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连作障碍因素对大豆养分吸收和固氮作用的影响

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摘要：采用分室装置，利用不同孔径的膜研究大豆连作条件下，化感物质、土壤有害生物和大豆胞囊线虫等因素不断累加对植株生长、生物固氮作用和矿质养分吸收和分配的影响。结果表明，随着各因素不断累加，植株的地上部、根系和根瘤干重逐渐降低；除Ca元素外，植株组织的P、K等矿质元素单位含量下降，吸收总量下降，地上部分配的养分比例下降。在化感物质和土壤有害生物因素的基础上接种线虫，对生物固氮和矿质养分的吸收和分配影响明显。

关键词：大豆；连作障碍；胞囊线虫；化感作用。

The effect of continuous cropping factors on soybean seedling growth and nitrogen fixation

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Abstract: Growth of citrus, apple and other fruit trees in replant woodlands may be significantly reduced due to a replant problem and now it has occurred in intensive cropping systems as well. Soybean is a main crop in the north-east part of China. When soybean is cropped continuously in the same field for years, the yield would be reduced by 10%～30% or more. The phenomenon is called soybean continuous cropping problem (SCCP). For easy management, farmers would rather plant soybean year after year than rotate with maize, or other crops. The area with continuous cropping problem is about 700 000 hm^2 only in the east part of the north-east China. Much work on the problem has been done in China since 1980s. However, the main reason why continuous cropping system causes growth problem remains unclear. Nematode, deleterious organism and allelopathic substances are now three factors under consideration, but which factor is the most important? An experiment was designed to answer the question.

The experiment was conducted in a greenhouse, in the campus of China Agricultural University, Beijing, China. A specific growth device was designed for the experiment. The device had two compartments, an outer and an inner cylinder in which soybean was planted. The outer cylinder was a Wargernel pot, and the inner one was a PVC tube (90mm×300mm) sealed completely at the bottom with a

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plastic sheet. Two windows(85mm×190mm)were made in opposite positions in the inner cylinder. These windows were covered either by plastic sheet(0μm), nylon net(30μm), or mixed cellulose ester membrane (Millipore < 0.22μm), which limited plant root growth in the inner compartment. There were 2 kg sterilized sandy soil placed in inner compartment, and 6.75kg black soil filled in outer compartment. Water was added to the water inlet of the Wargernel pot in three treatments in order to carry some substances in soil of outer compartment into inner one and its effect on the plant growth was examined. Water was applied directly to the top of the inner pots in the control.

Two soils were used in the experiment. The first soil, a Haphic Pheanozems(black soil)based on FAO-UNESCO classification, in which plant growth was seriously inhibitied, was collected from a field where soybean had been cropped continuously for wo years in Dancheng, Shuangcheng County, Heilongjiang Province, China. The second soil, a sandy soil, was sampled from Daxing County, Beijing. The sandy soil was autoclaved at 121℃ for 2h and then enough micronutrients and macronutrients were supplied to the sandy soil.

Four treatments were prepared as follwows: for the membrane treatment, the windows were covered by a mixed cellulose ester membrane(0.22μm), which only allowed first soil solutions to pass through but not the soil bacteria or fungi in the first soil; for the nylon treatment, the windows of inner cylinder were covered by nylon net(30μm), which permitted soil microbes to cross beside the soil solutions; for the third treatment, based on the nylon treatment, the suspension of SCN eggs was inoculated into inner compartment; in control, the windows were covered by plastic sheet(0μm)in order to separate completely the inner compartment from the outer one. Each treatment was replicated for 7 times.

In the experiment, four soybean seeds(Hefeng 25, a susceptible cultivar to SCN race 3)were sowed per pot, inoculated with *Bradyrhizobiom japoncium* 911 at the level 2×10^{8} cell pot^{-1}(provided by Department of Microbiology, China Agricultural University)and SCN at the level 2×10[illegible] egg pot^{-1}.

Six weeks after sowing, soybean seedlings were harvested. Total root length, nodule number, cyst number, and the dry weight of roots, shoots and nodules were noted. P, K, Ca, Mg, Fe, Cu, Zn, and B contents in roots, shoots and nodules were also measured with ICP (PE OPTIMA 3300). Several ceresin slides of nodule tissue for light microscopic observation were made. All data were analyzed with SAS(SAS, 1988). Means were compared using LSD at $P\leqslant0.05$ probability level.

The results showed that the dry weight of soybean root and shoot and the number of nodules were significantly depressed in the treatments other than in the control. The most profound inhibition was in the inoculation treatment. It was noticed that the inhibition was also significant in the membrane treatment even though no cysts were present. Compared with control, the nodule structures showed irregularly in nylon net and inoculation treatment.

For most nutrients, inoculation with SCN resulted in the lowest nutrient uptake and concentrations. Nutrient distribution within soybean plants as expressed by the percentage of nutrients in the shoots relative to the total nutrient uptake indicate that P, K, Mg distribution in inoculation, nylon net and membrane treatments increased compared with control, and Fe, Cu, Zn, B decreased.

In this paper, it was notable that allelopathic chemicals, deleterious microorganisms and presence of a large number of SCN affected soybean growth and caused SCCP. Why was the soybean growth inhibited severely when it was continuously cropped in the same field? It is supposed that after the whole growth stage in the first year, the rhizosphere ecology was changed so greatly that it was no longer suitable for soybean growth. One result was that a lot of allelochemicals were produced directly or indirectly in four ways including leaching from the shoot, shoot and root residues, root exudates and metabolites of microorganisms in rhizosphere, which will take effect immediately after seed was sowed in the following year. The other result indicated that the quality and quantity of microorganisms in the rhizosphere were

changed greatly, including the deleterious microorganism of soybean. Soybean is one of the exclusively hosts to SCN, and cyst in the soil would reach a high level after a growth cycle. In the second year, after sowing, the allelopathic substances would be absorbed by soybean. Some of the deleterious microorganisms would also take action at this time. Therefore, in the early stage the soybean development would be retarded, caused low root biomass and a few roots. The root developed in the condition will have weaker resistance and is easier for pathogen to infect than normal soybean in this stage. At the following stage, more nematodes and pathogens will also infact soybean and develop. During the process, they will not only destroy the root structure and restrain absorbing water and nutrient, but also compete for carbohydrate with the host. In a word, all the factors collectively caused the SCCP.

Key words: soybean continuous cropping problem; allelopathy; soybean cyst nematode (*Heterodea glycines*); soybean(*Glycine max* L.)

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同一地块连续种植相同植物的连作过程中植物常出现生长不良、品质变劣、产量降低等连作障碍现象[1]。近年来保护地蔬菜迅猛发展，2000年设施栽培面积已达到100万 hm²，蔬菜生产趋向规模化、工厂化、专业化，形成不少大蒜乡、黄瓜镇等蔬菜专业化生产基地，连作现象非常普遍[2]。目前我国存在连作现象的植物种类较多、面积较广，而且有些植物存在严重的连作障碍问题[3]。

东北是我国大豆的主产区，大豆连作非常普遍、危害严重。1998年，笔者调查发现在黑龙江哈尔滨市双城县约有133hm² 大豆由于连作障碍而颗粒无收。从20世纪80年代至今，关于大豆连作障碍减产的研究已经开展了很多。有关大豆连作减产的原因有多种提法，如大豆胞囊线虫、根腐病、养分亏缺以及土壤中有害物质等均可能引起减产[4]。目前对上述单一因素的研究比较深入，但综合考虑各个因素的研究鲜有报道。本文采用分室装置，利用不同孔径的隔膜研究连作障碍因素对大豆幼苗养分吸收和固氮作用的影响。

1 材料和方法

1.1 供试品种 合丰25号，对大豆胞囊线虫生理小种3号感病。

1.2 供试土壤 重茬土采自黑龙江省双城市单城乡一出现严重连作障碍而绝产的地块，该土壤样品中大豆胞囊线虫的胞囊数高达每百克鲜土156个。土壤为典型黑土，其农化性状为：全N 0.1858%、速效K 166.5 mg·kg⁻¹、Olsen-P 23.3 mg·kg⁻¹、pH 7.84。沙土采自北京市卢沟桥乡，土壤农化性状为全N 0.027%，速效K 47.9 mg·kg⁻¹、Olsen-P 3.2 mg·kg⁻¹、pH 7.80。

1.3 线虫采集 从1.2中重茬土中分离，将一定量病土加入水后搅拌，将悬浮液依次过20和80目筛后收集胞囊。在100目筛子上用橡皮塞压碎胞囊，用自来水冲洗至500目筛子上，加入少许高岭土，在2 000～2 500 r/min 离心5 min，弃去悬浮液，再加入40%蔗糖溶液将沉淀溶解，转速1 000 r/min 离心2～3 min，收集上清液备用。胞囊线虫卵的密度 n 为10 000 ml⁻¹，生理小种为3号。

1.4 根瘤菌培养 菌种 *Bradyrhizobium japonicum* 911，由中国农业大学生物学院微生物系提供。YMA培养基先接种斜面，然后接种到液体培养基，在28℃、180 r/min 培养72 h，接种密度 n 为 8×10^8 ml⁻¹。

1.5 试验装置 如图1，包括外室和内室两部分。外室为Wargernel盆，内具有明显连作障碍现象的黑土(重茬土)。内室为PVC管(90mm×300mm)，在管的中部对应的两侧各有一个开口(85mm×190mm)，内室底部用塑料纸和胶带纸完全密封，收获时从此打开以方便取样，内室装灭菌的沙土(湿热灭菌，121℃，2 h)。内室的开口上粘贴不同孔径的膜，它是内室和外室唯一的联系，每次从Wargernel盆的浇水口浇水，保证水先经过外室的重茬土，然后通过两个开口上的膜进入内室并作用于植物。对照处理内室则用塑料纸密封，与外室完全隔绝(没有重茬土的任何影响)，直接从PVC管上部浇水。

1.6 试验设计 根据内室开口上粘贴的膜孔径等的不同设计4个处理。对照中膜为塑料纸，保证外室与内室完全隔绝，没有重茬土的任何影响；处理1的膜为0.22μm微孔滤膜，土壤溶液可以通过此膜，而细菌、真菌等微生物不能通过，设计研究重茬土中化感物质对植物的影响，称为滤膜处理；处理2的膜为30μm尼

龙网,大豆根系不能穿过此膜,只能在内室生长,而外室重茬土中的土壤微生物包括病原微生物能够随水进入内室.线虫的二龄幼虫J2(体长375~500μm,体宽18~18.5μm)也可随机的移动进入内室侵染根系,因此本处在处理1中化感作用的基础上拟研究重茬土中土壤生物因素对植物生长的负面影响,称为尼龙网处理;考虑到重茬土中胞囊数每百克鲜土高达156个,处理3在处理2的基础上大量接种线虫,在化感作用和土壤生物作用基础上探索高接种量线虫对植物生长的影响,称为接种处理。所有处理均重复7次。

1.7 线虫接种 将直径12.5cm的滤纸折叠成呈小漏斗状,剪去下边锥形,将土用铁丝戳一锥形坑,将滤纸插入PVC管中,种子置于其中。2d后,将滤纸漏斗拿起来,每个种子分别接种5000个卵,每管共接种20 000个卵,2ml根瘤菌悬液(密度n为8×10^{8} ml^{-1})。

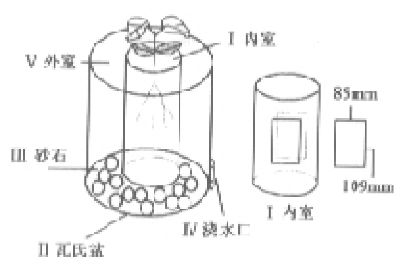
1.8 植物培养 供试土壤采自北京卢沟桥乡沙土,土壤风干后进行湿热灭菌(121 C,2 h)装入PVC管(直径75mm,高度381mm),每管装土1.8kg,肥料为(mg·kg^{-1})纯N 50、P_2O_5 50、K_2O 50、Mn 5、Zn 5、Cu 5、Fe 5、Mg 50。每管播种大豆4粒,出苗后定植2株。1999年4月5日播种,5月22日收获,并采样分析。

1.9 根瘤活性的测定 取整株植物放入250ml玻璃瓶中,加塞密闭,抽出25ml气体,加入C_2H_2 25ml,反应2 h后测定生成的C_2H_4含量(nmol C_2H_4·h^{-1}管$^{-1}$)。用气相色谱(SHIMADZU GC-14B)进行测定。

1.10 营养元素的测定 称取植物样品0.3000 g左右,580 C灰化7 h,用2 ml 1:1 HCl溶解,定容至20 ml。ICP(PE OPTIMA 3300)测定P、Ca、K、Mg、Fe、B、Cu和Zn。

1.11 根瘤组织的石蜡切片 4%的戊二醛溶液中固定试验材料,酒精梯度脱水,石蜡包埋并用Leica荧光相机照相。

1.12 所有数据均采用SAS方差分析,并进行LSD($P<0.05$)统计检验。



Ⅰ Inner, Ⅱ Wargernel pot, Ⅲ Gravel, Ⅳ Irrigation, Ⅴ Outer

图1 试验装置

Fig.1 Equipment for the experiment

2 结果与分析

2.1 生长参数的变化

由表1可看出,对照、滤膜处理、尼龙网处理、接种处理中植株地上部干重依次下降,各处理之间均达到显著水平。根干重呈现:对照>滤处理>尼龙网处理>接种处理。与CK、滤膜处理相比,接种处理和尼龙网处理中植株的总根长几乎下降了一半,差异显著。PVC管中为灭菌处理的沙土,因此CK、微孔滤膜处理大豆根系胞囊数为0,收获时仔细检查发现所有滤膜均保持完整。接种处理线虫胞囊数高达每管1586个。尼龙网处理在根部发现多达300个胞囊/管,这一方面可能由于尼龙网在线虫口针的作用下加大而容易通过,另一方面由于根系生长对线虫具有趋化性而引起的,但其与CK和微孔滤膜处理差异不显著,这可能由于线虫的随机移动性的误差造成的。接种线虫后,该处理中植株根系的根瘤数、根瘤干重和固氮酶活性显著降低,明显抑制大豆的生物固氮作用。

2.2 植株不同部位矿质元素的含量

2.2.1 地上部组织中矿质元素单位含量的变化 地上部单位干重的含P含量为:CK>尼龙网处理>滤膜处理>接种处理。与其它处理相比,接种处理中植株地上部单位干重的含K、Cu和Zn量显著低于其它处理,Ca则明显高于其它处理(表2)。

2.2.2 根中矿质元素单位含量的变化 与CK相比,其它处理根组织单位干重的含Fe量上升,Ca基本呈上升趋势。各处理中单位干重的含P、K和Mg含量变化与地上部趋势相同,其中接种处理中单位干重的含P量仅为对照的29.5%。

2.2.2 根瘤中矿质元 单位含量的变化 对照处理中,根瘤组织单位干重的含Zn量与其它处理差异显著。各处理中单位根瘤干重的含P、K和Mg量变化与根中趋势一致。

2.3 大豆植株矿质养分吸收总量的变化

植株的生物量与单位干重的矿质养分含量相乘得到矿质养分吸收总量。由表3可知，除Fe、P和Zn外，CK、滤膜处理、尼龙网处理、接种处理中植株所测营养元素的吸收总量呈现依次降低的趋势。虽然接种处理中各部位Ca含量较高，但各部位生物量则显著低于其它处理，所以植株Ca吸收总量仍然明显低于其它处理。由于单位含量和生物量都低，接种处理中所测 养元素的吸收总量比其它处理下降幅度很大，其P和K的养分吸收总量分别为对照的23.1%和40.7%。

表1 接种、尼龙网和滤膜处理对大豆生长的影响

Table 1 Effects of soybean cyst nematode infection and separations of sick soil from normal soil on soybean growth parameters (per tube)

处理 Treatment	根干重 Root dry weight(g)	茎干重 Shoot dry weight (g)	胞囊数 Cyst (Num.)	总根长 Total root length(cm)	根瘤干重 Nodule dry weight (g)	固氮酶活性 Acetylene reduction rate (nmol $C_2H_4\cdot h^{-1}$)	根瘤数 Nodule number
接种	1.04c	2.15d	1586a	2653b	0.14c[1)]	667.2b	161c
尼龙网	1.18c	2.89c	300b	2657b	0.34b	2950a	302b
滤膜	1.36b	3.47b	0b	4704a	0.40ab	3373a	301b
CK	1.62a	4.12a	0b	4664a	0.47a	2655a	446a

字母相同者表示差异不显著，字母不同表示差异显著(下同表1) Means within a column followed by the same letter are not significantly different at 5% level by LSD test, the same below

表2 接种、尼龙网和滤膜处理对根、地上部、根瘤中矿质养分含量的影响

Table 2 Nutrient concentration in soybean plants as affected by soybean cyst nematode infection and separations of sick soil from normal soil ($mg\cdot g^{-1}$DW)

处理 Treatment	P	K	Ca	Mg	Fe	Cu	Zn	B	
	接种	2.08c	23.98b	23.9a	5.52a	0.11a	0.014b	0.024c	0.041a
地上部 Shoot	尼龙网	3.87a	28.14a	20.7b	5.70a	0.13a	0.018a	0.036ab	0.037b
	滤膜	3.23b	29.13a	21.6b	5.75a	0.16a	0.017a	0.029bc	0.042a
	CK	4.10a	28.89a	20.1b	4.93b	0.13a	0.017a	0.041a	0.039b
	接种	2.06c	12.90b	15.0a	3.88b	1.17ab	0.023a	0.066a	0.020a
根 Root	尼龙网	4.94b	19.97a	11.4c	6.53a	0.86bc	0.023a	0.065a	0.017b
	滤膜	2.88c	15.02b	13.2bc	4.65b	1.36b	0.025a	0.054a	0.021a
	CK	6.97a	22.50a	12.0b	7.42a	0.75a	0.021a	0.057a	0.017b
	接种	4.86c	8.24c	12.4ab	4.23b	0.58a	0.019a	0.034b	0.013ab
根瘤 Nodule	尼龙网	6.36b	17.81a	10.7b	5.45a	0.73a	0.018a	0.035b	0.012b
	滤膜	5.44c	12.09b	11.7b	5.20a	0.74a	0.018a	0.035b	0.013a
	CK	7.74a	18.26a	14.3a	5.43a	0.70a	0.018a	0.060a	0.013ab

表3 接种、尼龙网和滤膜处理对大豆植株养分吸收总量的影响

Table 3 Total nutrient uptake by soybean plant as affected by soybean cyst nematode infection and separations of sick soil from normal soil ($mg\cdot g^{-1}$DW)

处理 Treatment	P	K	Ca	Mg	Fe	Cu	Zn	B
接种	7.34c	66.5c	68.5c	16.5c	1.58b	0.056c	0.124c	0.109c
尼龙网	18.85b	108.9b	76.9c	25.8b	1.64b	0.084b	0.189b	0.131b
滤膜	17.61b	128.6b	97.2b	28.56b	2.66a	0.102a	0.188b	0.178a
CK	31.73a	163.2a	108.6a	34.96a	2.03ab	0.113a	0.289a	0.196a

表4 接种、尼龙网和滤膜处理对矿质养分在大豆植株体内分配比例的影响(100%)

Table 4 Nutrient distribution soybean as expressed by the percentage of nutrients in shoots

处理 Treatment	P	K	Ca	Mg	Fe	Cu	Zn	B
接种	62.4a	78.3a	74.7b	72.2a	17.5b	51.8b	43.7b	79.6b
尼龙网	59.7ab	74.4ab	77.3a	63.6bc	23.3ab	60.0a	54.3a	80.7ab
滤膜	63.1a	78.6a	77.0a	70.1ab	20.6ab	59.7a	53.9a	81.3ab
CK	53.7b	72.7b	76.4a	58.6c	25.7a	62.5a	58.5a	82.6a

养分分配比例(%)＝100×地上部养分总量/植株的养分总量 Nutrient distribution soybean as expressed by the percentage of nutrients in shoots

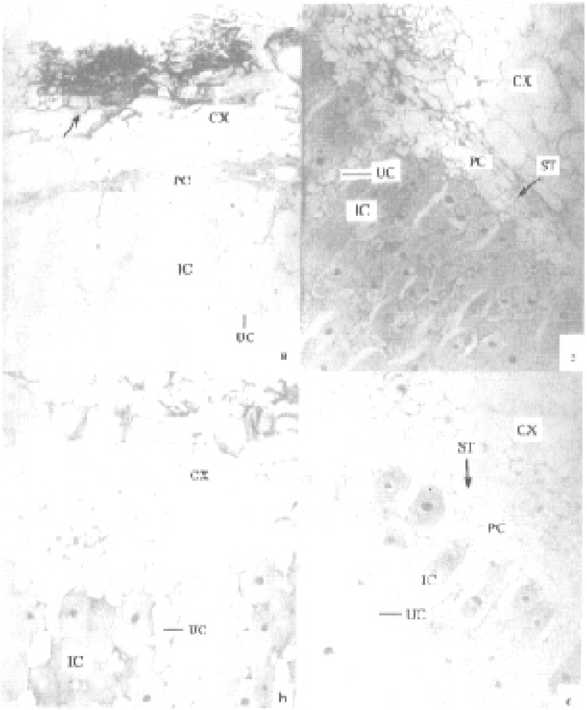


图 2　不同处理对大豆根瘤组织结构的影响

Fig. 2　Light micrographs of nodule of soybean in different treatments

UC　非侵染细胞 uninfected cell; IC　侵染细胞 infected cell; CX　皮层 cortex; ST　淀粉粒 starch granules; PC　侵染区周围的细胞层 cells periphery around the infected cells;→　组织坏死 necrosis tissue

2.4　养分分配比例的变化

与对照相比,接种处理中植株的 Ca、Fe、Cu、Zn 和 B 等养分在地上部的分配比例低,而 P、K 和 Mg 则有增加的趋势,其中接种处理加或减少的幅度比较明显,与 CK 差异显著。

2.5　瘤组织结构的变化

不同处理之间根瘤组织结构有明显的差别(图 2)。接种处理根瘤组织的厚壁细胞被破坏,甚至其以内的细胞出现坏死,与中央区相邻 4～5 层皮层细胞已经萎缩,几乎不含淀粉粒(图 2(a))。与其它处理相比,中央区侵染细胞发生萎缩,侵染细胞发育受到抑制。

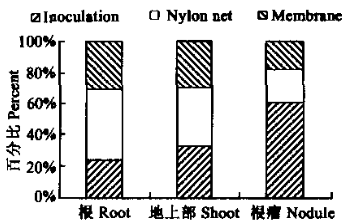
中央区非侵染细胞几乎完全萎缩。由图 2(b)可知,尼龙网处理细胞质稀少,中央区淀粉粒数目较少,厚壁细胞较多,细胞纤维化,甚至局部出现坏死,紧邻中央区的 4～5 层皮层细胞萎缩,这些细胞含有的淀粉粒亦较少。浸染细胞体积比较大,但淀粉粒很少。图 2(c)表明微孔滤膜处理根瘤结构完整,细胞质较多,图中可明显看到中央区含有大量淀粉粒,特别是近临中央区有 4～5 层皮层细胞含有大量的淀粉粒,形成淀粉粒层,保证了根瘤的能量供应。根瘤组织具有完整的厚壁细胞层。由图 2(d)可知,对照植株的根瘤中央区淀粉粒数目很多,细胞质浓厚,染色清晰,细胞结构完整。

3　讨论

本试验通过分室法利用不同孔径的膜材料造成不同因子作用的累加,初步探讨大豆连作碍产生的机制,对其它植物的连作障碍的研究具有一定的借鉴意义。当水溶液通过外室的重茬经过微孔滤膜

(0.22μm),即可得到无菌的重茬土土壤溶液,其对内室中的植物的作用是化感作用。线虫在根分泌物的趋化作用下向寄主移动[5],在尼龙网处理中,线虫在这种作用下穿过尼龙网侵染大豆。根据试验设计,随着各障碍因素逐渐累加大豆生长受到的抑制程度不断加大。图3已经证实了预先的设想。该图中计算CK和滤膜处理之间、滤膜处理和尼龙网处理之间、尼龙网处理和接种处理之间根干重的差值分别占CK和接种处理之间根干重的差值的百分比。同样的方法可以计算地上部干重、根瘤干重下降中各处理所占的比例。结果表明,根干重的减少中,滤膜处理、尼龙网处理、接种处理所占比例分别为44.8%、31.1%、24.1%;地上部干重下降值中,三者所占比例依次为33.1%、29.4%、37.5%;根瘤干重下降值中,三者所占比例依次为22.1%、18.2%、60.6%。从3个部位干重下降的比例来看,土壤溶液中的有害物质(化感作用)、土壤有害生物对大豆生长均有不同程度的抑制。本试验供试土壤中线虫含量很高,因此在尼龙网的基础上设计了线虫高接种量试验,结果表明线虫侵染引起根、地上部和根瘤3部分干重明显下降(表1和图3),尤其对根瘤干重和功能影响更大,进而使大豆生物固氮作用受到阻遏。由此可见,大豆连作障碍是多因素共同作用造成的现象。

本文中,重茬土的土壤溶液抑制大豆自身生长,是典型的自毒现象(表1)。韩丽梅等[6]证实大豆根残自毒作用的存在。对重茬土(与本文供试黑土属于同一类型)灭菌处理并不能完全消除连作障碍的存在,也反证了化感作用的存在[7]。研究发现葫芦科、豆科中多种植物也存在自毒现象[8,9]。



▨接种处理,□尼龙网处理,▧滤膜处理

图3 不同处理造成的植株根、地上部、根瘤干重降低程度的比较

Fig. 3 The effect of different treatmonts on the dry weight decline of nodule, root and shoot

与滤膜处理相比,尼龙网处理增加了土壤有害生物等因素的作用,根干重、地上部干重和总根长等明显减少,尤其是根干重、总根长显著下降,表明植物生长进一步受到抑制。连作条件下,大豆的根部病害加重[10]。王震宇等[11]研究表明在开花期以前,重茬大豆优势种群为镰刀菌(*Fusarium*),谷茬、玉米茬大豆则以青霉(*Penicillium*)、木霉(*Trichoderma*)占优势。马汇泉等[12]报道,禾谷镰刀菌等土壤习居菌复合侵染引起大豆根腐病。韭菜连作后病害发生严重[13]。

在土壤溶液和土壤生物因素作用的基础上,高接种量的线虫对大豆危害严重,尤其是地上部重量和根瘤生长显著受到抑制。根瘤干重、地上部干重、根瘤活性和根瘤数显著下降。Kennedy等[14]发现接种大豆胞囊线虫5号生理小种,根系产生的结瘤信息物质异黄酮量增多,根瘤数反而增加,但固氮酶活性下降与本文结果一致。线虫的侵染造成根瘤结构中淀粉粒越来越少,细胞萎缩严重,根瘤逐渐出现组织坏死和根瘤发育畸形(图2)。这可能与线虫作为库而跟根瘤竞争同化物有关[15,16]。

随着各种障碍因子的累加,植物生长受到的抑制程度逐渐加深,植株根系发育不良[8]。与对照相比,另外3个处理中各组织单位干重的含Ca量上升,K和P等含量则下降,而P含量降低严重影响根瘤的固氮效率。对于接种处理来说,根部单位干重的含Ca量上升,这与线虫体内Ca、P含量较高有关[17]。滤膜处理植株生长显著好于尼龙网处理,但其根、地上部和根瘤组织中单位干重的P和K等元素的含量却低于尼龙网处理,这种差异是否是由于滤膜处理中植株生物量大的稀释作用还是其它原因尚有待于进一步研究。

从本试验可看出,大豆连作障碍是由化感物质、土壤有害微生物、大豆胞囊线虫等多种因素综合作用的结果。大豆生长在发芽和幼苗生长期已经受到了抑制[18],导致前期根系发育不良,植株的抗性降低。在此基础上,线虫和病原微生物侵染大豆植株,使大豆受危害程度加剧,出现如生物量下降,养分吸收总量显著降低,固氮作用减弱,植株黄化等。至于土壤溶液中的化感物质是什么、大豆根系分泌物中或土壤溶液中是否存在刺激土壤病原微生物和大豆胞囊线虫生长的物质,有待于进一步研究。

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