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METABOLITES OF THE PATHOGENIC FUNGUS *Verticillium dahliae*.

X. INDUCTION OF PHYTOALEXINS IN THE COTTON PLANT BY METABOLITES IN THE PATHOGEN

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The capacity of ten metabolites isolated from the culture liquid and mycelium of the phytopathogenic fungus *Verticillium dahliae* Kleb. and identified by chemical and spectral methods or of known chemical nature for inducing the synthesis and accumulation of phytoalexins in the cotton plant has been investigated for the first time. It has been established that the maximum inducing capacity among the metabolites investigated in the concentrations tried is possessed by elaidic acid and di-2-ethylhexyl phthalate. A considerable amount of phytoalexins is also induced under the action on the cotton plant of PCL-1 and a substance of carbohydrate nature. In view of the inducing capacity of the lipid component the protein-lipoid-polysaccharide complex we have studied its total lipid and fatty acid compositions. It has been shown that the compositions of the classes of neutral lipids of the protein-lipoid-polysaccharide complex of the mycelium and the culture liquid do not differ fundamentally, while there are certain differences in the qualitative composition and quantitative amounts of fatty acids of the protein-lipoid-polysaccharide complex and of the culture liquid, with the exception of the $C_{16:0}$ and $C_{18:0}$ acids, the amounts of which are approximately the same.

The lipids and secondary metabolites (phytotoxins etc.) of the fungus *Verticillium dahliae* Kleb. play an important role in the pathogenesis of cotton wilt. With the aid of metabolites of phytophathogenic microorganisms it is possible to induce resistance of plants to diseases [1-7]. We have established previously that the capacity for evoking protective reactions of the cotton plant to wilt is possessed by a high-molecular-weight protein-lipoid-polysaccharide complex (PLPC) of *V. dahliae* and its individual components [8, 9].

In the present paper we give the results of further investigations of the metabolites of *V. dahliae* as inductors of the synthesis and accumulation of phytoalexins in the cotton plant.

The metabolites (I), (III), (IV) from the mycelium and (VII)-(X) from the culture liquid (CL) of *V. dahliae* were isolated and identified by the method described previously (see the literature to Table 1), and the method of isolation and information on the chemical na-

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ture of the metabolites (II) and (V) and the unidentified substance of the mycelium (VI) are given in the experimental part. Synthetic 9,10-dichlorostearic acid and the reagent trans-oleic (elaidic) acid were used.

The capacity for inducing phytoalexins under the action of the substances given above was determined on cotton plants of the varieties Tashkent-1 and Tashkent-2 grown on a sterilized substrate. The quantitative determination of the phytoalexins in the cotton plants was made by the TLC method on Silufol plates in the systems described previously [10]. The results of the determinations are given in Table 1.

It follows from Table 1 that the maximum amount of phytoalexins in the cotton plant is induced under the action, in the concentration shown, of PLPC, which is, according to the literature [7], a phytotoxic metabolite of *V. dahliae* and of its lipid component.

The inducing capacity of the PLPC of *V. dahliae* as of other high-molecular-weight inductors such as the lipoglycoprotein (LPG) from *Phytophthora infestans* [18, 19] etc., is apparently due mainly to their lipid component. There is little information in the literature on the lipid component of the PLPC — only the composition of its fatty acids (FAs) from the culture liquid has been determined [20].

We have established that the bulk of the lipids in the PLPC, as in LGP [18] are present in the bound form, and consists of the sum of the FAs, which can be separated by acid hydrolysis. However, chemically nonbound neutral lipids (NLs) have also been detected in the composition of the lipid component of the PLPC. There are statements that the inducing action of the LGP is connected with the neutral lipids since after their separation by extraction with solvents the LGP has lost its capacity for inducing phytoalexins, while the isolated neutral lipids do show this capacity [3].

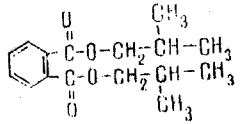
In the case of *V. dahliae* the inducing capacity is likewise, apparently, connected with the natural lipids of the PLPC of the mycelium in the culture liquid and it was therefore necessary to make a comparative study of just these neutral lipids. The method of isolating the PLPC from strain 614 and the lipid component from it by acid hydrolysis has been described previously [21]. Hydrolysis gave the total fatty acids (i.e., the "bound lipids") and the neutral lipids. The composition of the classes of neutral lipids was determined by the TLC method [22] from their R_f values in systems 1 and 2, and on the basis of their IR and PMR spectra. The quantitative ratio of the fractions as determined gravimetrically.

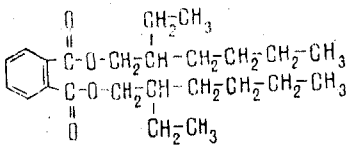
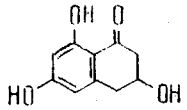
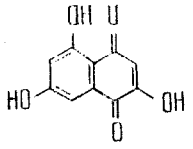
The composition of the total lipids of the PLPC of *V. dahliae* is as follows (%):

Class of Lipids	R_f	Mycelium	Culture Liquid
Carbohydrates (V)	0.90	2.4	2.8
Triacylglycerols (TGs)	0.57	26.0	21.3
Free fatty acids (FFAs)	0.50	67.3	73.0
Not identified	0.33	0.5	1.1
Free sterols (FSs)	0.25	1.8	0.8
Not identified	0.18	1.2	0.7
Not identified	0.00	0.8	0.3

The high content of the fraction identified as free fatty acids is due to the fact that it consists of the fatty acids of the "bound" and the neutral lipids. The other classes of lipids identified in the composition of the lipid component of the PLPC may be regarded as belonging to the neutral lipids. As follows from the figures given above, the compositions of the classes of neutral lipids of the PLPC of the mycelium and the culture liquid do not differ appreciably. The composition of the lipid component of the PLPC changes according to the method of extraction of the "bound" lipids — hydrolysis with 1% CH_3COOH [22] or with 1 N HCl [18]. Depending on the method used, the acid-containing fractions of the PLPC are hydrolyzed dissimilarly, which is reflected in the relative amount and qualitative composition of the fatty acids. The compositions of the intra- and extracellular lipids of strain 614 from which the PLPC was isolated have not been determined. However, by comparing our results with the compositions of the lipids of virulent and avirulent wild strains and mutants of *V. dahliae* [13, 16] it is possible to conclude that the composition of the lipid component of the PLPC from the mycelium differs from the composition of the fungal mycelium itself only by the absence of methyl esters of fatty acids. This is probably due to a difference in the strains investigated and in the conditions of their cultivation. The results of a determination of the qualitative composition and quantitative amounts of the acids of the PLPC iso-

TABLE 1. Accumulation of Phytoalexins in the Cotton Plant Induced by Metabolites of *Verticillium dahliae*

Inductor	Structure	Source of isolation	Concentration of inductor	Concentration of phytoalexins, μg/g of tissue	Literature
Suspension of spores, pathogenic strain	Sum	Strain V_1	10 μg/ml	84,7—88,6 (sativane)	[11]
Suspension of spores, non-pathogenic strain	Sum	Strain V_2	10 μg/ml	45,9—48,8 (sativane)	[11]
PLPC	Not determined	Mycelium, strain of the Yangi-Yul' population	2 mg/ml	30,5±0,8 (hemigos-sypol)	[8]
Polysaccharide component of the PLPC	"	"	2 mg/ml	25,0±0,5 (hemigos-sypol)	[8]
Protein component of the PLPC	"	"	2 mg/ml	21,2±0,3 (hemigos-sypol)	[8]
Lipid component of the PLPC	Sum	"	0,2 mg/ml	77,9±1,3 (hemigos-sypol)	[8]
9,10-Dihydroxystearic acid	$CH_3-(CH_2)_7CH(Cl)-CH(Cl)-(CH_2)_7COOH$ (I)	Mycelium, strain L-1	3,5 mM 35,4 mM	— —	[15]
Elaidic acid	$CH_3-(CH_2)_7-C(H)=C(H)-(CH_2)_7-COOH$ (II)	Mycelium, strain L-1	1,4 mM 2,3 mM 2,9 mM	8,7 9,7 11,2 (hemigossypol)	
Halogen-containing compound	Not determined (III)	Mycelium, strain L-1	1 mg/ml 10 mg/ml	Tr. + (hemigossypol)	[17]
Diisobutyl phthalate	 (IV)	Mycelium, strain L-1	3,54 mM 35,61 mM	Tr. + (hemigossypol)	[16]
Substance of hydrocarbon nature	Not determined (V)	Mycelium, strain L-1	0,05 % 0,08 %	11,0 14,49 (hemigossypol)	

Unidentified substance	Not determined (VI)	Mycelium, strain L-1	0,05 % 0,08 % 0,1 %	7,57 9,75 14,0 (hemigossypol)	
Di-2-ethylhexyl phthalate		CL, strain L-1	1,30 mM 2,05 mM	7,5 16,25 (hemigossypol)	[12]
3,6,8-Trihydroxy-3,4-dihydro-1(2H)-napthalenone (scytalone)	(VII) 	CL, mutant P-196	5,15 mM 51,54 mM	Tr. (hemigossypol)	[13]
2,5,7-Trihydroxy-1,4-naphthoquinone (flaviolin)	(VIII) 	Cl, strain XL 1, 3	4,85 mM 48,54 mM	Tr. + (hemigossypol)	[14]
PCL-1	(IX) Not determined (X)	Cl, strain L-1	0,2 mM 2 mM	+ ++ (hemigossypol)	[14]

Note. +) Synthesis of phytoalexins in the cotton plant observed; ++) amount of phytoalexins sufficient for suppressing the parasite; -) absence of activity.

lated by hydrolysis with 1% CH_3COOH are given below, and for comparison the fatty acid composition of the lipid component of the PLPC from the culture of *V. dahliae* determined previously [20] is also given (%, GLC):

Acid	Mycelium	FAs	FAs [20]
X_1	—	—	12,9
$C_{12:0}$	1,7	—	2,3
X_2	1,8	—	1,0
$C_{14:0}$	3,5	5,3	5,0
$C_{15:0}$	6,4	4,4	—
$C_{16:0}$	24,9	27,8	22,7
$C_{16:1}$	—	8,2	—
$C_{17:0}$	5,6	3,3	—
$C_{18:0}$	15,4	13,5	6,2
$C_{18:1}$	14,0	22,4	23,3
$C_{18:2}$	10,4	11,2	—
$C_{18:3}$	4,8	3,9	11,8
X_2	1,4	—	—
X_3	2,0	—	—
X_4	1,7	—	4,8
X_5	6,4	—	3,8

Thus, in qualitative and quantitative compositions the fatty acids of the lipid component of the PLPC from the mycelium and the culture liquid have definite differences, with the exception of the $C_{16:0}$ and $C_{18:0}$ acids, the amounts of which are approximately the same. In addition, it must be mentioned that the lipid components of the PLPC from the mycelium and the culture liquid contain a considerably smaller amount of unsaturated acids than the neutral lipids of the mycelium itself [13, 16]. The unbound fatty acids possess inducing properties [23, 24], and therefore it may be concluded that it is precisely the free fatty acids present in the neutral lipids from the PLPC that may exhibit them.

Spectral results (IR and PMR spectra) show the presence of a trans-unsaturated fatty acid in the free fatty acid fraction of the protein-lipoid polysaccharide complex from the mycelium. Taking into account the results that we have obtained on the reducing capacity of elaidic acid, it may be assumed that the action of the lipid fraction of the PLPC is connected with the presence of trans-unsaturated acids in it.

The inducing effect of the lipid component of the PLPC is apparently due not only to the free fatty acids from the neutral lipids but also to other lipid and lipophilic compounds. It was necessary to study the capacity of these substances for inducing the synthesis and accumulation of phytoalexins independently of the sources of their isolation, all the more since, as mentioned above, the composition of the neutral lipids of the PLPC does not differ appreciably from that of the neutral lipids of the mycelium itself, and an extract of lipids from the mycelium probably possesses inducing capacity, as is shown indirectly by information on this property of a lipid extract from the mycelium of *Phytophthora infestans* [25].

As we have reported previously [24], the lipid fractions from the mycelium and culture liquid of *V. dahliae* contain substances of aromatic nature (phthalates, naphthoquinones, and other pentaketides), and also some more polar lipid classes of organic compounds. A series of aromatic compounds and pentaketides possesses a phytotoxic action [24]. A series of aromatic compounds and pentaketides possesses a phytotoxic action [24]. As is well known, phytotoxic metabolites in concentrations below the threshold of their toxic action are capable of inducing the resistance of plants to diseases [6]. Consequently, in the first place as phytoalexin inductors we tested the polar compounds (II and IV-VI, see Table 1) from the mycelium of *V. dahliae*.

Compounds (II) and (V) and an unidentified substance (VI) proved to be the most active. The results obtained are in harmony with available information on the presence of phytoalexin inductors of similar nature [26, 27]. The protein-lipoid-polysaccharide complex from the culture liquid, just like the PLPC from the mycelium and the culture liquid itself of the majority of *Verticillium* isolates [28] induces the synthesis of terpenoid phytoalexins in the cotton plant. In selecting from the metabolites of the culture liquid compounds for testing as phytoalexin inductors we considered the results of investigations performed by ourselves previously on the metabolites of the culture liquid of virulent strains for which, in contrast to the avirulent strains, the production of extracellular lipids and specific second-

ary metabolites is characteristic [13, 29]. In the fraction of these extracellular metabolites we detected juglone [30] and compounds biogenetically related to it (flaviolin, etc.), and also various pigments. Tests for phytotoxicity showed that the most pronounced action of the cotton plant is possessed by solutions of the red pigment PCL-1 (X). For a number of avirulent mutants (P-196, brm-1 [13, 31], etc.) scytanol accumulates in considerable amount, no extracellular lipids and PCL-1 are produced, and the synthesis of melanin is blocked [31]. Thus, the production of PCL-1, flaviolin (IX), and di-2-ethylhexyl phthalate (VII) is characteristic for virulent strains and that of scytalone (VIII) is characteristic for avirulent strains. The comparative study of their inducing capacities was carried out by known methods [10]. It was found that, in actual fact, these phytotoxic metabolites from the culture liquid, just like compounds (II), (V), and (VI) from the mycelium, are, in concentrations below the toxicity threshold, inductors of phytoalexins in the cotton plant. A comparison of the capacity of these metabolites for inducing phytoalexins (Table 1) showed that the most effective are the phytotoxic pigment PCL-1 (X) and di-2-ethylhexyl phthalate (VII). A comparison of the inducing capacity of the individual components of the PCL-1, consisting of the peptide moiety bound to flaviolin and of free flaviolin (IX) gives grounds for considering that it is the peptide moiety of the molecule that is responsible for the given effect in this case, which agrees with literature information [26] on the presence of inductors of peptide nature in fungi. Scytalone (VIII) does not possess an appreciable inducing capacity in the concentrations tested.

Phytotoxic metabolites, such as PCL-1 (X) from the culture liquid of *V. dahliae*, fusaric acid from *Fusarium oxysporum*, and some others, when they act on the roots, stems, or leaves of the cotton plant, cause chemiluminescence the energy substrate of which consists of lipids [32, 33]. As a result of peroxidation processes that they induce in addition to the specific action, reactive oxygen-containing products (peroxides, free radicals, etc.) are formed in the tissues. Under these conditions, the metabolism of the cells of the plants changes, which leads to the formation of a whole group of biogenetically related substances possessing a greater or smaller degree of fungitoxicity [34]. In the case of the cotton plant, such compounds are biogenetically related to gossypol (Scheme 1) and their structure forms a taxonomic characteristic of the plant [35]. The same compounds are responsible for the antioxidant activity of cotton-plant tissues [32]. Consequently, it is possible that in some cases because of an increased synthesis of induced phytoalexins (Scheme 1) the actions of phytotoxins will lead to a decrease in the synthesis of gossypol. At the same time, because of the decrease in the synthesis of the antioxidant gossypol and in view of the participation of phytoalexins in the protective reaction of the cotton plant, the oxidizability of the lipids is greatly increased, a consequence of which is apparently the outburst of chemiluminescence observed under the action of phytotoxins.

At the present time, a number of publications has appeared which enable peroxides and free radicals to be assigned the role of initiators of the damage to plants by wilt [32, 36-39]. At concentrations below the toxicity threshold peroxides and free radicals are formed in very small amounts and the balance of antioxidants and lipids is maintained. At higher concentrations of phytotoxins oxidative enzyme systems, including oxygenase-bound cytochrome P-450 [40] are activated in the cells of the cotton plant and other higher plants. It must be expected that the compounds considered by us, also, in concentrations at which their phytotoxic action is shown will lead to an increase in the activity of oxidative enzyme systems, and at very high concentrations there may be an abandonment of enzymatic oxidation for the nonenzymatic (free-radical) route. Consequently, under the action of phytotoxins the free-radical) route. Consequently, under the action of phytotoxins the free-radical oxidation of lipids that is observed even in normally functioning tissue may be considerably activated, and this may lead to a pathological state — namely to the withering of the cotton plant, one of the phenomena of which is the reaction of "hypersensitivity" of the tissues to the pathogen (the formation of necroses on the leaves). This is also shown by information that has appeared in the literature on the connection of the hypersensitivity reaction with the oxidation of lipids [41, 42].

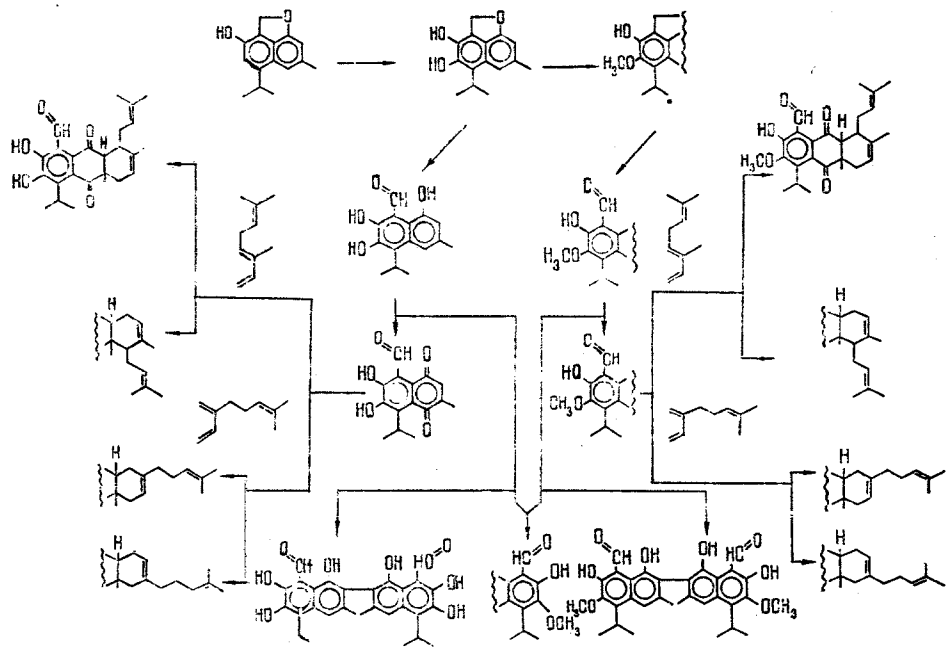
The results obtained permit a conclusion concerning possible measures for preventing the cotton plant from being affected by wilt by using metabolites of the phytopathogenic fungus *V. dahliae* as inductors of its protective reactions. These metabolites can be used for the pre-sowing treatment of the seeds or for the direct treatment of the cotton plants themselves.

EXPERIMENTAL

The conditions for recording the IR, PMR, and mass spectra were similar to those described previously [12, 16].

Cultures of *V. dahliae* of the Yangi-Yul' strain L-1 and strain 614 were investigated. The method of growing the fungus and the procedure for the primary treatment of the fungal mycelium and the culture liquid were similar to those described previously [16, 17].

The lipids were isolated by treating the liquid-nitrogen-fixed and carefully comminuted mycelium with 20 volumes of chloroform–methanol (2:1, v/v). The solvent was evaporated off in a IR-1M rotary evaporator. The chloroform–methanol extract was treated with hexane. This gave a hexane extract and a residue, and the evaporation of the hexane gave the neutral lipid fraction.



Scheme 1. Suggested route of the biosynthesis of antibiotic terpenoids of the cotton plant [28].

The neutral lipids were analyzed qualitatively and preparatively on silica gel L 5/40 + 1% of gypsum in the hexane–diethyl ether–acetic acid (70:30:1) system (system 1). The chromatograms were revealed by spraying the plates with 50% H_2SO_4 and heating them at 150°C. The analytical chromatography of the combined neutral lipids according to classes was also performed on Silufol plates in the heptane–methyl ethyl ketone–acetic acid (41:9:0.5) system (system 2) [43]. The spots were revealed with iodine vapor. The fatty acids were methylated with diazomethane.

The gas–liquid chromatography of the methyl esters of the fatty acids was performed on a Khrom-4 chromatography with a flame-ionization detector using a stainless steel column filled with Chromaton N-AW-DMCS with 15% of Reoplex 400. The column was 2.5 m long and its diameter 4 mm, temperature 198°C, rate of flow of carrier gas (helium) 62 ml/min, of H_2 60 ml/min, and of air 60 ml/min.

Trans-Oleic (elaidic) acid was identified in the free fatty acid fractions. After methylation with diazomethane the fatty acid esters obtained were separated by TLC on silica gel L5/40 with the addition of 10% gypsum and 3-5% of $AgNO_3$ (on the weight of the silica gel) in benzene (System 3). The substances were revealed with 50% H_2SO_4 followed by heating. The spots were identified by comparison with markers. A fraction that had solidified locally with R_f 0.82 was isolated.

The mass spectrum of the methyl ester isolated corresponded to the spectrum of the 18:1 methyl ester described in the literature [16]. The IR spectrum showed a strong absorption

band in the 970-960 cm^{-1} region (—C(H)=C(H)— -trans) [22]. The PMR spectrum of the fraction under investigation was identical with the spectrum of methyl elaidate in admixture with oleic acid in the same proportion of ∿3:1 in which it was obtained from the combined material. The ^{13}C NMR spectrum contained, in addition to the peaks characteristic for oleic acid, signals at 133.0 and 35.0 ppm unambiguously showing the presence of a trans- —CH=CH— group. In the IR spectrum of a hydrolysate of the PLPC the absorption band characteristic for the trans acid described above was observed, and in the PMR spectrum there were signals in the region of trans-olefinic protons which must obviously be assigned to the protons of elaidic acid.

Substance (V) was isolated from the residue of the chloroform—methanol extract obtained after the separation of the neutral lipids with the aid of hexane. The preparative thin-layer chromatography of the residue was carried out on silica gel L 5/40 + 1% of gypsum in the isopropanol—water (1:1, v/v) system (System 4) (R_f 0.55). The spots were revealed with an ammoniacal solution of $AgNO_3$. The substance was finally purified by recrystallization from methanol. In this process, substance (IV) remained in the mother liquor. The IR spectrum of (V) contained absorption bands at 1640 cm^{-1} (>C=O), and 3200-3400 cm^{-1} (br., —OH), which are characteristic for carbohydrates. The PMR spectrum of this compound has a complex multiplet in the region from 5 to 6 ppm, which also shows its carbohydrate nature. The signals of the ^{13}C nuclei in the ^{13}C NMR spectrum of this compund were located in the region characteristic for the carbon nuclei of carbohydrates (60-75 ppm).

The induction of phytoalexins was investigated on cotton plants of the varieties Tashkent-1 and Tashkent-2 (grown in vegetation vessels on sterilized vermiculite enriched with Belousov's nutrient medium [45]). In the phase of 6-8 true leaves, aqueous-aqueous alcoholic or Tween-80 solutions of the substances were introduced by means of sterile capillaries into the xylem vessels of the stem of the cotton plant. All the solutions tested were prepared in a wide range of concentrations (0.005-0.2%). The amount of solution introduced into each capillary was 0.15 ml. As controls we used plants without the introduction of the substance, plants infected with a suspension of spores of the fungus, and plants into the stems of which the solvent had been introduced. The experiment was performed in duplicate.

SUMMARY

The capacity of ten metabolites of the phytopathogenic fungus *V. dahliae*, of which three have been identified in the composition of the metabolite for the first time, for inducing the synthesis and accumulation of phytoalexins in the cotton plant has been investigated.

The total lipid composition of the protein-lipoid-polysaccharide complex of the fungus has been studied. It has been shown that the lipids of the complex from the mycelium and from the culture liquid of *V. dahliae* do not differ appreciably in composition.

It has been established that, of the metabolites investigated, in the concentrations tested, the maximum inducing capacity is possessed by elaidic acid and di-2-ethylhexyl phthalate and, to a smaller degree by the phytotoxic pigment PCL-1.

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