

苯丙烯酸对黄瓜幼苗膜脂过氧化作用的影响

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摘要:以山东密刺黄瓜(*Cucumis sativus* L.)为试材,分别采用大棚土壤和露地土壤进行盆栽模拟试验,首次研究了不同浓度的苯丙烯酸对不同土壤栽培条件下黄瓜幼苗膜脂过氧化作用的化感效应。结果表明:不同浓度的苯丙烯酸对大棚土培幼苗不同时期的 SOD 活性的化感效应均为抑制作用,并随着处理浓度的增加抑制作用增强。浓度大于 50 mg/kg 时,对露地土培幼苗 6 叶期 SOD 活性的化感效应均为抑制作用。浓度大于 100 mg/kg 时,对两种土培幼苗 CAT 的化感效应均为抑制作用,并随着处理浓度的增加抑制作用增强。苯丙烯酸对不同土壤、不同时期黄瓜幼苗的 MDA 均为促进作用,并随着处理浓度的增加促进作用增强。苯丙烯酸使黄瓜幼苗的电解质外渗率和伤害率增加,浓度大于 50 mg/kg 时的大棚土培幼苗和浓度大于 100 mg/kg 时的露地土培幼苗,电解质外渗率与对照及处理间均存在显著差异($p < 0.05$),伤害率与对照及处理间均存在极显著差异($p < 0.01$)。大棚土培幼苗 MDA 含量和电解质外渗率的化感强度均大于露地土培幼苗。

关键词:苯丙烯酸;黄瓜;化感效应;超氧化物歧化酶;丙二醛;电解质外渗率

Effects of cinnamic acid on peroxidization of the plasma membrane of cucumber seedlings

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Abstract: Cucumber is one of the most important vegetable crops grown under greenhouse conditions in China in terms of total production. Continuous cropping systems have become common practice in many vegetable-growing areas, especially under plastic greenhouse conditions, giving rise to a series of problems for sustainable production of cucumber with high quality and high yield. The autotoxic effect has been considered as an important obstacle to continuous cropping of cucumber from previous investigations. Cinnamic acid was found to have an autotoxic effect on cucumber in solution culture. However, whether the autotoxic effect also occurs in soils and whether the effect is long lasting and dependent on the concentration of cinnamic acid is still unclear. To answer these questions, field experiments were conducted with cucumber (*Cucumis sativus* L.) growing under plastic greenhouse and open field conditions. The autotoxic effect of cinnamic acid was investigated at varying concentration levels in the two experimented conditions.

To prepare cucumber seedlings for treatment of cinnamic acid, soils were taken from two vegetable fields at the Horticultural Experimental Station of Northeast Agricultural University. One field was in a plastic greenhouse where cucumber had been grown continuously for 18 years. The other was an open field with no previous history of cucumber cultivation. Pots were filled with 400g of either soil containing cinnamic acid of 0, 25, 50, 100 or 200 mg/kg, respectively. Healthy and uniformly sized cucumber seedlings at the two-leaf stage pre-cultivated in vermiculite medium were transferred to the nursery pots. The pots were immediately placed in the two fields from which the soils had been collected. In each field there were 4 cinnamic acid level treatments. One treatment occupied a 0.3 m² area of soil with 20 plants, separated from other plots by a border area. Three replicates were set up in a randomized design. Plant samples were taken at growth stages of 4, 5 and 6

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leaves, for analysis of SOD, CAT activity and MDA concentration. The permeability of the plasma membranes of the leaves was measured in terms of solute leakage at the 6-leaf stage.

The allelopathic effect of cinnamic acid was measured by the Williamson method using the expression $RI=1-C/T$ when $T \geq C$ or $RI=T/C-1$ when $T < C$, where C and T stand for the comparison value and the treatment value, respectively. When $RI > 0$, it indicates a stimulation effect and $RI < 0$, an inhibition effect. The absolute value of RI indicates the strength of the allelopathic effect.

The results indicate that the allelopathic effect of cinnamic acid differed with enzyme and soil. In the case of seedling SOD activity, cinnamic acid showed an inhibitory effect at all concentration levels under greenhouse conditions. Furthermore, the strength of the inhibitory effect increased with cinnamic acid concentration. Under open field conditions the inhibitory effect occurred when cinnamic acid concentration was above 50 mg/kg. CAT activities of the plants were inhibited when cinnamic acid addition levels were higher than 100 mg/kg, and the degree of inhibition increased with the cinnamic acid concentration in both fields. Cinnamic acid exerted an overall stimulatory impact on MDA content of the leaves at all concentrations in both fields. Furthermore, the strength of the stimulatory effect increased with cinnamic acid level added to the soil. Cinnamic acid above the level of 50 mg/kg in the greenhouse and 100 mg/kg in the open field led to higher permeability of plant plasma membranes and actually destroyed the cell membrane at the highest concentration in this experiment. The allelopathic effect of cinnamic acid was greater in the greenhouse than in the open field.

The results indicate that cinnamic acid can break the balance in the plant tissue between the free radicals produced in the cells and the capacity of the plants to clear free radicals, resulting in a decrease in the activities of the membrane-protective enzymes of cucumber followed by accumulation of MDA. As a result of these reactions, cell membrane permeability decreased and solutes leaked out of the plant tissues.

Key words: cinnamic acid; cucumber; allelopathic effect; SOD; MDA; plasma membrane permeability

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黄瓜是设施栽培的主要蔬菜作物之一,连作现象十分普遍,连作障碍严重。许多研究表明,作物的连作障碍与作物产生的化感物质密切相关^[1~9]。黄瓜产生的他感物质对连作黄瓜本身的生长发育具有很强的抑制作用(即自毒作用)。Yu 和 Matsu^[6]的试验证明,黄瓜根系中含有苯丙烯酸、对羟苯甲酸、苯甲酸、2,5-二羟苯甲酸等酚酸类物质,当黄瓜连续种植时,根系分泌的酚酸类物质积累达到一定程度,就会抑制下茬黄瓜的生长,产生自毒作用(autotoxic effect)。

自 McCord 和 Fridovich 提出自由基伤害学说以来,现已广泛应用于研究需氧生物细胞的毒害机理。人们发现植物处于干旱^[10]、低温^[11]和 SO₂^[12]等逆境胁迫下,细胞内氧自由基产生和清除的平衡受到破坏,自由基的增加会导致细胞膜的伤害,造成膜脂过氧化。黄瓜根系分泌物、根系提取液和自毒物质对水培黄瓜保护酶活性和光合作用具有显著影响,增加了根系膜质过氧化^[13,14],而自毒物质在土壤条件下对幼苗的影响如何,目前报道较少。本研究分别在露地菜田土壤和大棚连作土壤栽培条件下,模拟黄瓜自毒作用逆境胁迫,研究其对黄瓜幼苗根系膜质过氧化的影响,为揭示自毒作用的生理生化机制奠定基础。

1 材料与方法

1.1 试验材料

供试品种为山东密刺黄瓜(*Cucumis sativus* L.),供试苯丙烯酸(肉桂酸)(cinnamic acid)由北京原平皓生物技术有限公司提供。采用的栽培基质为蛭石,供试营养液为霍格兰营养液。供试土壤采集于东北农业大学园艺实验站,分别是种植 18a、每年种植一茬黄瓜的大棚土壤和未种植过黄瓜的露地菜田土壤,供试土壤的基础肥力见表 1。

表 1 供试土壤农化性状

Table 1 Agri-chemical properties of the tested soils									
供试土壤 Soil	有机质 OM (%)	全氮 Total N (%)	全磷 Total P (%)	缓效钾 Slow exch K (mg/kg)	碱解氮 Alkaline N (mg/kg)	速效磷 Avail. P (mg/kg)	速效钾 Avail. K (mg/kg)	EC 值 (ms/cm)	pH
大棚土壤 Greenhouse soil	4.65	0.34	0.28	1072.40	207.80	239.80	460.20	0.67	7.44
露地土壤 Open field soil	3.26	0.22	0.14	951.10	150.80	178.60	329.00	0.34	7.66

1.2 试验方法

1.2.1 土壤处理 把采集来的大棚土壤和露地土壤去杂过筛,将苯丙烯酸用无水乙醇溶解,分别以 0(不加苯丙烯酸)、25、50、

100 mg/kg 土和 200 mg/kg 土的苯丙烯酸处理两种土壤(各处理溶液中乙醇浓度保持一致),然后分别装 400g 土于 10cm×10cm 营养钵中,放置过夜待用。

1.2.2 黄瓜幼苗预培养 将浸种催芽后的种子播于 5 cm×5 cm 盛有蛭石的营养钵中,不分小区,以保证基本相同的栽培条件和幼苗的整齐度,该区面积为 2 m²,栽培株数为 800 株。平均每 2d 浇灌霍格兰营养液 1 次。待幼苗长到 2 叶 1 心时进行处理。

1.2.3 试验设计与处理方法 挑选生长一致、健壮的幼苗移入盛有苯丙烯酸处理土壤的营养钵中开始处理,各处理均采用小区栽培,每处理均设 3 个重复,每个小区面积为 0.3 m²,栽培株数为 20 株。各小区均设有保护行,采用完全随机排列,常规管理。在 4、5 和 6 片叶期在每个处理的 3 个重复小区中分别取 3 株幼苗根系混合,进行 SOD、CAT 活性分析和 MDA 含量测定,在 6 片叶期取第 3 片叶进行电解质外渗率测定,重复 5 次。

1.3 测定项目与方法

超氧化物歧化酶(SOD)活性测定采用氮蓝四唑光化还原法^[15]。过氧化氢酶(CAT)活性测定采用碘量滴定法^[16]。丙二醛(MDA)含量采用硫代巴比妥酸显色法测定^[15]。电解质渗出率采用相对电导率法^[16],电解质渗出率(%)=(浸泡液电导率值/煮沸后电导率值)×100;细胞膜伤害率(%)=[(处理电导率-对照电导率)/(处理煮沸后电导率-对照电导率)]×100;化感作用效应敏感指数(RI)采用 Williamson^[17]的方法, $RI=1-C/T(T\geq C)$; $RI=T/C-1, (T<C)$, C 为对照值, T 为处理值。当 RI>0 时,表示促进作用,当 RI<0 时,表示抑制作用。RI 绝对值的大小代表化感(自毒)作用强度。

1.4 数据处理

该试验原始数据的处理采用 Excel 软件完成,差异显著性测验采用 SAS 软件完成。

2 结果与分析

2.1 苯丙烯酸对黄瓜幼苗根系超氧化物歧化酶(SOD)活性的化感效应

图 1 和 2 是苯丙烯酸对大棚土培和露地土培幼苗根系 SOD 活性的化感效应及其时间变化。结果表明,不同浓度的苯丙烯酸对大棚土培和露地土培幼苗的化感效应是不同的。除浓度为 25 mg/kg 的低浓度对大棚土培幼苗第 4 和第 6 叶期 SOD 的化感效应为促进效应外,其它处理均表现出抑制作用,并随着处理浓度的增加抑制作用增强。对露地土培幼苗的 SOD 活性的化感效应在第 6 叶期为抑制作用,随着处理浓度的增加抑制作用增强,其它处理均表现出促进作用,随着处理浓度的增加,促进作用减弱。大于 50 mg/kg 浓度处理对 3 个叶期大棚幼苗 SOD 活性均具抑制作用,而对露地幼苗则依叶期的不同而有促进或抑制作用。低浓度苯丙烯酸促进露地幼苗 SOD 活性,证明其诱导 SOD 活性提高而有利于清除氧自由基。其次,苯丙烯酸对大棚土培和露地土培幼苗 SOD 活性的化感强度是不同的,在第 6 叶期大棚土培的化感强度大于露地土壤。例如,处理浓度为 25 mg/kg 时,大棚土培幼苗的 SOD 活性的化感指数为-0.056,而露地土培幼苗 SOD 活性的化感指数则为 0.002,处理浓度为 200 mg/kg 时,大棚土培幼苗的 SOD 活性的化感指数为-0.473,而露地土培幼苗 SOD 活性的化感指数则为-0.214。

2.2 苯丙烯酸对幼苗 CAT 活性的化感效应

图 3 是苯丙烯酸对大棚土培黄瓜幼苗 CAT 活性的化感效应,结果表明,除浓度为 25 mg/kg 和 50 mg/kg 在幼苗第 4 片叶

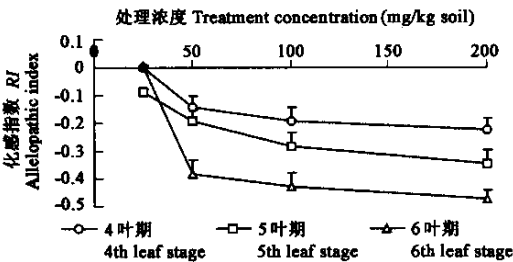


图 1 苯丙烯酸对大棚土培幼苗根系 SOD 活性的化感效应
Fig. 1 Allelopathic effects of cinnamic acid on SOD activity in roots of cucumber seedlings cultured in greenhouse soil

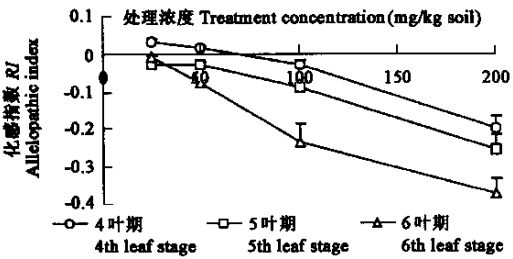


图 3 苯丙烯酸对大棚黄瓜幼苗根系过氧化氢酶活性的化感效应
Fig. 3 Allelopathic effects of cinnamic acid on catalase activity in roots of cucumber seedlings cultured in greenhouse soil

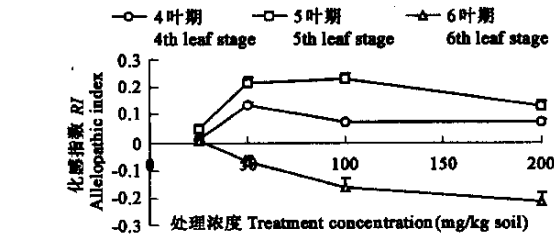


图 2 苯丙烯酸对露地土培黄瓜幼苗根系 SOD 活性的化感效应
Fig. 2 Allelopathic effects of cinnamic acid on SOD activity in roots of cucumber seedlings in Open field soil

时的化感效应为促进效应外,其它处理在各个时间均为抑制作用,25 mg/kg 经过一定的处理时间后可得到一定程度的恢复,自 50 mg/kg 处理开始随着处理浓度的增加和时间的延长抑制作用增强。

图 4 是苯丙烯酸对露地土培黄瓜幼苗 CAT 活性的化感效应。结果表明,25 mg/kg 和 50 mg/kg 处理在第 4 和 5 片叶时表现为抑制作用,在第 6 片叶时表现为促进作用,说明得到了一定程度的恢复。自 100 mg/kg 开始随着处理浓度的增加和时间的延长抑制作用增强。

上述结果表明,大棚土壤可因苯丙烯酸的加入而加重其毒害作用。较低浓度的苯丙烯酸对黄瓜幼苗伤害的程度较轻,随着处理时间的延长植株可得到一定的恢复,而高浓度苯丙烯酸毒害作用较大,使植株最终难以抵御而表现出保护功能的削弱。

2.3 苯丙烯酸对幼苗根系 MDA 含量的化感效应

图 5 和图 6 分别是苯丙烯酸对大棚土培和露地土培幼苗 MDA 含量的化感效应,结果表明,苯丙烯酸对土培幼苗 MDA 活性的化感效应均表现为促进作用,即 MDA 含量增加,当处理浓度为 200 mg/kg 时,在第 4 叶期和第 6 叶期,大棚土培幼苗的化感指数分别为 0.148 和 0.367,露地土培幼苗的化感指数分别为 0.084 和 0.283,对大棚土培幼苗的化感作用强度均大于露地土培幼苗($p < 0.05$),与 SOD 的抑制效应规律一致。

以上结果表明,低浓度的苯丙烯酸处理后,在保护酶系统的作用下,氧自由基得到一定程度的清除,膜质过氧化程度较轻;高浓度处理产生的氧自由基因保护酶的清除能力削弱而不能得到及时的清除,对细胞膜将产生毒害作用,这种毒害作用随着处理时间的延长和浓度的增加而增加。

2.4 苯丙烯酸对黄瓜幼苗电解质外渗的影响

表 2 可见,苯丙烯酸使黄瓜幼苗相对电导率增加,苯丙烯酸浓度越高,相对电导率越大。不同土壤条件下苯丙烯酸导致电解质外渗的趋势相一致,但强度略有不同,其中连作 18a 大棚土壤栽培条件下分别较对照增加 0.65%、12.76%、26.38% 和 50.32%;露地菜田土壤栽培条件下分别较对照增加 0.61%、1.34%、17.93% 和 38.29%。显著性分析结果表明,与对照比较,连作 18a 大棚土壤栽培时,苯丙烯酸浓度为 50mg/kg 时电导率达到显著性差异($p < 0.05$),伤害率在各处理间达到了极显著差异($p < 0.01$)。而露地菜田土壤栽培则在 100mg/kg 时电导率和伤害率与对照差异显著。黄瓜叶片电解质渗出量增多,说明外源苯丙烯酸浓度较高可对黄瓜幼苗产生逆境胁迫,造成细胞膜受损,膜透性增大,离子渗漏。膜透性增大引起的电解质渗透被认为是逆境下对植物伤害的直接表现^[18]。

图 7 是大棚土培和露地土培幼苗在 6 叶期时相对电导率的化感效应。图表明,大棚土培的化感强度明显大于露地土培。浓度为 25 mg/kg 时,化感指数相差不大,分别为 0.0055 和 0.0061,在浓度为 50、100 和 200 mg/kg 时大棚土培的化感指数分别为 0.113、0.208 和 0.335,露地土培幼苗的化感指数分别为 0.013、0.152 和 0.227,说明相同浓度的苯丙烯酸对大棚土培幼苗细胞膜的伤害程度大于露地土培。

3 讨论

近年来的研究结果证明,植物在逆境条件下产生更多的氧自由基,加剧膜质过氧化而导致膜系统受到破坏^[10~12,19,20]。SOD 和 CAT 则对这些自由基具有清除作用,从而在一定程度上忍耐、减缓或抵抗逆境胁迫^[21]。本研究中,低浓度(25 mg/kg)苯丙烯酸处理土壤^{万方数据}和 CAT 具有一定的促进作用,表明植株为免受逆境伤害作出了适应性反应。但高浓度(100 mg/kg 和 200 mg/kg)处理,均使 SOD 和 CAT 活性降低,表明植物受逆境胁迫加重,产生的氧自由基已超出了 SOD、CAT 等保护酶系统

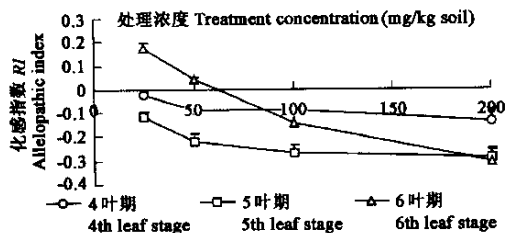


图 4 露地土培条件下苯丙烯酸对黄瓜幼苗根系过氧化氢酶活性的化感效应

Fig. 4 Allelopathic effects of cinnamic acid on catalase activity in root of cucumber seedlings cultured in open field soil

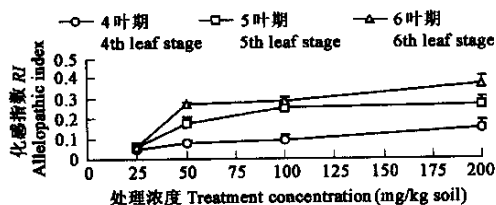


图 5 苯丙烯酸对大棚土培幼苗根系 MDA 含量的化感效应

Fig. 5 Allelopathic effects of cinnamic acid on MDA content in roots of cucumber seedlings cultured in greenhouse soil

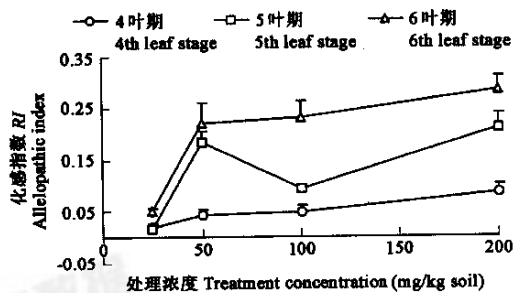


图 6 苯丙烯酸对露地土培幼苗根系 MDA 含量的化感效应

Fig. 6 Allelopathic effects of cinnamic acid on MDA content in roots of cucumber seedlings cultured in open field soil

表 2 苯丙烯酸对黄瓜幼苗电解质外渗的影响

Table 2 Effects of cinnamic acid on permeability of plasma membrane in leaves of cucumber seedlings				
处理浓度 Treatment concentration (mg/kg)	大棚土培 Culture in greenhouse soil		露地土培 Culture in open field soil	
	相对电导率(%)	伤害率(%)	相对电导率(%)	伤害率(%)
	Relative conductivity rate	Rate of injury	Relative conductivity rate	Rate of injury
0	32.45±4.01d		35.45±3.62c	
25	32.63±4.24d	2.54±1.22D	36.03±3.72c	3.56±1.46C
50	36.59±3.83c	8.12±2.08C	36.29±4.41c	2.67±1.12C
100	41.01±5.22b	15.16±3.21B	42.23±4.50b	7.73±3.66B
200	48.78±6.03a	34.56±5.09A	49.52±5.00a	14.17±3.68A

* 同一列数据中不同字母表示差异显著,小写字母表示 $p<0.05$,大写字母表示 $p<0.01$ Numbers in the same column with different letters indicate a significant difference; The minuscule represent $p<0.05$, The capital represent $p<0.01$

的清除能力,因此,导致膜脂过氧化产物 MDA 含量的增加,膜系统受损,电解质外渗。

苯丙烯酸对大棚土培的化感强度大于露地土培的化感强度,如大棚和露地土培幼苗电解质外渗率产生差异显著性作用的浓度分别为 50 mg/kg 和 100 mg/kg,说明大棚土培的自毒临界浓度比露地土培低的多,其原因可能一是种植 18a 黄瓜的大棚土壤中已积累了一定的酚酸类物质,外加酚酸后比没有酚酸积累的露地土壤的更易达到临界浓度;二是酚酸自毒作用强度与土壤环境密切相关,如 pH、EC 值^[22]等,EC 值越大、pH 越小,自毒作用越强。从表 1 中可知,大棚土壤的 EC 值大于露地土壤,pH 值小于露地土壤,因此,大棚土培的自毒作用强度大于露地土培,外加同等浓度的酚酸后,仍然是大棚大于露地。此外,酚酸物质进入土壤后,由于土壤的吸附、螯合以及微生物的作用,酚酸物质可能会发生数量和结构的变化,从而会影响它们的化感效应^[23~25],关于苯丙烯酸进入不同土壤后的动态变化还有待于进一步研究。

本文是通过室内模拟实验研究了苯丙烯酸对黄瓜幼苗膜脂过氧化的影响,与实际生产还存在一定的差距,而且实际设施连作土壤中的酚酸类物质不是只有苯丙烯酸,因此,设施连作土壤中的酚酸种类和实际浓度还有待进一步研究。

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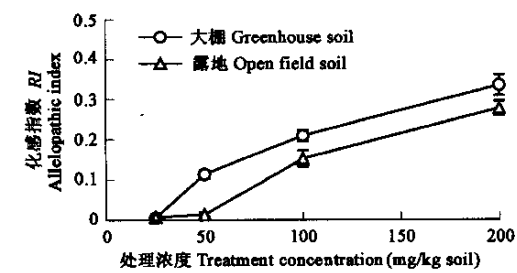


图 7 苯丙烯酸对土培黄瓜幼苗叶片相对电导率的化感效应
Fig. 7 Allelopathic effects of cinnamic acid on permeability of plasma membrane in leaves of cucumber seedlings cultured in soil

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