Canton Thurgau in Switzerland. The experimental design in these sites was a split-plot with four replications. The crop rotation is winter wheat (*Triticum aestivum*), maize (*Zea mays*), winter wheat and canola (*Brassica napus* L.). The amount of fertilizer applied to different treatments was the same with the obvious difference that in the no-till method the fertilizers are left on the soil surface and not mixed into the soil. Some chemical and physical properties of the soils are shown in Tables 1 and 2.

Table 1. Some properties of a dystric gleysol soil which has been under different tillage intensity experiments.

Sand (%)	23.5
Loam (%)	35.2
Clay (%)	35.7
Humus (%)[a]	1.5 - 6.6
Organic C (%)[a]	0.9 - 2.6
pH (water)[a]	6.0 - 7.7
Olsen-P (mg/kg)[a]	35.2 - 69.2

[a]Values are the range observed in different plots in 1994 in soil samples taken from 0-25 cm depths.

Table 2. Distribution of P (mg/kg soil[a]) in different depths in soil under different tillage treatments since 1987.

Depth (cm)	No-till	Plowed
0-5	1.80	0.98
5-10	0.97	1.05
10-15	0.92	0.95
15-20	0.79	0.92
20-30	0.21	0.56
30-40	0.11	0.15

[a]Measured through CO_2 -saturated water extract method.

Soil samples were taken from the top 20 cm in May 1996, sieved through a 5-mm sieve, and mixed with an equal portion of 2-mm quartz sand. Bahiagrass (*Paspalum notatum*) was grown on these soils in a growth chamber (30°/25°C day/night;18h photoperiod at light intensity of 450 µE. m^{-2}. s^{-1}). After two months, roots from the pots show ing colonization by indigenous mycorrhizae were used as inocula for phosphorus uptake studies. These inocula were taken as representing the mixture of indigenous soil fungi

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under different soil tillage intensities. Observations of spores from these pot cultures have shown that the majority of them belong to a mixture of *Glomus mossea, G. clarum,G. claroideum* and *G.caledonium* . *Glomus intraradices* was obtained from the Federal Research Station at Wädenswil (Switzerland).

Culture vessels similar to those described by Rhodes and Gerdemann (1975) were constructed (Fig. 1). Briefly, these consisted of 9-cm-diameter Petri dishes (with 2-cm height) from which a 15x20-mm window (hyphae window) was cut on one side and closed with a 20-µm nylon net (to provide an opening for the plants to grow out of). Each Petri dish was placed inside a rectangular box (12x8x3 cm) so that the hyphae window was located at a distance of 20mm from the box's edge-wall. The space outside the Petri dish was the root compartment and that inside the Petri dish constituted the hyphae compartment (Fig. 1). Soils from plowed and no-till plots were first mixed in 1:1 ratio with quartz sand sterilized with γ-rays and placed in the root and hyphae compartments of each culture vessel. Inocula consisted of root segments (ca. 3g fresh weight) of Bahiagrass colonized by indigenous mycorrhizal fungi from plowed or no-till soils or by *G. intraradices* obtained from Wädenswill Experiment Station in Switzerland. Inocula were placed in the root compartment in front of the hyphae window, covered with a 1-cm layer of sterilized quartz sand and ten surface-sterilized and pregerminated seeds of white clover (*Trifolium repens* var. Milkanova) were planted. Control treatments did not receive any mycorrhizae. All treatments were replicated 3 times. In order to provide comparable microbial populations in all treatments, all vessels received one mL of a soil-peptone suspension as described by McGonigle and Miller (1996). Briefly, 20 g of a 1:1 mixture of non-sterilized soil from no-till and plowed fields were shaken with 100 mL of a 0.1% sterile Difco Bacto-Peptone for 3h, filtered through a 20µm sieve and used.

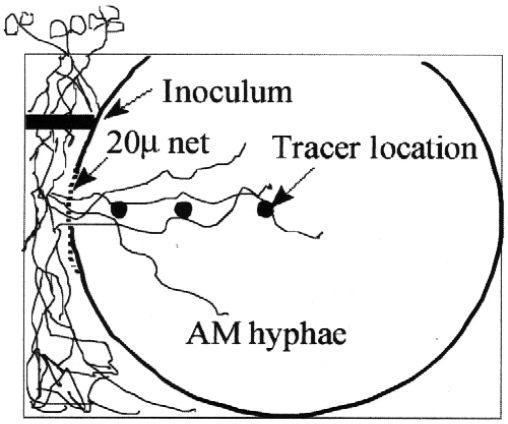

Figure 1. Diagram of experimental set-up.

Plants were grown in a growth chamber of 20°/15°C day /night temperature, 16h photoperiod and light intensity of 320 µE. m^{-2}. s^{-1}. Uptake of P from different distances by fungal hyphae was tested by injecting 74 kBq of ^{32}P (as orthophosphate in 100 µL of water) into the hyphae compartments (2 cm below the soil surface) at 1-, 2.5- and 4-cm distances from the hyphae window 23, 37 and 46 days after planting. After 72 h, culture vessels were opened, and the tops and roots harvested. All the tops and part of the roots were dried at 85°C for 48 h. Plant materials were ashed at 450°C for 6 h, dissolved in 1 mL of 1N HCl, mixed with scintillation cocktail and the activity measured with a Packard scintillation counter. Root colonization with mycorrhiza was measured with a subsample of roots and the staining method of Phillips and Hayman (1970) and the magnified intersections method of McGonigle *et al.* (1990b).

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Table 3. Results of ANOVA ($P > F$) for the effects of fungi and time after planting on the % colonization of white clover roots.

Source	Hyphae	Arbuscules	Vesicles
Fungi	0.0001	0.0001	0.0001
Time	0.004	0.12	0.04
Fungi x Time	0.001	0.01	0.0007

RESULTS

Root Colonization

Non-mycorrhizal control treatments were all free of mycorrhizal structures in their roots. Different mycorrhizae colonized white clover roots to different degrees. There existed significant time and fungi interactions (Table 3). On the first sampling date (23 days after planting), roots inoculated with fungi from no-till plots showed less hyphae than those inoculated with fungi from plowed fields or with *G. intraradices* (Fig. 2). At later dates, however, this difference disappeared. Arbuscule production was highest in roots inoculated with *G. intraradices* at the last sampling date of 46 days.

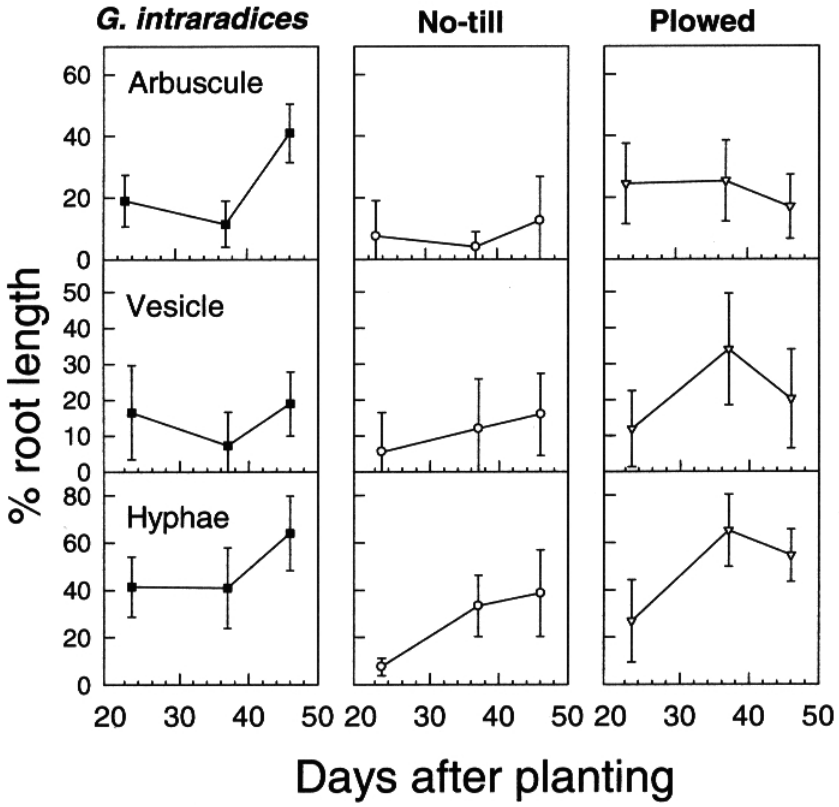

Figure 2. Progress of root colonization by fungi from no-till, plow-fields or *G. intraradices* at different times after planting. Roots of non-mycorrhizal control plants were free of mycorrhizal structures.

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Table 4. Results of ANOVA for the effects of different mycorrhizae (fungi), distance from the roots where ^{32}P was placed and the time after planting on the total amounts of ^{32}P in the roots or leaves of white clover.

Source	F- ratios for leaf-^{32}P	F-ratios for root-^{32}P
Fungi	61.1 **	31.1 **
Distance	289.9 **	110.5 **
Time	570.7 **	253.4 **
Fungi x distance	71.4 **	7.2 **
Fungi x time	59.0 **	54.0 **
Distance x time	188.4 **	3.0 *
Fungi x distance x time	67.2 **	11.1 **

* and ** indicate significance of F at 0.05 and 0.01 levels, respectively.

Total Phosphorus Uptake

Fungi, distance from root surface where ^{32}P was placed, time after planting and the interactions between these factors were all significant for the transport of ^{32}P to plant leaves and roots (Table 4). Non-mycorrhizal control plants contained very low amounts of ^{32}P (<300cpm) which indicated negligible mass flow of ^{32}P to the roots. For clarity of figures and discussions, the data from control plants are not included in the figures and discussions.

In general, less ^{32}P was transported to the plants the farther away from the root the ^{32}P was placed. Fungi differed in their capacity for ^{32}P transport based on distance to white clover roots. Differences between fungi became more pronounced as the absorption of ^{32}P was measured in the older plants, i.e,

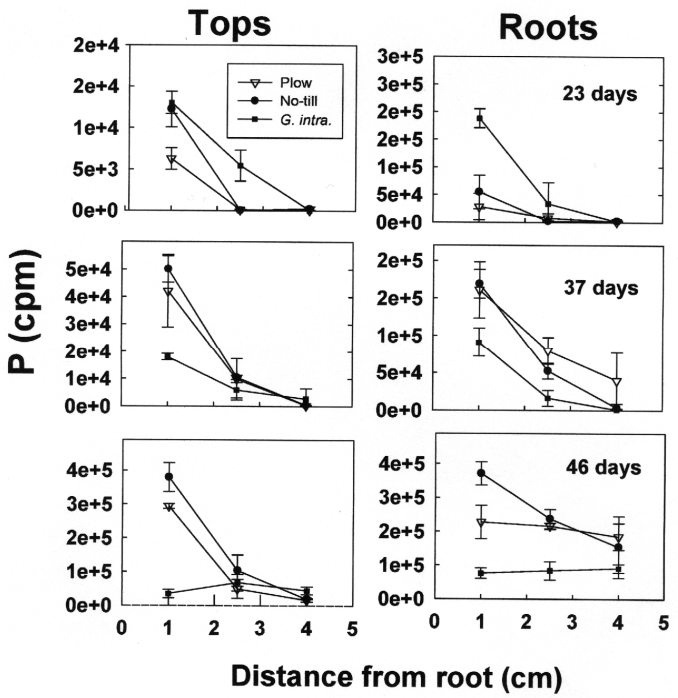

Figure 3. Total counts of ^{32}P in the tops (leaves and stems) and in the roots of white clover plants inoculated with fungi from no-till, plow-fields or *G. intraradices* and exposed to ^{32}P placed at different distances from their roots in 23, 37 and 46 days after planting.

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plants which were longer in contact with mycorrhizal fungi (Fig. 3).For example, 23 days after planting, and when ^{32}P was placed at 1cm distance, tops of plants inoculated with fungi from plowed fields contained significantly less ^{32}P than those inoculated with fungi from no-till plots or with *G. intraradices.* The amount of ^{32}P in the roots, however, was considerably more in the plants inoculated with *G. intraradices* than those inoculated with plowed and no-till fungi (Fig. 3). As plants got older and their roots more colonized by mycorrhizal hyphae, a different picture emerged.For example, 46 days after planting, and when ^{32}P was placed at 1 cm from root surface, tops of plants inoculated with plowed and no-till fungi contained 8-10 times more ^{32}P as compared with those inoculated with *G. intraradices* (Fig. 3).

Partitioning of ^{32}P between Tops and Roots

Based on the amount of ^{32}P in the tops (Fig. 3) and in the roots (data not shown), we calculated the relative partitioning of total ^{32}P to the tops. Fungi affected the partitioning of ^{32}P to the tops which became more pronounced as ^{32}P was placed at farther distances from the roots and as the

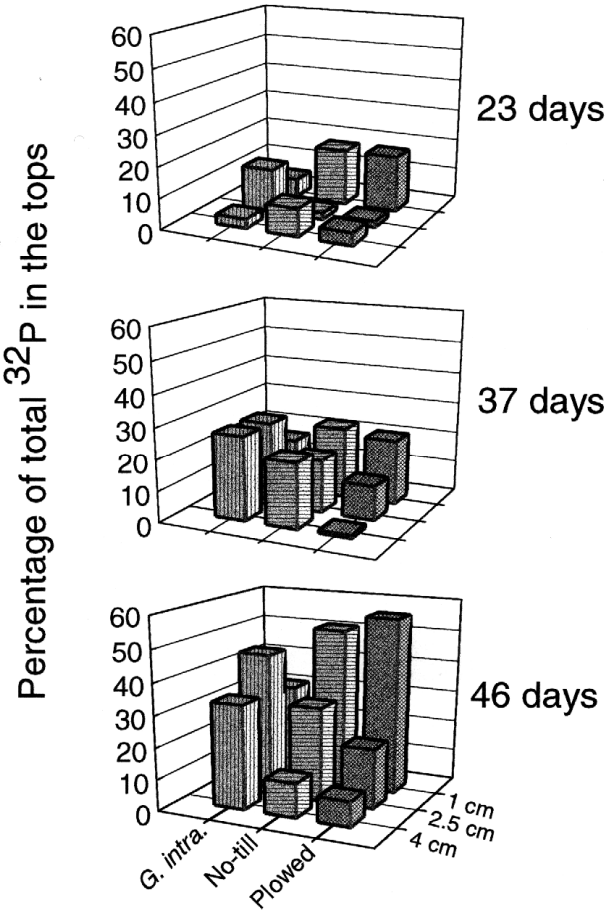

Figure 4. Percentage of total ^{32}P absorbed by white clover roots and transported to the tops as affected by the mycorrhizal fungi used and the distance from the root surface where ^{32}P was placed inside the hyphae compartment.

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plant-symbiont got older (Fig. 4). For example, when ^{32}P was placed at 1 cm from the roots of 23-, 37- or 46-day-old plants, those inoculated with fungi from plowed fields transported 18, 21 and 56% of their total absorbed ^{32}P to the tops, respectively. The corresponding values for plants inoculated with *G. intraradices* were 6, 17 and 31%, respectively. Progressively less ^{32}P was transported to the tops as ^{32}P was placed farther away from the roots. For example at 46 days after planting, placing the ^{32}P at 1, 2.5 and 4 cm from the roots resulted in 51, 30 and 11% of total absorbed ^{32}P to be transported to the tops. At 46 days, and when ^{32}P was placed at a 4-cm distance from the roots, less ^{32}P was transported to the tops in plants inoculated with fungi from no-till and plowed fields as compared with *G. intraradices*. The reverse was true if ^{32}P was placed at 1-cm distance from the roots. In other words, indigenous fungi from these P-rich Swiss soils were more effective in causing higher transport of ^{32}P to plant tops when the P-source was in close vicinity of the roots, while *G. intraradices* was more effective in allocating ^{32}P to the tops from locations farther away from the roots. Tillage intensity did not seem to have any consistent effect on the ^{32}P transport by indigenous fungi.

DISCUSSION

Mycorrhizal fungi may increase the partitioning of ^{137}Cs (Horrill and Clint, 1994), ^{90}Sr (Entry *et al*., 1994) and Cu and Zn (Weissenhorn *et al*., 1995), between plant tops and roots. In some cases this effect was so strong that in the non-mycorrhizal plants all of the ^{137}Cs remained in the roots and none was transported to the plant tops (Horrill and Clint, 1994). We are not certain as to the mechanisms involved in the partitioning of P observed in this study and thus the following are just our speculations. Differences observed between fungi isolates in the partitioning of ^{32}P might be due to differences in the amount of absorbed radioisotope which was retained in the hyphal structures (hyphae, vesicles, arbuscules or spores) within the roots and that delivered to the host at different times. Jakobsen and co-workers showed that *Scutellospora calospora* transported less ^{32}P to plants but accumulated more ^{32}P in its hyphae and thus had a much higher specific radioactivity in its hyphae as compared with *Acaulospora laevis* or *Glomus* sp.

The external hyphae network of mycorrhizal fungi is reported to reach its upper order of branching and development in 5-7 days which may also coincide with the formation of phosphorus depletion zones (Friese and Allen, 1991). The hyphae network, however, undergoes a constant process of formation and dieback. This may account for the differences observed between fungi in the absorption from different distances but could not explain the differences observed in the P-distribution between roots and tops.

Arbuscles as the main site for fungus /plant metabolite exchange,complete their development in 4-5 days and then rapidly collapse (Brundrett *et al*.,1985).The ratio of active arbuscles to the amount of hyphae and vesicles at the time ^{32}P injection should ultimately affect the amount of ^{32}P translocated to the tops and the amount stored in the vesicles or hyphae.

VAM infection also increases the amount of vascular tissue,lignification of the xylem and the number of vascular bundles (Daft and Okusanya,1973).Under low P conditions , mycorrhizal plants have higher hydraulic conductivity,water potential,transpiration rate and lower stomatal resistance than non-mycorrhizal plants (Allen,1982;Nelson and Safir ,1982).Thus,plants with higher P nutrition would be able to translocate ^{32}P to the tops more easily.

Although mycorrhizal fungi are known to be able to absorb organic-P, the prevalent view is that they absorb the same labile-P as that absorbed by the roots. The identity of the organic or inorganic solutes transported by mycorrhizal fungi, however, is not known with any certainty (Smith & Read, 1997, p. 389). Absorbed P is thought to be

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transformed into polyphosphates within the mycelia and stored in the vacuoles and could constitute a considerable reserve of phosphorus in mycelium and in mycorrhizal roots (Smith and Read, 1997, p. 388). Considering the report that polyphosphate accumulation in mycelia could vary at different growth stages, being low in the young mycelia and linear in the stationary phase (Smith & Read, 1997, p. 390), one may speculate that the effects observed in this study might have been due to the differences in fungi with respect to the rates of polyphosphate formation and/or in the rates of their delivery to the host roots. This is in line with the observation that mycorrhizal species differ in their effect on the root-shoot transport of radio-caesium which was attributed to the caesium-binding capacity or ionic regulation between different fungi (Horrill and Clint, 1994).

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توزیع ^{32}P بین ریشه و اندامهای هوایی شبدر سفید: اثر قارچهای میکوریز و فاصله قرارگیری از ریشه

چکیده

در این آزمایش گلخانه ای اثرهای *Glomus intraradices* و ایزوله های قارچهای بومی دو خاک شخم خورده و شخم نخورده در جذب^{32}P از فاصله های ۱، ۲/۵ و ٤ سانتیمتری از ریشه های شبدر سفید *(Trifolium repens)* ۲۳، ۳۷ و ٤٦ روز بعد از کاشت مقایسه شده است. اسپورهای قارچهای بومی عمدتاً مخلوطی بود از قارچهای *Glomus mosseae* ، *G. clarum* ، *G.caledonecum* و *G. Claroideum*. شدت کلونیزاسیون ریشه ها از نظر مقادیر هیف، وزیگل و آربوسکول اختلاف معنی داری نشان داد. جذب ^{32}P از فواصل مختلف به نوع قارچ و سن گیاه بستگی زیادی داشت. قارچهای بومی از نظر انتقال ^{32}P در فاصله کوتاه موثرتر از *G. intraradices* بودند. مثلاً هنگامی که^{32}P در فاصله یک سانتیمتری از ریشه قرار داده شده بود، انتقال آن توسط قارچهای بومی ۱۰-۸ برابر بیشتر از آن توسط *G. intraradices* بود. این تفاوتها هنگامی که ^{32}P در فاصله های ۲/۵ و ٤ سانتیمتر قرارداده شد، مشاهده نگردید. با افزایش سن گیاه و قارچ همزیست به طور نسبی مقادیر^{32}P بیشتری به اندامهای هوایی گیاه انتقال داده شد و اختلاف بین قارچها از این بابت بیشتر شد. در گیاهان ۲۱، ۳۷ و ٤٦ روزه هنگامی که^{32}P در فاصله یک سانتیمتری ریشه قرار داده شده بود، به ترتیب ۱۸، ۲۱ و ٥٦٪ ^{32}P جذب شده به شاخ و برگها انتقال داده شد. با افزایش فاصله ^{32}P از سطح ریشه مقادیر کمتری از کل ^{32}P جذب شده به شاخ و برگها انتقال داده شد. به طور مثال ٤٦ روز بعد از کاشت هنگامی که ^{32}P در فاصله های ۱، ۲/۵ و ٤ سانتیمتری ریشه شبدر (تلقیح شده با ایزوله های مزرعه بدون شخم) قرارداده شده بود، به ترتیب ٥۱، ۳۰ و ۱۱ درصد از ^{32}P جذب شده به شاخ و برگها انتقال یافت. نتیجه گیری می شود که قارچهای میکوریز ممکن است تحت تاثیر درازمدت عملیات خاک ورزی اثرات متفاوتی بر توزیع فسفر جذب شده در داخل گیاه شبدر داشته باشند.

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