Novel Phosphoglucans from the Cytoplasm of Phytophthora palmivora and Their Selective Occurrence in Certain Life Cycle Stages*

Ming Chang Wang and Salomon Bartnicki-Garcia

From the Department of Plant Pathology, University of California, Riverside, California 92502

SUMMARY

The cytoplasm of Phytophthora palmivora is rich in soluble \( \beta-(1 \rightarrow 3) \)-glucans of which two different types can be recognized. The glucans extracted from the mycelium are all neutral molecules. In the asexual reproductive stages (sporangia, zoospores, and cysts) neutral glucan is also present but the main component is a family of novel phosphoglucans. By ion exchange chromatography, five different phosphoglucon fractions were detected with glucose to phosphate ratios ranging from 33:1 to 18:1. The phosphate was largely removed from the phosphoglucans by phosphonoesterases. Phosphodiesterase had no effect. On enzymatic dephosphorylation, all phosphoglucans yielded a neutral glucan similar to, if not identical with, the neutral glucan concurrently found in the cytoplasm. The mobility of phosphoglucans in gel filtration was highly affected by the ionic strength of the eluant. The phosphoglucans have an average degree of polymerization of \( \sim 30 \) and contain one or two phosphate groups linked by monooester linkage to the C-6 hydroxyl of a glucose residue(s). The absence of phosphoglucans in the mycelium, their subsequent appearance in the sporangia, and their partial utilization by the zoospores during encystment suggest that these polymers may play a major role in the biochemistry of cellular differentiation.

Previous studies from our laboratory indicated that \( \beta-(1 \rightarrow 3) \)-glucans play an important role in the biochemistry of differentiation of Phytophthora species. The mycelial walls of these fungi are made largely of \( \beta-(1 \rightarrow 3) \)-glucans (1-3). Cellulose is present but the predominant polymer is a highly insoluble, noncellulosic, \( \beta-(1 \rightarrow 3) \)-glucan with branches at C-6 (4, 5). The cytoplasm in the mycelium of Phytophthora cinnamomi contains no glycogen; instead, a soluble \( \beta-(1 \rightarrow 3) \)-glucan with branches at C-6 is the storage carbohydrate (6). A similar glucan was isolated from the mycelium of Phytophthora infestans (7) and appears to be present in other genera of the Oomycetes (8).

During cellular differentiation (encystment) or carbon starvation, cytoplasmic glucans are utilized for the synthesis of a new cell wall glucan. A preliminary study of the nature and metabolism of cytoplasmic glucans by encysting zoospores of Phytophthora palmivora revealed the presence of anionic glucose polymers (9). The present communication describes the initial characterization of these polymers as phosphoglucans and their selective occurrence in some developmental stages of the life cycle of P. palmivora (Fig. 1), namely, sporangia, zoospores, and cysts, and their absence from vegetative mycelium.

There are but few examples of phosphorylated glucans in nature (11). These include onuphic acid, a polymer of glucose phosphate isolated from the tube of a marine annelid (12-14), and a polysaccharide isolated from Mycobacterium tuberculosis made principally of repeating units of \( \alpha,\alpha'-\)trehalose 6,6'-diphosphate (15). In addition, the amylopectin from certain plant starches contains small amounts of phosphate bound in a monooester linkage to some glucose residues (16). Other phosphohexosans, e.g. phosphomannans (17-19), phosphogalactans (20), and phosphoglucogalactans (21), are produced by various yeasts. This appears to be the first account of phosphoglucans in fungi.

EXPERIMENTAL PROCEDURE

Microbiological Procedures—The test organism was a papaya strain of P. palmivora formerly designated as P. parasitica P 113 (9) and obtained through the courtesy of M. Aragaki (University of Hawaii). The methods described earlier (9) were routinely used for the maintenance of the organism and the production of mycelia and asexual propagules (sporangia, zoospores, and cysts). To minimize premature leakage of carbohydrate a slight modification was made in the zoospore-harvesting procedure, namely, the use of cold 70% ethanol (v/v) for washing the zoospore pellet.

Mycelia were grown in glucose-asparagine medium (100 ml per 500-ml Erlenmeyer flask) at 25° for 7 days with occasional shaking. Liquid cultures were inoculated with four 3-mm discs taken from the periphery of a mycelial colony (4 to 6 days old) grown on V-8 juice agar medium. Mycelial mats were collected on a sintered glass filter and rinsed several times with cold distilled water before extraction.

Extraction of Glucan Reserves—Zoospores, cysts, sporangia, or mycelia were suspended in 10 volumes of 70% ethanol, refluxed in a water bath at 97° for 20 min, cooled, and centrifuged. The pellet was rinsed once with 10 volumes of 70% ethanol. The
supernatant and the washing were combined. The residue was suspended in 10 volumes of water and heated at 97°C for 20 min. The supernatant and the single washing that followed were combined. These ethanol and water extracts (up to 50 ml each) were pooled together and dialyzed against 4 liters of distilled water overnight at 20°C. The nondialyzable portion was used for fractionation as described below.

**Fractionation and Purification of Anionic Polysaccharides**—DEAE-Sephadex, A-25, Cl⁻ form, was equilibrated against 5 mM Tris-HCl buffer, pH 7.6, and packed into a column (2 x 30 cm). The nondialyzable glucan fraction was directly applied to the column and rinsed with 200 ml of 5 mM Tris-HCl buffer, pH 7.6. Anionic glucans were eluted by a two-step linear gradient (in Tris buffer): first, a 1000-ml gradient from 0 to 0.3 M NaCl; second, a 500-ml gradient of 0.3 to 0.6 M NaCl. Fractions of 8 ml were collected; their ultraviolet light absorbance and their carbohydrate content (anthrone) were determined.

The eluates of each major carbohydrate fraction were freeze-dried, dissolved in approximately 20 ml of distilled water, and dialyzed against several changes of distilled water at room temperature. Each fraction was concentrated and applied, in 2.0 ml of water, onto a Sephadex G-75 column (1.8 X 105 cm; void volume = 87 ml) and eluted with distilled water; 3-ml fractions were collected. Purified phosphoglucons were then decalcinated through a column (1.8 X 5.0 cm) on Dowex 50 (H⁺ form), concentrated to 2 to 3 ml, and subjected to a second gel filtration in Sephadex G-75.

A phosphomannan from *Pichia pinus* NRRT. Y-2579, a gift of M. E. Slodki (United States Department of Agriculture, Northern Utilization Research and Development Division, Peoria, Illinois) was also purified by DEAE-Sephadex chromatography as above for use in enzymatic digestion studies. A purified phosphomannan from *Kloeckera brevis* was kindly supplied by C. E. Ballou (University of California, Berkeley).

**Chemical Methods**—Total carbohydrate was determined with anthrone reagent (22) using α-glucose as a standard. Glucose was assayed with glucose oxidase (Glucostat “Special,” Worthington Biochemical Corp., Freehold, New Jersey). Reducing end group determinations were made by the Somogy-Nelson colorimetric method (23). Inorganic and total phosphate were estimated by the method of Dryer et al. (24).

Complete hydrolysis of glucans was done by pre-soaking in 70% H₂SO₄ (w/v) for 3 hours at 20°C, diluting the acid to 0.85 N, and then heating to 105°C for 10 hours. Hexoses in the hydrolysates were converted to the corresponding alditol hexaacetates; these were separated and quantitated in a Perkin-Elmer gas chromatograph, model 990, using a Pyrex glass column (3 mm inner diameter X 180 cm) packed with Gas-chrom Q 100/120 mesh and coated with 3% ECNSS-M (25).

Partial acid hydrolysis was performed with 0.2 or 1 N HCl at 97°C for 1 hour. The hydrolysate was neutralized with 1 N KOH and the products of hydrolysis were separated by gel filtration on a Sephadex G-15 column (2.5 X 166 cm) equilibrated with H₂O. Fractions of 4 ml were collected and their carbohydrate content was assayed with anthrone.

**Physical Methods**—Optical rotation was measured with a Bendix automatic polarimeter, model 1100. Ultraviolet light absorption spectra of glucans in aqueous solutions were scanned with a Beckman DB spectrophotometer. Estimates of molecular weight were made by gel filtration according to the procedure of Arturson and Granath (26) using a Sephadex G-75 column calibrated with *Leuconostoc mesenteroides* dextrans: T 40 (Mw = 42,400), T 20 (Mw = 22,300), and T 10 (Mw = 9,300) purchased from Pharmacia A.B., Uppsala, Sweden.

**Enzymatic Digestions**—Phosphoglucons were digested by purified acid phosphatase (potato; Calbiochem), alkaline phosphatase (intestinal; Calbiochem), phosphodiesterase (spleen; Worthington Biochemical Corp.), and phospholipase C (Sigma Chemical Co.).

The mixture for digestion with acid phosphatase contained 1 mg of phosphoglucon and 1 mg of acid phosphatase in 4 ml of 0.04 M sodium acetate buffer, pH 4.2; the mixture was incubated at 30°C for 3 hours. Phosphoglucons (1 mg) were also incubated with 1 mg of alkaline phosphatase, 20 μmoles of MgCl₂, and 0.02 μM Tris-HCl buffer, pH 7.6, in a final volume of 4 ml at 30°C for 3 hours. The incubation of phosphoglucons (1 mg) with spleen phosphodiesterase (1.7 units) was done in 4 ml of 0.075 M Tris-HCl buffer, pH 7.6, at 30°C for 1 hour. The possibility that the acid or alkaline phosphatase preparations contained phosphodiesterase activity was tested against RNA core (27, 28).

Phosphoglucons (1 mg) were digested with phospholipase C (1 mg) and CaCl₂ (10 μmoles), in 0.05 M Tris-HCl buffer, pH 7.6, in a final volume of 4.0 ml at 30°C for 1 hour.

After digestion with the above enzymes, the reaction mixtures were heated at 97°C for 3 min and assayed by the following two methods: (a) to detect dephosphorylated products, the reaction mixtures were passed through a column of Dowex 1 (acetate form) and the amount of neutral glucan in the filtrate was determined by the anthrone method; (b) to detect changes in molecular dimensions the reaction mixtures were first freeze-dried, redissolved in 2 ml of water, and then fractionated by gel filtration on Sephadex G-75 as already described.

Glucose 6-phosphate was assayed in a neutralized (NaOH) acid hydrolysate of phosphoglucon using a spectrophotometric assay with glucose 6-phosphate dehydrogenase (29, 30). The enzyme was a purified preparation kindly supplied by D. Holten from the Biochemistry Department (31).

**RESULTS AND DISCUSSION**

**Extraction and Fractionation of Cytoplasmic Glucans**—Preliminary investigations indicated important differences in the properties of cytoplasmic glucans from different stages in the life cycle of *Phytophthora palmivora*. The asexual life cycle of *Phytophthora palmivora* is shown in Fig. 1.
FIG. 2. Ion exchange chromatography profiles of soluble glucans from the cytoplasm of four different stages in the life cycle of *Phytophthora*. The glucan fractions were isolated as indicated in the text and chromatographed on DEAE-Sephadex columns. Arrows indicate application of sample (S), rinse with Tris buffer (R), first gradient of 0 to 0.3 M NaCl (I), and second gradient of 0.3 to 0.6 M NaCl (II). Fractions were 8 ml. Absorbance values represent glucan concentration as determined with anthrone reagent; values were normalized so that in all four graphs the sum total of neutral glucan (N) and phosphoglucans (P I to P V) is the same.

## TABLE I

<table>
<thead>
<tr>
<th>Soluble Glucans</th>
<th>% Cell Dry Wt</th>
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<tbody>
<tr>
<td>Mycelium</td>
<td>Sporangia</td>
</tr>
<tr>
<td>Neutral</td>
<td>33.56 ± 0.10</td>
</tr>
<tr>
<td>Anionic</td>
<td>Nil</td>
</tr>
<tr>
<td>Total</td>
<td>33.56 ± 0.10</td>
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Properties and Characterization of Anionic Glucans—Most of the characterization work was done with polysaccharides isolated consistently detected in the extracts from zoospores and cysts (Fig. 2). In the sporangial sample, there were well defined peaks for P I, P II, and P III, but the other two components, if present, did not show up as peaks (Fig. 2). P-III was the major phosphoglucon component in zoospores and cysts but not in sporangia.

As a reference compound, the phosphomannan of *Pisca pinus* (32) was chromatographed on DEAE-Sephadex under identical conditions and found to elute at about the same place as P-IV.

The proportions of neutral and acidic glucans were obtained from DEAE-Sephadex fractionations as shown in Fig. 2. Values represent the mean ± S.D. of several fractions (five for zoospores, three for cysts and sporangia, two for mycelium).
Sephadex column—the least strongly adsorbed glucans had less adsorbed by Dowex 1 (acetate form).

...from zoospores. Following separation on DEAE-Sephadex, each fraction (Fig. 2) was subjected to one or two cycles of gel filtration and deacetylation. Only small amounts of purified phosphoglucans were available for these studies; e.g. the final yield of zoospore phosphoglucan, P-III, from 100 Petri dish cultures was about 10 mg.

The anionic glucans (P-I to P-V from zoospores or cysts) in aqueous solutions, at pH 4.0, were adsorbed onto Dowex 1 (acetate form) but not onto Dowex 50 (H₄ form) columns. The purified anionic glucans from zoospores (P-I to P-V) showed no ultraviolet light absorption maxima in the region 210 to 340 nm and were free of contaminating nucleic acid and protein. Upon acid hydrolysis, all five anionic glucan fractions from zoospores yielded glucose as the sole monosaccharide. This was established by gas-liquid chromatography separation of alditol acetates. Also, a determination of glucose with glucose oxidase and subjected to a second, longer treatment (8 hours) with the enzyme; again about two-thirds of the material underwent dephosphorylation. These results indicate that most, perhaps all, of the phosphate is bound to the glucan by monoester linkage. The exact reason for the inability of the alkaline phosphatase to remove all phosphate groups is not known. Other workers also found that phosphomonoesterases fail to split off all of the predicted phosphate monoesters in onuphic acid (13) or potato starch (33). During storage at 1°C and handling in solution, it went partial conversion to neutral glucan. Up to 65% of P-I was thus degraded. Decomposition was minimized by storing samples in the freeze-dried state. Thus, P-I suffered only 15% conversion and with the other phosphoglucans only a small percentage, if any, was converted to neutral glucan. This is evident in Fig. 3 where the P-III and P-IV samples show a minor peak of neutral glucan (before digestion with phosphatase). It is not certain whether this degradation results from contaminating enzymes or spontaneous hydrolysis of some labile phosphate groups.

Characterization of Anionic Glucans as Phosphoglucans—Significant amounts of phosphate were found in all anionic glucans (Table II). The phosphate content of the various phosphoglucans, determined after the first cycle of gel filtration, fluctuated from 13 to 24 glucose residues per phosphate mole. After decationization followed by a second gel filtration, higher ratios were obtained, 18:1 to 33:1. This increase probably reflects the removal of phosphate-containing contaminants, although the possibility of depolymerization during handling cannot be ruled out (see below). Also, exact phosphate values were difficult to determine in the small samples available. Nevertheless, after the second gel filtration, the ratio of glucose to phosphate correlated with the order of elution from the DEAE-Sephadex column—the least strongly adsorbed glucans had less phosphate than the more strongly adsorbed ones. The neutral glucans had no detectable phosphate (>0.1%) and were not adsorbed by Dowex 1 (acetate form).

The phosphorylated nature of these anionic glucans was confirmed by digestion with either acid or alkaline phosphatase which converted a major part of the phosphoglucans into neutral glucan (Table III and Fig. 3). Spleen phosphodiesterase and phospholipase C had little or no such effect (Table III). A mixture of P-III and P-IV from zoospores was digested for 8 hours with phosphodiesterase and then subjected to gel filtration on Sephadex G-75 equilibrated with 50 mm glycine-HCl buffer (pH 3.5). There was no evidence of phosphoglucone cleavage into smaller molecular fragments.

The alkaline phosphatase-resistant fractions from P-II, P-III, and P-IV were separated by gel filtration (Fig. 3), combined, and subjected to a second, longer treatment (8 hours) with the enzyme; again about two-thirds of the material underwent dephosphorylation. These results indicate that most, perhaps all, of the phosphate is bound to the glucan by monoester linkage. The exact reason for the inability of the alkaline phosphatase to remove all phosphate groups is not known. Other workers also found that phosphomonoesterases fail to split off all of the predicted phosphate monoesters in onuphic acid (13) or potato starch (33). During storage at 1°C and handling in solution, it was observed that the phosphoglucans, particularly P-I, underwent partial conversion to neutral glucan. Up to 66% of P-I was thus degraded. Decomposition was minimized by storing samples in the freeze-dried state. Thus, P-I suffered only 15% conversion and with the other phosphoglucans only a small percentage, if any, was converted to neutral glucan. This is evident in Fig. 3 where the P-III and P-IV samples show a minor peak of neutral glucan (before digestion with phosphatase).

Interestingly, after removal of phosphate by phosphomonoesterase digestion there was a sharp change in the gel filtration mobility of the glucan; the broad, asymmetrical fast moving peak of phosphoglucon was converted to a sharp, symmetrical slower moving peak of neutral glucan which eluted at the same place as the neutral glucan originally present in the cytoplasm (Fig. 3). This glucan product was not adsorbed by Dowex 1 (acetate form), an indication that it was fully dephosphorylated. The drastic change in gel filtration mobility following depoe
Phosphoglucan was initially regarded as evidence of depolymerization of the phosphoglucons and, hence, the possibility was considered that the phosphoglucons were chains of neutral glucan "subunits" linked by phosphodiester bridges. This idea could not be experimentally confirmed. First, as shown above, spleen phosphodiesterase had no effect on the P. palmivora phosphoglucons. Second, the possibility that the phosphomonoesterase preparations employed had some phosphodiesterase activity was unlikely since neither the acid nor the alkaline phosphatase degraded RNA core. Moreover, phosphomannans of Pichia pinus (32) or K. brevis (19), with bona fide phosphodiester linkages, were not attacked by acid or alkaline phosphatase when tested under the same conditions as shown in Table III.

Eventually, we discovered that the disparity in gel filtration mobility between the phosphoglucons and the neutral glucan did not represent a change in degree of polymerization of the glucan but anomalous gel filtration behavior of the phosphoglucons under the conditions employed (see next section).

**Molecular Weight and Behavior on Gel Filtration**—The neutral glucans isolated from mycelium, sporangia, zoospores, or cysts gave a sharp symmetrical peak when passed through a Sephadex G-75 column equilibrated with distilled water (Fig. 4). The mobility of these glucans corresponds to $M_w \approx 5000 \pm 300$ (degree of polymerization $\sim 30$) using a column calibrated with L. mesenteroides dextrans.

By contrast, each of the five different phosphoglucon fractions (dissolved in distilled water) gave asymmetrical elution profiles on the same column (Fig. 3) and eluted much earlier than the neutral glucan. Initially, this was considered as evidence of greater molecular size and dispersity (10) of the phosphoglucons as compared to the neutral glucan. However, when the phosphoglucons were subjected to gel filtration in 50 mM glycine-HCl buffer at pH 3.5 or 50 mM glycine-NaOH buffer at pH 9.5, they all behaved as homogenous substances and they eluted as sharp peaks slightly ahead of the neutral glucan (e.g., Fig. 5) to give the apparent molecular weight $M_w$ estimates shown in Table II. Conceivably, the anomalous migration of the phosphoglucon in the salt-free environment was due to ionic interaction with residual anions in the Sephadex gel (34) which partially blocked the movement of the polymer into the gel particles, an interaction nullified by raising the ionic strength of the medium.

It is also conceivable that changes in ionic strength brought about marked alterations in the shape, size, and solvation of the phosphoglucon molecules and that these were largely responsible for their unusual behavior in gel filtration. Skalka (35), who found that ionic strength greatly influenced the migration of heparin through Sephadex columns, favored the latter explanation. Likewise, the gel filtration properties of brain sialomucopolysaccharides, another example of an anionic polysaccharide, are markedly dependent on ionic strength (36). The abnormal behavior of the phosphoglucons of *P. palmivora* in Sephadex

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**Fig. 3.** Gel filtration profiles of phosphoglucon fractions P-III and P-IV before (●) and after (○) digestion with alkaline phosphatase. (P-I and P-II gave similar results; P-V was not tested). Separation was on a Sephadex G-75 column equilibrated with distilled water. Fractions of 3 ml were collected and their glucan content was determined with anthrone reagent. The peaks at Fraction 61 correspond to neutral glucan.

**Fig. 4.** Gel filtration profile of the neutral glucan from zoospores. Separation on Sephadex G-75 column equilibrated with distilled water. (Neutral glucans isolated from mycelium, sporangia, and cysts yielded nearly identical profiles.)
from zoospores. Separation on a column of Sephadex G-75 equilibrated with 50 mM glycine-HCl buffer at pH 3.5. (A similar behavior was noticed for P-I, P-II, P-IV, and P-V.)

G-75 columns eluted with distilled water is advantageous in one respect—it permits a clean cut separation of phosphoglucan from neutral glucan (Fig. 3). Otherwise, with eluants of higher ionic strength, the two polymers would run very close to each other, making their separation impractical.

Determination of number average molecular weight, $M_n$, by reducing end group determination (Somogyi-Nelson), indicated that the neutral glucan had an $M_n$ of 5600 corresponding to an average degree of polymerization of 36. The $M_n$ values for the five different phosphoglucans from zoospores were in the range 7600 to 7900 and therefore substantially higher than the corresponding $M_n$ estimates (Table II). This reversal of the expected relationship ($M_n > M_w$) probably arises from an overestimation of $M_w$ due to a lower color rendition from a mole of phosphoglucan as compared to a mole of glucose standard. However, the possibility that $M_w$ values are at fault cannot be ruled out; the accuracy of the $M_w$ determinations depends on how closely the $\beta-(1 \rightarrow 3)$-glucans studied here resemble, in molecular shape and density (34), the L. mesenteroides dextrans used as standards; this point has not yet been established.

Acid Hydrolysis of Phosphoglucans—Neither loss of anionic property (lack of adsorption onto Dowex 1 (acetate form)) nor cleavage of glucosyl bonds (increase of reducing power by Somogyi-Nelson) was observed when autohydrolysis was attempted on the dephosphorylated glucans isolated from P-II, P-III, and P-IV (as in Fig. 3) gave almost the same ratios of methylated glucose derivatives as the neutral glucan isolated from the zoospores. Both of these glucans are $\beta-(1 \rightarrow 3)$-linked polymers with a single branch at C-6 and $M_w \sim 5000$ (average degree of polymerization $\sim 30$). In the phosphoglucan, 1 or 2 glucose residues are esterified at C-6 with a phosphoryl residue via monoester linkage. Since, at most, two phosphate groups are present per glucan molecule (Table II), the occurrence of five different phosphoglucan fractions necessitates further explanation. Conceivably, the multiplicity of fractions (Fig. 2) results from differences in the location of the phosphorylated glucose residue(s) in the polymer, or, perhaps, from differences in the fine structure of the glucan.

The phosphoglucans of P. palmivora appear to be a new kind of phosphorylated homoglucon significantly different from other phosphoglucans of natural origin (see introductory section) in two or more of the following properties: molecular weight, glucosidic linkages, glucose to phosphate ratio, absence of phosphodiester linkages, and absence of monosaccharides other than glucose.

Biological Significance—Cytoplasmic glucans comprise a quantitatively major portion of the dry weight of P. palmivora (Table I) and appear to be actively mobilized during differentiation (9). The neutral glucan found in the mycelium represents one-third of the total dry weight. In two subsequent developmental stages of the fungus (sporangia and zoospores), the total amount of soluble glucan in the cell remains high (20 to 25% dry weight). In these stages, particularly the zoospore, the principal polysaccharides are phosphoglucans. There appears to be a progression in the accumulation of the different phosphoglucan fractions. In the sporangia, P-I and P-II predominate but in the next stage (zoospore) P III and P IV become evident components. Finally, in the conversion of zoospores to mature cysts, we see a 50% decrease in the total soluble glucan content (Table I); both phosphoglucan and neutral glucan are partly consumed during encystment. This is not surprising since encystment takes place in the absence of nutrients and, as shown

earlier, cyst wall formation is dependent on internal glucan reserves (9). Eventually, the phosphoglucan of the cyst must be completely consumed (or diluted out), for none can be detected in the mycelium. This sequence of appearance and disappearance of phosphoglucans during the asexual life cycle of P. palmivora suggests a major role of these polymers in biochemical differentiation.

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Phosphoglucans were also absent in the mycelium of Phytoph-\nhora cinnamomi and Phytophthora parasitica (to be published).
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