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Wrap-and-plant technology to manage sustainably potato cyst nematodes in East Africa

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Renewable eco-friendly options for crop protection are fundamental in achieving sustainable agriculture. Here, we demonstrate the use of a biodegradable lignocellulosic banana-paper matrix as a seed wrap for the protection of potato plants against potato cyst nematode (PCN), *Globodera rostochiensis*. Potato cyst nematodes are devastating quarantine pests of potato globally. In East Africa, *G. rostochiensis* has recently emerged as a serious threat to potato production. Wrapping seed potatoes within the lignocellulose banana-paper matrix substantially reduced *G. rostochiensis* field inoculum and increased potato yields by up to fivefold in Kenya, relative to farmer practice, whether or not impregnated with ultra-low doses of the nematicide abamectin (ABM). Markedly, ABM-treated banana paper at ~1,000 times lower than conventional recommendations reduced PCN inoculum. Assays and analyses revealed that the lignocellulose matrix disrupts parasite–host chemical signalling by adsorbing critical PCN hatching and infective juvenile host location chemicals present in potato root exudate. Recovery experiments confirmed adsorption of these host location chemicals. Our study demonstrates the use of waste organic material to sustainably manage PCN, and potentially other crop root pests, while increasing potato yields.

Potato (*Solanum tuberosum*) is a major food crop worldwide. In sub-Saharan Africa, it is a key source of income for millions of smallholder farmers[1], where pests and diseases are persistent production constraints[2]. In East Africa, potato is currently under threat from potato cyst nematodes (PCNs; *Globodera rostochiensis*), destructive quarantine pests recently detected in Kenya, Rwanda and Uganda[3–5]. In Kenya, *G. pallida* has also been recorded[4], but in only a small number of fields, while *G. rostochiensis* is highly prevalent and has caused substantial production declines of ~60%;[6] extrapolations from models indicate alarming losses, in the range of 4.2–21.8 t ha^{-1} (ref. [7]). The prevailing subtropical conditions, with successive cropping of a susceptible cultivar, has led to particularly high PCN densities[7]. With marked declines in potato productivity, farmers are pushed to clearing forests, in an unsustainable manner, to create more productive fields free of PCN and other pests. With extensive cross-border trade of potato between countries in East Africa, *G. rostochiensis* is being viewed as a pest of regional importance[8].

Globally, PCN is subject to strict phytosanitary regulations[9]. The life cycle comprises an infective juvenile hatching from the egg to infect host roots, where they establish a fixed feeding site for the developing female. Females produce 300–500 eggs within their body cavity, which swells and hardens into an outer protective casing, the cyst, as they mature (and die) protecting the eggs against environmental and biological stresses, in addition to pesticides. To hatch, the eggs respond to chemical cues from host root exudates; in the absence of a host, they can remain dormant in the soil for many years. They are consequently intractable pests and difficult to manage[7,10–12]. Despite internationally coordinated efforts, PCNs continue to plague potato crops worldwide, although some successes in their management have been observed[13–15]. Synthetic nematicides, such as abamectin (ABM), can be effective, but the protective cysts of PCNs limit their impact[16,17]. Adoptable, innovative solutions that are environmentally benign, safe to use, profitable and applicable to smallholder farming systems are therefore desperately needed. The special host–pest relationship of PCN, which relies on chemical cues to stimulate egg hatch and juvenile host location, presents potential management opportunities through targeting these vulnerable life stages[15,18,19].

Incorporation of renewable, eco-friendly crop protection options is a current approach towards the sustainable intensification of agriculture. Previous studies have demonstrated the potential of a biodegradable lignocellulosic matrix (LCM) to deliver microdoses of agrochemicals to the target rhizosphere[20–22]. A banana-fibre matrix, with its unique combination of lignin and cellulose, proved the most suitable substrate for ABM loading in the wrap and plant technology (W&P)[20]. The matrix allowed slow and sustained release of ABM over weeks, while remaining intact in the soil but allowing root propagation[20,22]. This approach can enable delivery of an effective dosage of ABM, which is otherwise known for its poor mobility in soil, up to 1,000 times less than the commercially recommended application rates of the registered product Tervigo[20]. The ABM-loaded LCM (ABM–LCM) provides a targeted delivery of high relative concentrations of nematicides to the rhizosphere,

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minimizing environmental contamination and non-target effects. Assessment of the LCM to reduce infection by plant parasitic nematodes (PPNs), such as the yam nematode (*Scutellonema bradys*) on yam (*Dioscorea rotundata*)[23] and *Meloidogyne hapla* on tomatoes[20], has earlier provided an indication of its use for potential protection of crops against other PPNs.

In this study, we compared ABM-loaded paper with its controls and with farmer practice for the management of *G. rostochiensis* on potato. We further used behavioural and chemical analysis to investigate the mode of action. Our findings reveal a remarkable new strategy for managing PCN, which delivers ultra-low dosages of nematicides and concomitantly disrupts the plant host–pest chemical signalling.

Results

We monitored the effect of ABM–LCM compared with the controls: untreated LCM (no active ingredient loaded; u-LCM), soil drenching with ABM alone and farmer practice (absolute control).

PCN damage to potatoes reduced by W&P. The productivity of the potato crops (kg plot^{-1}) varied significantly between the two seasons ($P<0.001$), requiring independent analyses of the data collected during 2016 (rainfall 858.9 mm) and 2017 (rainfall 458.3 mm) (Fig. 1a,b and Table 1). No significant differences ($P=0.867$) were observed between the two study sites, Haraka and Kinangop, however. The analyses show that those treatments involving W&P had significantly higher yields across both cropping seasons (Fig. 1a). Among the four treatments studied, the highest yields were consistently obtained with the ABM–LCM and the lowest with the farmer-practice control. All treatments demonstrated a significant increase in tuber yield and mass of root systems per plant across the two seasons compared with the absolute control, with ABM–LCM consistently providing greater tuber yields per plant ($P<0.001$, $\chi^2=344.7$, d.f.$=3$) and mass of root system ($P<0.001$, $\chi^2=282.2$, d.f.$=3$) compared with other treatments (Table 1). The plots with ABM–LCM-wrapped tubers produced 4.4-fold and 5.2-fold increase in yields compared with farmer practice during 2016 and 2017, respectively, equivalent to ~85% (34 t ha^{-1}) of the indicated yield potential for Kenya (40 t ha^{-1}) (ref. [7]). The u-LCM (3.0-fold and 3.4-fold) and ABM alone (3.0-fold and 1.4-fold) also provided significantly better yields in both seasons, respectively, compared with the control. None of the treatments resulted in any penalty to potato germination and growth. During the 2016 season, the number of tubers per plant was also significantly higher for all treatments, compared with the farmer-practice control, although this was not observed in 2017 ($P<0.001$, $\chi^2=223.9$, d.f.$=3$).

The soil cyst densities at harvest differed significantly between treatments (2016: $P<0.001$, $\chi^2=23.9$, d.f.$=3$; 2017: $P<0.001$, $\chi^2=28.2$, d.f.$=3$) in both seasons (Fig. 1b). Use of the ABM–LCM led to the lowest PCN cyst density, which was ~17.4-fold and 1.6-fold lower than control plots in 2016 and 2017 seasons, respectively, followed by the ABM alone (2016: ~9.8-fold; 2017: ~1.5-fold) and u-LCM (2016: ~8.8-fold; 2017: ~1.4-fold).

In addition to PCN, root knot nematodes (*Meloidogyne* spp.) are an important PPN, which was also consistently recovered from field sites. Analysis of the reproduction between planting (Pi) and harvest (Pf) from across field sites showed that the ABM–LCM treatment reduced ($P=0.02$, $\chi^2=9.9$, d.f.$=3$) root knot nematode multiplication to 0.10 compared with 2.56 for farmer practice in 2017. It was also lower in u-LCM and ABM drenching alone than in the control. In 2016 season, root knot nematode multiplication was again lower (0.06) in the ABM–LCM treatment than in the control (0.50).

PCN hatching reduced by LCM. Since PCN hatch and host location depend on host root exudates[24], we investigated the chemical composition of potato root exudates in the presence and absence of the LCM and how this affects the assailable stages in the nematode development. The number of infective second-stage juveniles (J2s) hatching on a weekly basis differed between treatments (3-week-old root exudates, F ratio with (4,15) degrees of freedom: week 1, $F_{(4,15)}=5.288$, $P=0.007$; week 2, $F_{(4,15)}=6.819$, $P=0.002$; week 3, $F_{(4,15)}=7.266$, $P=0.002$; week 4, $F_{(4,15)}=12.3$, $P<0.001$; week 5, $F_{(4,15)}=3.173$, $P=0.04$; week 6, $F_{(4,15)}=5.835$, $P<0.001$; week 7, $F_{(4,15)}=25.76$, $P<0.001$; week 8, $F_{(4,15)}=279.2$, $P<0.001$), as did the cumulative juvenile hatch after 8 consecutive weeks, which reflected the general trend during the 8 weeks. Root exudates of 3- to 6-week-old potato plants influenced PCN hatching (Fig. 2a–d), with root exudates from 5-week-old plants eliciting 1.5-fold, 1.2-fold and 1.3-fold higher hatching compared with the exudates from 3-, 4- and 6-week-old plants (Fig. 2c). The u-LCM + exudates showed the greatest hatch reduction ($P<0.001$), with up to 85% and 70% lower hatch, compared with exudates alone and ABM–LCM, respectively. However, there was no significant difference in hatch stimulation between the ABM–LCM and u-LCM using root exudates from 3-, 4- and 6-week-old plants (Fig. 2a,d). The control (distilled water) elicited only minimal hatching, which did not differ significantly between the three treatments. The viability test carried out on the remaining eggs also showed no significant differences between the treatments.

PCN chemotaxis impeded by W&P. When presented with a choice, PCN infective juveniles preferred the chamber treated with the potato root exudate (stimulus) obtained from the different plant ages compared with distilled water (control): 4-week-old (B: $\chi^2=7.9$, d.f.$=1$, $P=0.005$), 5-week-old (C: $\chi^2=21.0$, d.f.$=1$, $P<0.001$) and 6-week-old (D: $\chi^2=31.2$, d.f.$=1$, $P<0.001$) potato plants (Fig. 2e–h). However, the presence of the LCM significantly reduced attraction of infective juveniles to the host chemical stimulus. Furthermore, the proportion of infective juveniles recovered from the stimulus chamber varied significantly across treatments ($P<0.001$), with the ABM–LCM and the u-LCM significantly reducing ($P<0.001$) juvenile response by 98% and 94%, respectively, compared with the mesh control (no LCM treatment) using root exudates from 5-week-old plants (Fig. 2g). Likewise, 5% fewer juveniles were recovered from the chamber loaded with the ABM–LCM than from the u-LCM. Juvenile recovery was 65% lower from the distilled water chamber in the ABM–LCM treatment compared with the mesh control. However, there was no difference between the mesh control and u-LCM. There were no differences between the proportions of juveniles recovered from the different treatment release chambers. This trend was also observed when the root exudates obtained from 3-, 4- and 6-week-old plants were used for assays (Fig. 2e,f,h).

PCN development delayed by W&P. When PCN infective juveniles invade the host roots, they establish a fixed feeding site (syncytium), where they undergo two additional moults (third stage (J3) and fourth stage (J4)) before maturing into an adult. Whereas at weeks 2, 4 and 6, juvenile recovery from roots did not differ among the three treatments, at week 8, a marginally significant effect ($P=0.08$) was observed between the u-LCM and the control, with a 48% lower juvenile count in the u-LCM (Fig. 3a–d).

At weeks 2 and 6, the counts of J3s and J4s were not significantly different between the different treatments, but at weeks 4 and 8, significantly ($P<0.001$) fewer juveniles were recorded from the ABM–LCM and u-LCM by factors of 0.25 and 0.27 (week 4) and 0.37 and 0.49 (week 8), respectively, compared with the control. At week 4, the proportion of females was not significantly different between the treatments; however, by week 6, 24% and 22% fewer females were recorded in the ABM–LCM ($P=0.006$) and u-LCM ($P=0.004$), respectively, and by week 8, 36% fewer females ($P<0.001$) were found across both matrix treatments.

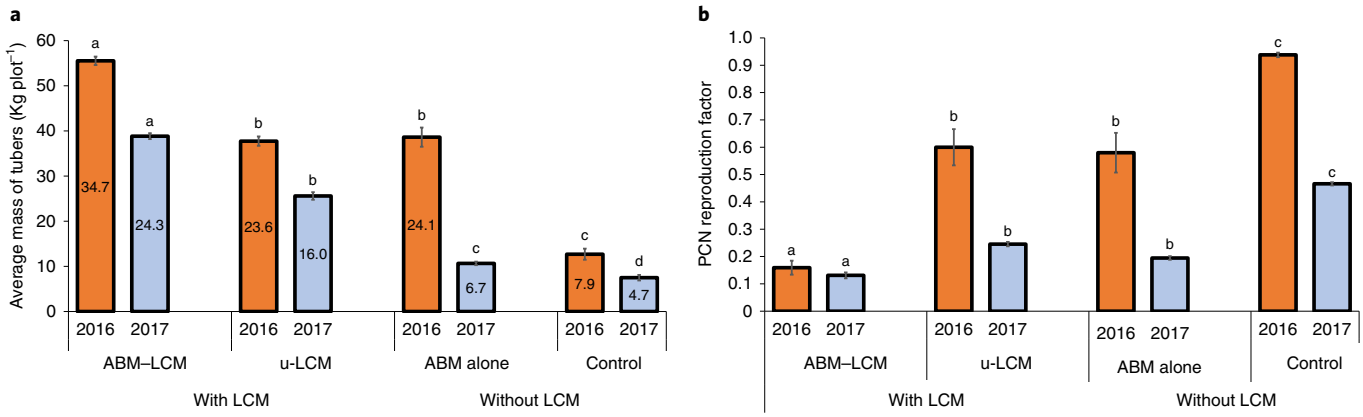

Fig. 1 | Effect of W&P on potato yield and PCN reproduction from field trials conducted at four experimental sites in 2016 and 2017. a, Average potato yield (kg) per plot (the figures in the bars represent an extrapolation of the yield to tonnes per hectare). **b**, Reproduction factor of *Globodera rostochiensis* cysts per 200 ml of soil in field experiments on implementation of the experimental treatments. Different lower-case letters on the bars represent significant differences between the treatments in an individual year at 5% significance level ($n=8$). Error bars represent the s.e.m.

Table 1 | Effects of W&P on potato growth and productivity including germination rate, number of tubers, mass of root system, number of stems and plant height

Field trial

Season	Treatment	Germination rate per plot (%)	Number of tubers per plant	Mass of root system (g plant^{-1})	Mass of tubers (g) plant^{-1})	Number of stems per plant	Plant height (cm)
2016	ABM–LCM	86.6 ± 4.22 ^{a}	11.2 ± 0.26 ^{a}	5.7 ± 0.12 ^{a}	978.9 ± 18.00 ^{a}	—	40.0 ± 0.68 ^{a}
	u-LCM	88.1 ± 3.78 ^{a}	6.5 ± 0.17 ^{c}	3.1 ± 0.09 ^{c}	659.5 ± 12.10 ^{b}	—	43.4 ± 0.69 ^{bc}
	Abamectin alone	79.7 ± 3.69 ^{a}	7.4 ± 0.16 ^{b}	4.1 ± 0.10 ^{b}	669.7 ± 12.32 ^{b}	—	41.3 ± 0.62 ^{ab}
	Control	87.4 ± 2.74 ^{a}	5.7 ± 0.15 ^{d}	2.1 ± 0.08 ^{d}	262.0 ± 6.90 ^{c}	—	44.8 ± 0.78 ^{c}
2017	ABM–LCM	94.8 ± 2.27 ^{a}	7.6 ± 0.17 ^{a}	7.7 ± 0.11 ^{a}	600.1 ± 13.21 ^{a}	5 ± 0.11 ^{a}	57.5 ± 0.59 ^{a}
	u-LCM	94.4 ± 1.59 ^{a}	7.4 ± 0.16 ^{a}	5.0 ± 0.13 ^{c}	382.0 ± 9.85 ^{b}	5 ± 0.11 ^{a}	53.4 ± 0.43 ^{b}
	Abamectin alone	95.0 ± 1.36 ^{a}	7.4 ± 0.17 ^{a}	5.8 ± 0.11 ^{b}	166.3 ± 2.31 ^{c}	4 ± 0.11 ^{a}	57.9 ± 0.54 ^{a}
	Control	91.5 ± 1.39 ^{a}	7.5 ± 0.15 ^{a}	3.0 ± 0.11 ^{d}	164.7 ± 4.27 ^{c}	4 ± 0.10 ^{a}	56.0 ± 0.45 ^{a}

Values in columns represent the mean ± standard error of the different treatments. The different lower-case letters per column represent significant differences in data between the treatments in an individual year at 5% significance level. For data collected from filed plots, $n=8$; for data collected per plant, $n=112$.

PCN host stimulants/attractants adsorbed by LCM. Chemical analysis of the potato root exudates identified a wide diversity of compounds, including the known PCN hatching factors solanoeclepin A, steroidal glycoalkaloids, α-solanine, α-chaconine and the steroidal alkaloid solanidine[25], as well as several amino acids, fatty acids, benzoic acid derivatives, hydroxycinnamic acids and phytohormones (Supplementary Table 1). Exposure of the root exudates to both the ABM–LCM and u-LCM led to a reduction of up to 98% of the levels of most of the compounds, including the PCN hatching factors solanoeclepin A, α-solanine, α-chaconine and solanine in the root exudates (Fig. 4a and Supplementary Table 1). However, solanoeclepin A, α-chaconine, α-solanine and solanidine were detected in the ABM–LCM and u-LCM following their exposure to the root exudates (Fig. 4b). In the recovery experiments, extracts obtained from the LCM boosted egg hatch by ~60-fold, compared with distilled water, confirming the adsorption of root exudate hatching factors by the LCM.

When exposed to pure α-solanine, α-chaconine and solanidine, the LCM clearly demonstrated its adsorption of these compounds. The ABM–LCM and u-LCM adsorbed 98% and 93% of α-chaconine, 46% and 49% of α-solanine and 49% and 9% of solanidine, respectively. When exposed to root exudates, synthetic cellulose also adsorbed up to 25% of the PCN hatching factors α-solanine, α-chaconine and solanidine (Fig. 4a and Supplementary Table 1), similar to the LCM.

Chemical analysis of the LCM that had been wrapped around seed potato tubers in the field and recovered at up to 8 weeks after planting also showed traces of the PCN hatching factors α-chaconine, α-solanine and solanidine. The main hatching factor solanoeclepin A, however, was not detected in the LCM at 8 weeks. The decomposition of the matrix over the duration of the season showed that the LCM gradually degraded over time but could still be detected at 8 weeks (Fig. 5).

Discussion

Our study demonstrates a highly promising option for the sustainable management of PCN. Earlier assessment of various organic fibres as potential carriers for nematicidal products identified banana fibre (from the waste rachis) as the most suitable[20,21]. Unexpectedly, the characteristics that make banana fibre an ideal candidate for this purpose also appear to provide a platform to disrupt chemical communication between PCN and potato. Banana fibre, with its unique combination of lignin and cellulose, tubular morphology and porosity, retains nematicides (for example, ABM) for long periods, enabling ultra-low-volume application of the active ingredient and its subsequent slow release[21]. Consequently, micro-dosages

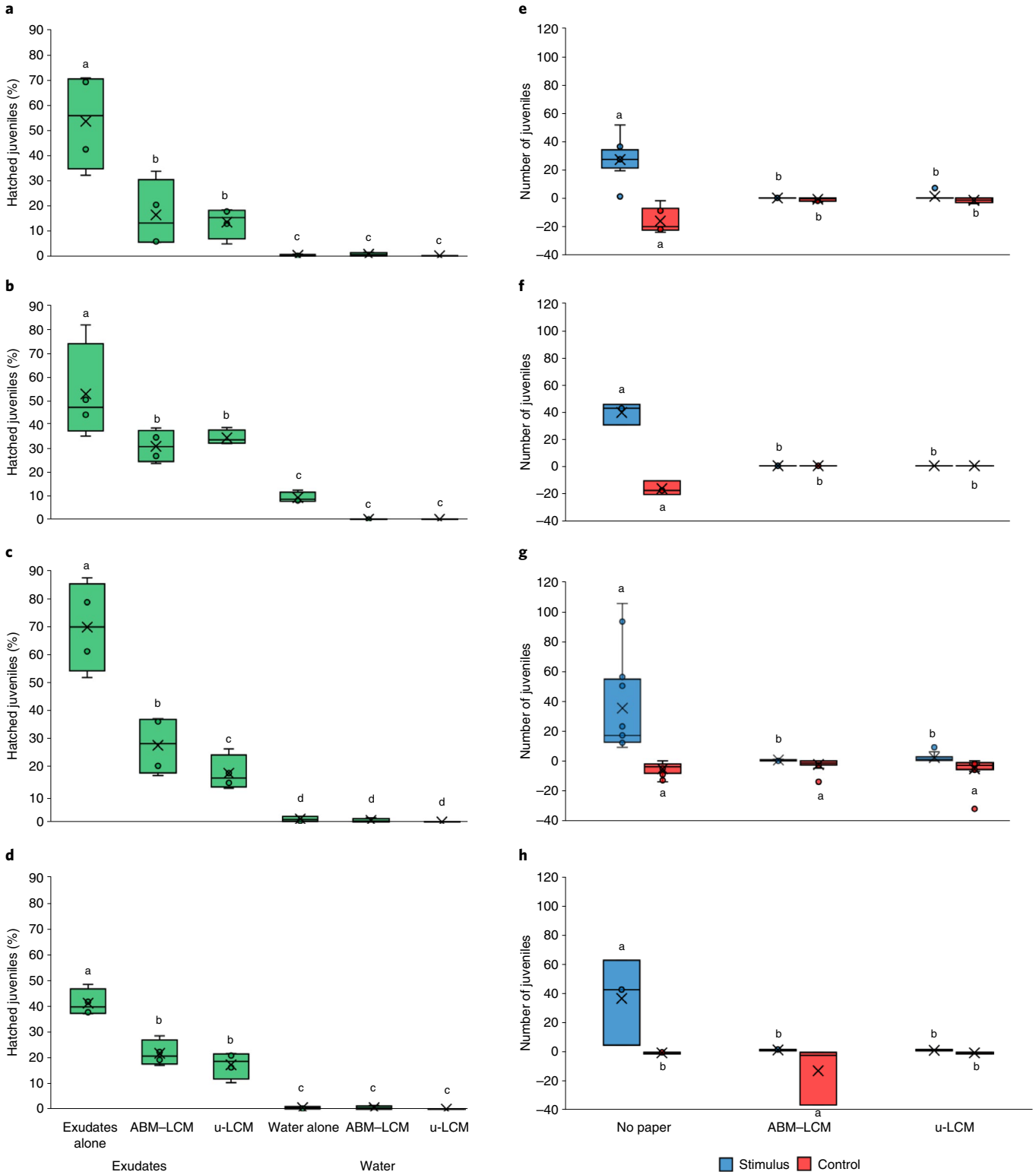

Fig. 2 | Behavioural response of *Globodera rostochiensis* to W&P treatments when exposed to potato root exudates from differently aged plants. **a**–**d**, Hatching response of juveniles in the presence of different treatments when exposed to potato root exudates from 3-week-old plants (**a**), 4-week-old plants (**b**), 5-week-old plants (**c**) and 6-week-old plants (**d**) ($n=4$). **e**–**h**, Chemotaxis responses of juveniles to root exudates (stimulus) in the presence of the three treatments, ABM–LCM, u-LCM and no LCM, compared with absolute control (moist sand) using exudates from 3-week-old plants ($n=6$) (**e**), 4-week-old plants ($n=3$) (**f**), 5-week-old plants ($n=12$) (**g**) and 6-week-old plants ($n=3$) (**h**); *n* represents the sample size, and different lower-case letters on the box plots represent significant differences between the treatments at 5% significance level. The vertical lines on the box plots indicate variability outside the upper and lower quartiles, and any point outside those lines is considered an outlier. The symbol X on the box plots indicates the sample mean; the small circles represent individual data points.

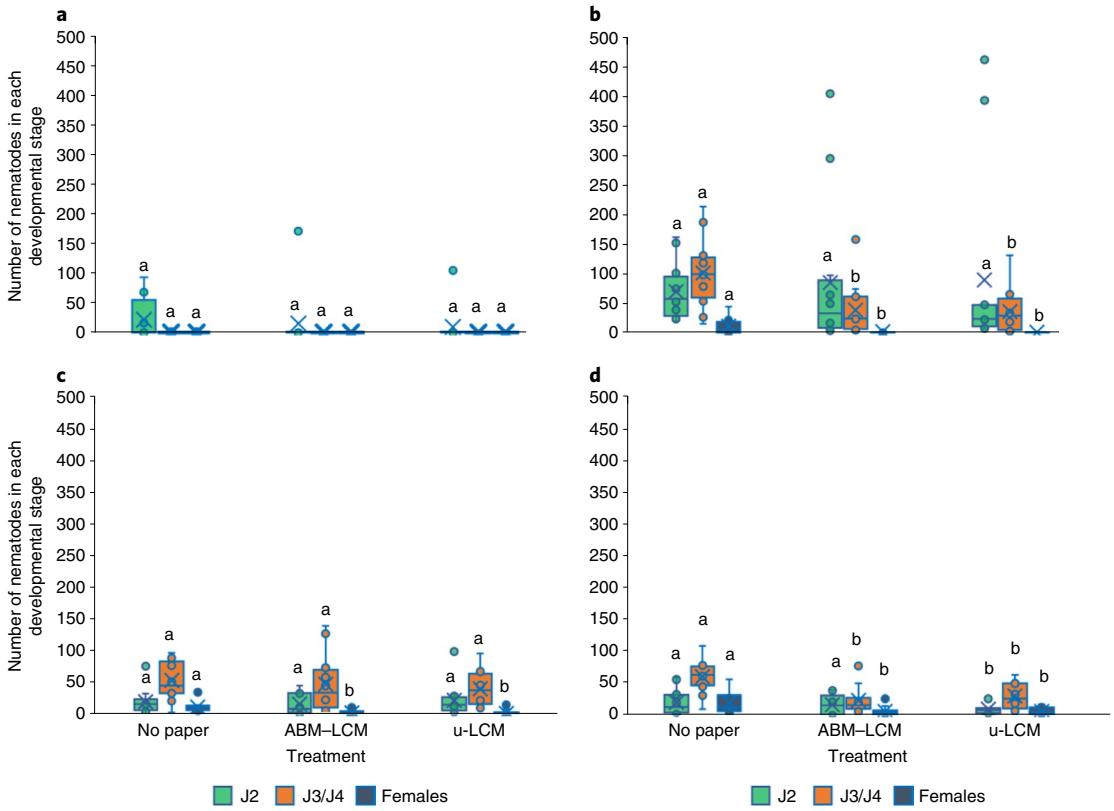

Fig. 3 | Developmental stages of PCN found in plants of different ages following application of the different treatments at planting. a, 2-week-old plants. **b**, 4-week-old plants. **c**, 6-week-old plants. **d**, 8-week-old plants. Comparison made across the treatments for each developmental stage with different lower-case letters on the box plots representing significant differences between the treatments at 5% significance level. The symbol X on the box plots indicates the sample mean; the small circles represent individual data points.

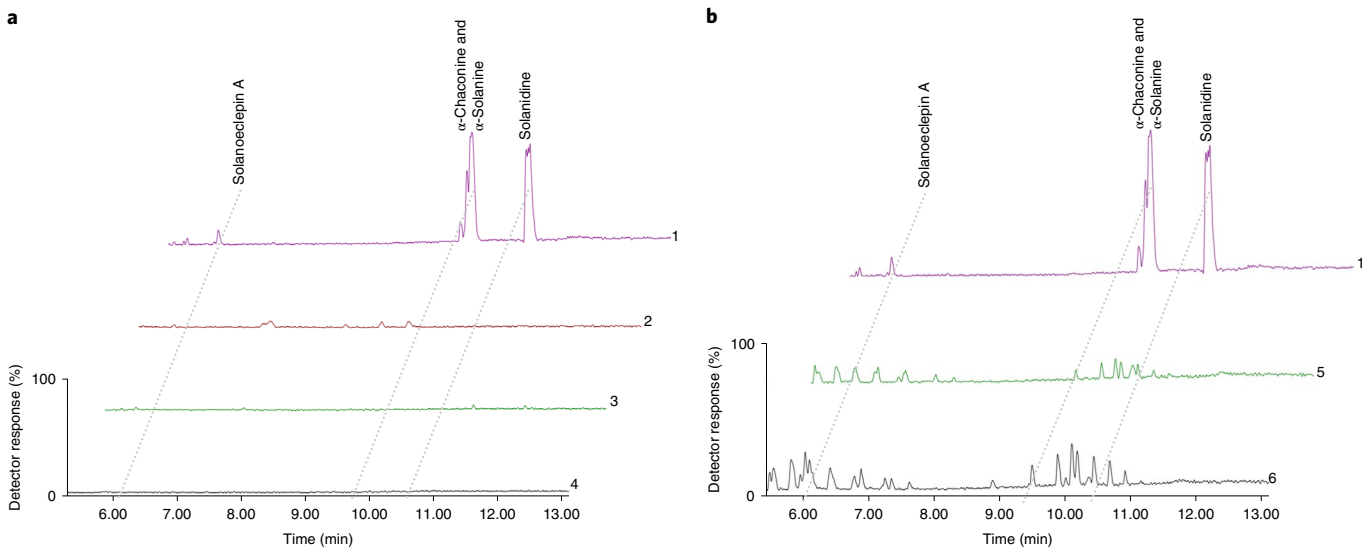

Fig. 4 | Change in root exudate chemical profile following interaction with LCM. a, Liquid chromatography triple quadrupole mass spectrometry (LC-QqQ-MS) chromatograms showing composition of potato root exudates before exposure (1) and after exposure to cellulose (2), u-LCM (3) and ABM–LCM (4). **b**, LC-QqQ-MS chromatograms showing the composition of extracts of u-LCM (5) and ABM–LCM (6) exposed to potato root exudate compared with unexposed root exudate (1) with the identified PCN hatching factors.

of nematicides can be applied directly to the target root zone by enclosing seed material in a banana-fibre LCM impregnated with nematicides. The difference in results observed between ABM–LCM and soil drenching with ABM provides evidence of increased ABM efficiency when applied on LCM at a fraction of the label rate. The same properties also appear to enable effective adsorption of

Fig. 5 | Degradation of the LCM in soil over 8 weeks. a, Photo of the W&P technology in a field study. **b**–**e**, Photos showing the penetration of roots through the LCM and its gradual decomposition after 2 weeks (**b**), 4 weeks (**c**), 6 weeks (**d**) and 8 weeks (**e**) of potato growth.

key chemical components of root exudates essential to successful PCN parasitism. The combination of these factors makes for a very effective PCN management option. In terms of crop production, LCM, with or without ABM, greatly improved current farmer practices with no negative effect on seed germination. From our results, improved production using LCM can be directly associated with the reduced challenge from PCN, with PCN reproduction effectively reduced compared with farmer practice.

Our study further demonstrated that reduced PCN hatch in the presence of ABM–LCM and u-LCM was due to LCM adsorption of key PCN hatching factors, rendering them unavailable for nematode recognition. However, when exposed to low-potency root exudates (from 3-, 4- and 6-week-old plants), which equates to reduced hatching factor presence, hatching response was similar between ABM–LCM and u-LCM. When exposed to increased potency root exudates (5-week-old plants), u-LCM more effectively reduced hatching[24,26]. This could mean that LCM impregnation with ABM influences adsorption properties and should be further investigated. The similarity in egg hatch between the water treatments indicates that LCM presence does not influence spontaneous hatch of PCN in water. These results indicate that when seed potatoes are wrapped in LCM, untreated or treated with ABM, PCN hatch is reduced during the first 8 weeks, which translates into decreased PCN reproduction.

Host location is an important factor in successful nematode parasitism, and disruption of host plant–nematode chemical interaction has received increasing attention as a strategy for nematode management[27–30]. Our results demonstrate that enclosing seed potato in ABM–LCM or u-LCM disrupts the host-finding process of PCN juveniles, reducing their chance of infection and successful establishment in potato roots. Previous studies have identified the compounds solanoeclepin A, α-solanine, α-chaconine and solanidine, present in root exudates of potato and tomato, that stimulate PCN hatching (hatching factors)[24,25,31]. Cellulose contains a number of hydroxyl moieties that form inter- and intra-molecular hydrogen bonds between the same and neighbouring cellulose moieties[32], which are properties that enable cellulose to be used in removal of various substances, including organic materials, water and metal ions[33,34]. Analysis of root exudates before and after exposure to LCM revealed that most of these compounds were strongly adsorbed by LCM (Supplementary Table 1), possibly via hydrogen bonding to the abundant hydroxyl moieties in the LCM[35]. Chemical analysis of LCM after exposure to root exudates confirmed the presence of hatching factors on LCM, which, once re-extracted, stimulated egg hatch. However, in contrast to 25% adsorption of PCN hatching factors on cellulose only, u-LCM showed a high adsorption rate for the hatching factors (93% for α-chaconine). Besides hydrogen bonding with the –OH moieties of the cellulose in LCM, this exceptionally high adsorption can be attributed to the sorption characteristics of highly porous fibres in LCM, as well as the involvement of polyphenolic entities in the 12% lignin content of LCM in developing intermolecular bonds with the hatching factors. This adsorption by LCM was further confirmed using standard α-solanine, α-chaconine and solanidine. Chemotaxis bioassays suggest that use of both ABM–LCM and u-LCM prevented perception of attractant chemical cues emerging from the root exudate stimulus side by juveniles, disrupting chemo-attraction. The low proportion of juveniles recovered from both distilled water and stimulus sides in LCM treatments (Fig. 2e–h) indicates that LCM may also act as a physical barrier, preventing juvenile chemotactic migration. Such barrier properties could be attributed to LCM's unique tortuous structure, consisting of a network of tubular microfibrils[21] and low porosity (indicated by a high air resistance of 45 ± 12 Gurley seconds per 100 ml). The LCM hampered the chemotactic recognition of its host by PCN but did not entirely prevent it. This lapse allowed the crop to develop a more robust root system before a later infection occurred, retarding PCN hatch and reducing soil PCN inoculum at harvest when the W&P technology was used.

We conclude that use of banana-fibre paper can effectively reduce the impact of PCN and lead to much improved potato yields. This phenomenon is achieved through a combination of interacting mechanisms across nematode life-cycle developmental stages, such as (1) preventing diffusion of chemical cues used by PCN to identify and locate host roots, (2) disrupting detection of hatching factors, reducing egg hatch, and (3) retarding the juvenile moulting process, delaying maturity to adult females and extending the life cycle of PCN. LCM does this by strongly adsorbing root exudate components, rendering them unavailable for nematode chemoreception. The initial objective of our study was to identify a biodegradable matrix that could deliver micro-dosages of nematicides to the target root zone in a field setting and provide a sustainable nematode management option for smallholder farmers. This has been achieved. Given that banana fibres in general are composed of a network of tubular microfibrils and a distinctive combination of lignin and cellulose, it is anticipated that fibre from different genotypes other than Cavendish bananas would work equally well, but this would need to be confirmed. As LCM can also be treated with ultra-low dosages of chemical nematicides, an environmentally sensitive, safe-to-handle and climate-smart mechanism for managing a particularly pervasive pest has been demonstrated. The incorporation of LCM in integrated pest management programmes would be particularly relevant in the context of sub-Saharan African food security.

Methods

LCM fabrication and characterization. Banana fibre from the rachis of Cavendish banana plants was procured from the agro-industrial unit of Earth University,

Costa Rica, and was processed in the Forest Biomaterials Department at North Carolina State University. Lignin content and air resistance of the matrix were measured as reported in a previous article[21]. Briefly, lignin content of the matrix was measured following TAPPI (Technical Association of Pulp and Paper Industry) T236 test protocol. We evaluated porosity of LCM via the Gurley air resistance method following the TAPPI T460 standard protocol. A high air resistance of the LCM is indicative of its low porosity and vice versa.

Experimental sites. Field experiments to evaluate the effectiveness of W&P to protect PCN-susceptible potato cv. 'Shangi' against *G. rostochiensis* (the most prevalent PCN species in Kenya) attack were carried out under rainfed conditions during the main wet season from May to August (2016) and April to July (2017) in Kenya at four sites: Haraka A (00.78537° S, 036.60429° E), Haraka B (00.77588° S, 36.61652° E), Kinangop A (00.58985° S, 036.61740° E) and Kinangop B (00.58854° S, 36.61234° E), Nyandarua County. Farms were selected on the basis of their continuous cultivation of potato over the previous five years; all field sites were situated at elevations >2,500 m above sea level and had clay and sandy loam soils. Physico-chemical and soil texture analyses (Supplementary Tables 2 and 3) were conducted for each site at planting and harvest at the laboratory of the Kenya Agricultural and Livestock Research Organization in Nairobi, using a composite sample from across each site pre-planting and from a composite sample for each treatment per site at each harvest. No remarkable differences in soil composition between treatments were observed (Supplementary Table 4). The accumulated rainfall for the county was 859.9 mm and 458.3 mm for 2016 and 2017, respectively.

Field experiments. Plant parasitic nematode densities were assessed at both Pi and Pf. For both Pi and Pf, nematode infestation was assessed using a 200 ml sub-sample from a composite sample of ~1 kg removed from five randomly selected soil sampling points per plot from ~20 cm depth in each field. PCN cysts were extracted using the Fenwick can method[9]. As no differences ($P < 0.05$) were observed between the Pi infestation levels of PCN cysts and other nematodes, a completely randomized design was implemented. The PCN juveniles and other nematodes were identified to the genus level using morphometric traits, while the molecular-based European and Mediterranean Plant Protection Organization diagnostic protocol PM 7/40(3)[9] was used to determine the PCN species.

The experiment involved four treatments: ABM–LCM (seeds 'wrapped' with LCM impregnated with ~0.8 ng cm^{-2} of abamectin (100 ng ABM per sheet), u-LCM (not impregnated with ABM), ABM alone (drenching the soil with ABM Tervigo (8 l ha^{-1}) following the commercial recommendations (0.19 ml active ingredient per potato seed)) and farmer practice (absolute control, which received no additional application of nematicide or wrapping). Quality-declared cv. Shangi seeds were planted in 4 × 4 m plots spaced 30 × 75 cm (65 seeds per plot) with a 1 m distance between plots and four replicate plots per treatment. Plots were prepared individually by hand-hoe. Treatments involving the LCM used a single sheet (10 × 12.5 cm) in which the potato tuber was wrapped loosely. For the non-LCM treatment, two 10 l suspensions of Tervigo were applied per plot onto the unwrapped tubers in the furrow and top drenched after covering with soil; the potato seeds remained unwrapped.

For all treatments, di-ammonium phosphate (NPK 18/46/0) fertilizer was applied at planting (500 kg ha^{-1}); a foliar fertilizer (NPK 20/20/20; Diamond Plant Fertilizer, Kerapros Ltd) (2.5 ml l^{-1}) was applied 6 weeks after planting and the foliar fungicide Mistress 72 wettable powder (1.5 g l^{-1}) (Cymoxanil 8% + Mancozeb 64%; Osho Chemicals Ltd) for early and late blight disease control was sprayed every 2 weeks after sprouting. Weeds were removed manually on three occasions. No additional irrigation was provided.

The experiment was terminated at 110 days post-planting. Data were collected on percentage germination per plot, plant height, stems per plant, root mass, yield and number of tubers per plot (kg plot^{-1}) measured from all harvested tubers. The final juvenile (J2-Pf) and cyst (Cy-Pf) densities per plot and of *Meloidogyne* species were determined as described.

Laboratory-based experiments. The experiments were conducted using potato root exudates from cv. Shangi planted in 2 l plastic pots in sterilized sand (autoclaved at 121 °C for 40 min, Astell Scientific autoclave) in the screenhouse at 23 ± 2° C and 60–70% relative humidity at the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya (1.2219° S, 36.8967° E). Plants were watered three times weekly with a nutrient solution prepared according to ref. [36]. Potato root exudates were collected from 3- to 6-week-old plants using the dipping method[37]. Batches of five potato plants per treatment were gently uprooted, rinsed in water, placed into 500 ml of distilled water and their exudates collected over 24 h. The exudates were filtered through Whatman no. 1 filter paper and stored at −80° C for use over a period of 8 weeks for the hatching assay.

For the chemotaxis assays, freshly collected exudates within 24 h after collection were used for each assay. Cysts used in the assays were obtained from a farmer's field shortly following harvest of potatoes in Nyandarua County, Kenya (00.78537° S, 036.60429° E). The soil was air dried, and cysts were extracted as described previously. The collected cysts were dried on a milk filter paper before handpicking with the aid of a stereomicroscope (LEICA M125).

Chemical reagents. LC-MS grade methanol (LC-MS LiChrosolvR, Merck (99.97%)), formic acid (98–100%), water (LC-MS Chromasolv), α-solanine (95%), solanidine (95%) were sourced from Sigma-Aldrich and α-chaconine (95%) from PhytoLab.

Potato cyst nematode hatching bioassays. The PCN hatching assay was conducted with and without the LCM as illustrated in Supplementary Fig. 1a. Two test solutions, distilled water and potato root exudates retrieved from plants grouped into four ages (from plants aged 3, 4, 5 and 6 weeks old), were used to evaluate the egg hatching response. Exudates were collected from different plants for each age group and each group replicated four times. Six treatment combinations were then assessed against each exudate group: exudates alone (no LCM; positive control), ABM–LCM + exudates, u-LCM + exudates, distilled water alone (no LCM; negative control), ABM–LCM + water and u-LCM + water. For each replicate, five cysts were placed in container A and were held in place by a nylon mesh that permitted hatching juveniles to pass through. The experiment was arranged in a randomized design with four replicates per treatment. For treatments involving the LCM, the base of container B was lined with the matrix; for the treatments without matrix, a nylon mesh was used. The experiment was arranged in a six-well culture plate labelled as container C (Supplementary Fig. 1a) into which the test solution was added and maintained in the dark for 8 weeks. The number of juveniles emerging from cysts were counted weekly and the test solution replenished. At 8 weeks, eggs remaining in the cysts were assessed for viability[38].

Potato cyst nematode chemotaxis bioassays. PCN eggs were stimulated to hatch using freshly collected potato root exudates, and freshly hatched juveniles were collected daily on a 20 µm sieve, rinsed and held in distilled water for use. The responses of hatched infective juveniles to potato root exudates in the presence and absence of LCM were tested in a dual-choice sand bioassay (Supplementary Fig. 1b), according to ref. [37], with some modifications. Root exudates from 5-week-old plants were used. Each chamber was filled with 5 g of sterile sand. Sand in chambers A and B was mixed with 1 ml of freshly collected exudate (<24 h) and distilled water, respectively. The effects of u-LCM or ABM–LCM were compared with a nylon mesh partition between the chambers. Chamber C contained 3 mg of moist autoclaved sand and 500 µg of water containing 200 J2s. Each chamber was suspended in water and juveniles collected on 20 µm sieves. The juveniles recovered after 48 h were counted and scored under a stereomicroscope as either positive responders to stimuli or negative responders/non-responders depending on the chamber in which they were recovered. The experiment was arranged in a randomized design with three replicates per treatment. The experiment using root exudates from 5-week-old plants was conducted six times.

Potato cyst nematode development experiments. The effect of the LCM on PCN development was assessed using wrapped and unwrapped seed potatoes (cv. Shangi) inoculated with PCN in 2 l pots filled with autoclaved sand. Treatments included potatoes wrapped in ABM–LCM, potatoes wrapped in u-LCM and unwrapped potatoes (control). The experiment was arranged in randomized design with six replicates per treatment. The pots were inoculated with 20 cysts at planting and maintained for 8 weeks in the screenhouse at 23 ± 2° C and 60–70% relative humidity at *icipe*. Plants were watered three times weekly with a nutrient solution prepared according to ref. [36]. At 2-week intervals for 8 weeks, six replicates per treatment were randomly selected and the number of each development stage of PCN on the roots recorded. The experiment was conducted twice.

The different nematode developmental stages present in the roots were assessed after staining with acid fuchsin[39]. Briefly, the uplifted roots were gently rinsed in distilled water to remove soil debris. The roots were chopped into 1–2 cm segments, placed in 1.5% sodium hypochlorite solution for 4 min, agitating occasionally, then rinsed in tap water followed by distilled water. The clean roots were placed in 30 ml of water containing 1 ml of acid fuchsin (3.5 g in 25% acetic acid) (BDH), which was heated to boiling, cooled and rinsed under running water before placing in heated glycerine acidified with a few drops of 5 N hydrochloric acid. After cooling, root segments were pressed between two microscope slides, and the different nematode development stages were counted under a stereomicroscope at ×40 magnification.

Root exudate chemical composition after exposure to LCM. The chemical composition of root exudates from 5-week-old plants was assessed following exposure to the LCM in vitro. A 0.05 g of LCM (u-LCM and ABM–LCM) was immersed in 1 mg ml^{-1} of freeze-dried root exudate for 24 h. The LCM was removed and the remaining solution centrifuged to remove any remaining particles. This experiment was replicated three times. Chromatographic separation was then performed using an ACQUITY ultra-performance liquid chromatography (UPLC) I-class system (Waters Corp.) fitted with an ACQUITY UPLC BEH C18 column (2.1 × 150 mm, 1.7 µm particle size; Waters Corp.) according to the method by ref. [25]. Briefly, the mobile phase comprised water acidified with 0.01% formic acid (solvent A) and methanol (solvent B) and followed a gradient system. The gradient system used was 0–2 min: 5% B; 2–4 min: 40% B; 4–7 min: 40% B; 7.0–8.5 min: 60% B; 8.5–10.0 min: 60% B; 10–15 min: 80% B; 15–19 min: 80% B; 19.0–20.5 min: 100% B; 20.5–23.0 min: 100% B; 23–24 min:

95% B; 24–26 min: 95% B. The flow rate was held constant at 0.2 ml min^{-1}. The UPLC was interfaced with an electrospray ionization Waters Xevo TQ-S operated in full-scan MS in positive ionization modes, and data were acquired over the m/z range 100–2,000.

Identification of the compounds present in root exudates pre- and post-exposure to the LCM was performed using a Thermo Scientific Q Exactive Mass Spectrometer coupled to a Vanquish UHPLC System by gradient elution using an ACE Excel 2 C18-PFP column (2.1 µm, 100 mm). The mobile phase used was composed of water acidified with 0.1% formic acid (solvent A) and 0.1% formic acid in acetonitrile (solvent B) and followed a gradient system. The gradient system used was 0–3 min: 100% A; 3–23 min: 80% B; 23.0–26.5 min: 80% B; 26.5–30.0 min: 100% A. Solvent flow rate was at a constant 0.35 ml min^{-1} and 2 µl of the sample injected. Full-scan MS analysis was performed in positive ion mode at mass resolution 35,000 scanning from m/z 70–1,000.

This adsorption experiment was repeated using individual standards of PCN hatching factors α-solanine, α-chaconine and solanidine. A 10 µg ml^{-1} concentration of the standards was prepared separately in a 1.5 ml Eppendorf tube, and 0.05 g of the ABM–LCM and u-LCM were exposed to the standards for 24 h. Both the LCM-exposed and unexposed standards were analysed to compare differences. This experiment was conducted only once.

For comparison with the LCM, the chemical composition of root exudates following exposure to cellulose was analysed in an in vitro experiment. Exudates from 5-week-old plants were used, with three replicates per treatment. After freeze-drying (see the preceding), 1 mg of exudate was dissolved in 1 ml of methanol/water (3/7 v/v), and 0.05 g of cellulose was immersed in the solution. After 24 h, the solution was centrifuged and the supernatant collected and analysed, as described. This experiment was conducted only once.

Identification of root exudate chemicals adsorbed by LCM. Following exposure to 30 ml of 1 mg ml^{-1} root exudates for 24 h, 2.0 g of the LCM (u-LCM and ABM–LCM) was removed, dried and placed in 5% methanol in a sonicator bath at room temperature for 30 min. The extract was then freeze-dried, and 1 mg ml^{-1} of the extract was reconstituted in 30% methanol, centrifuged (Spectrafuge 16M) at 14,000g for 10 min and then analysed for chemical composition as described using three replicates.

The bioactivity of the LCM extract was also assessed using a hatching bioassay to determine whether the extracts remained active. Five pre-soaked cysts were placed in 200 µl of the u-LCM and ABM–LCM extracts per well, using a Linbro 96 multi-well sterile plate, with three replicates per treatment. Emerging juveniles were counted on a weekly basis over 4 weeks and compared with a negative water control. This experiment was conducted only once.

An assessment of the LCM longevity and ability to adsorb PCN hatching compounds under field conditions was undertaken in the field at *icipe*. Potatoes were planted following the procedure for the field evaluation of the LCM described in the preceding using ABM–LCM and u-LCM with three replications per treatment. Plants were uprooted on a 2-week cycle for 8 weeks, and the physical state of the matrix was observed and photographed. Matrix fragments were also analysed to detect and determine the presence of hatching factors using liquid chromatography triple quadrupole mass spectrometry analysis.

Statistical analysis. Data from field experiments were first checked for normality and equality of variances before analysis using the Kruskal–Wallis test to determine differences among the treatments and a pairwise Wilcox test used for a pairwise comparison between treatments. The numbers of juveniles hatching in the bioassays were fitted in a quasi-Poisson with negative binomial models to determine the differences between the treatments. The number of weekly hatched juveniles was log transformed and subjected to analysis of deviance and multiple comparisons of the means performed using Tukey's honestly significant difference test. Comparisons between the treatments were also performed after fitting a linear mixed model, and the mean interactions of the treatments were analysed using least squares means. The number of responding juveniles from the dual-choice assays was analysed using the proportionality test to check the effect of the treatments on the attraction potential of the stimulus. The differences across the treatments were determined for each of the three chambers separately, including stimulus, control and the release chamber. The numbers of juveniles recovered from the stimulus chamber and the release chamber were fitted in a generalized linear model (GLM) with a negative binomial distribution, and those recovered from the control chamber were fitted in a zero-inflated model with a negative binomial distribution. A pairwise comparison of the means was performed when there were significant differences in the means.

The different stages of nematode development were represented as a mean of six replicates and subjected to ANOVA after fitting in a GLM with a negative binomial distribution. The means were adjusted using least-square means and separated using Tukey's honestly significant test. Data from the repeated experiments were pooled, as no differences were observed between them, and analysed to assess treatment effect on the development of PCNs. The analyses were conducted separately for each week and for each developmental stage. The data were fitted in a GLM assuming a negative binomial distribution with the exception of J2 counts at week 2, for which a zero-inflated model with negative binomial distribution was used and the female count at week 4 was fitted with the zero hurdle model to address both dispersion and zeros in the data. All the models took experiment and treatment as covariate.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data supporting the findings of this study are available within this paper and the Supplementary Information. Source data are provided with this paper.

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Author contributions

C.O., T.P., S.K., L.P., R.M., D.G., E.D. and T.S. contributed to the design and manufacture of the lignocellulose matrix. B.T., D.C. and L.C. conceived and designed the experiments. J.O., O.M., L.C. and D.C. performed most of the experiments. S.A.C., J.O., A.H., M.N. and B.T. performed the chemical analysis. M.T., L.C. and J.O. analysed the data. B.T., L.C. and D.C. contributed reagents. D.G. reviewed the draft manuscript. J.O., L.C., D.C., C.O. and B.T. wrote the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Software and code

Policy information about availability of computer code

Data collection	No software was used
Data analysis	The data analysis was performed in R studio. R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

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All studies must disclose on these points even when the disclosure is negative.

Sample size	For the field trials, within each experimental plot (16 m2) fourteen (14) plants were randomly selected and labelled after emergence; these plants were measured and controlled along the experimental period until harvesting time; variables to analyze crops' performance was evaluated periodically (every two weeks). At harvest, from each of the 14 experimental plants monitored, analyses to assess nematodes incidence were conducted by collecting 10 g of root. One composite sample was created for each individual plot by mixing 200 cm3 of soil and 10 g of roots from each of the (14) individual plants studied. From these composite samples, data on nematode infection was obtained from one (1) soil sample of 100 g, and the extraction is 5 g of roots and 5 g of potato peels per plot. Each sample of soil, root and potato peel per plot was counted at least twice under the microscope. Researchers collected data from all the plants (65 planted seeds) in each plot to gather information on plants germinability (%). For the pot trials, data related to the phenologic development nematode in the potato crop were collected from every plant (n=6) per treatment. For the lab-based bioassays and chemical analysis sample sizes used was adopted from similar articles in literature.
Data exclusions	No data were excluded from the analyses in the field trials since none of the plants selected for individual monitoring in each plot after emergence died at the end of the experiment. No data was excluded from the PCN development and chemotaxis bioassays and during chemical analysis. For the weekly comparison of treatments in the hatching bioassay, no hatching was observed with the use of the untreated lignocellulose matrix and so the data was not included in the analysis
Replication	Field trials: In every season, trials were replicated twice (in two different farmers' fields) and trials were repeated for two seasons. In total, trials were established in 4 different farmers' fields with a similar history of potato cultivation during 2016 and 2017. The lab-based bioassays were done using root exudates from plants at different ages (from 3 weeks to 6 weeks). For the chemotaxis experiment using root exudates from 5-weeks old plants, the experiment was replicated 5 times. The pot trials: The experiment was replicated twice, and the two experiments were established in the same screenhouse with a difference of 15 days between each other.
Randomization	Pot trials: were located within the screen house using a randomized block design. Field trials: in the open field, due to the homogeneous infestation of the soil with plant-parasitic nematodes, the lack of inclination of the field and the absence of physical elements (e.g. trees, rocks, shelters) in the experimental area, plants were distributed using a complete randomized design.
Blinding	Field trials: In each location, we gave every treatment and plot number a unique code (e.g. Tervigo@ plot 5 in Haraka = H13) that we recorded on an excel file. Plants within each field were labelled as H13.1, H13.2, etc., until the end of the season and the data collection process. Laboratory supporting staff worked using these codes. Plot trials: Every treatment had its code (e.g. A), and repetition was labelled from 1 to 10. Experiment one was marked as '.1' and experiment two as '.2' (e.g. A8.1 - treatment A, plant 8, experiment 1). Laboratory supporting staff worked using these codes.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging