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Effects of harvest injuries on storage rot of potato tubers infected with *Phytophthora infestans*

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Abstract We explored the effects of harvest damage on potatoes infected with *Phytophthora infestans* in 2015 and 2016. Injured tubers were inoculated with zoosporangia suspensions and incubated at 18°C in the dark for 4 weeks. In 2015 and 2016, 38.5% and 74.4%, respectively, of injured tubers inoculated with *P. infestans* rotted and hyphal masses were apparent on the tuber surfaces. Tubers in the uninjured group rarely rotted even when there were numerous *P. infestans* zoosporangia on the inoculated tuber surface. The percentage of rotten tubers in the injured/no inoculation group caused by other types of fungi or bacteria increased rapidly, to approximately 20% within one week; however, there was very little increase during the subsequent incubation. Conversely, the percentage of rotten tubers increased with incubation time in the injured/inoculation group and this phenomenon was significant in 2015. These results imply that not only the presence of *P. infestans* but also surface harvest injuries affect potato storage rot. Storage rot can be minimized by reducing surface injuries and/or decreasing blighted plant material and the population density of *P. infestans* in the soil at the time of harvest during commercial potato production.

Keywords *Phytophthora infestans* · Late blight · Tuber rot · Harvest injury · Storage disease

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Several pathogens that cause potato tuber rot have been reported; among these, *Phytophthora infestans*, the causal agent of potato late blight, is one of the most important in terms of commercial losses. In Japan, most potato tuber rot is caused by *P. infestans* (Kitazawa and Tomiyama 1967). Genotypes JP-3 and JP-4 have been identified in Hokkaido, Japan, since the early twenty-first century (Kashima et al. 2012; Akino et al. 2014; Osawa et al. 2016a). Both genotypes are of mating type A1; thus, the spread of late blight in potato fields in Japan occurs most likely via zoosporangia rather than oospores. Following infection by *P. infestans*, tubers are secondarily infected by bacteria and fungi (Ozaki 1989).

Tuber infection by *P. infestans* has been reported to occur through eyes, lenticels, wounds, intact periderm, hilum (Jones et al. 1912; Lacey 1967; Darsow 2004), and sometimes growth cracks (Lapwood 1977). The susceptibility of tubers to infection by *P. infestans* is said to change during the growing season. As the tuber matures, lenticels become less susceptible and eyes become more susceptible (Zan 1962). The resistance of tubers increases with time after harvest; thus, the highest level of susceptibility occurs when tubers are inoculated on the day of harvest (Stewart et al. 1983). Tubers may be infected by *P. infestans* during growth (Lapwood 1977; Sato 1980), at harvest (Nærstad et al. 2010), or during subsequent handling (Dowley and O'Sullivan 1991).

A reduction in tuber blight would reduce potato loss during storage. The objective of our study was to evaluate the importance of infection at harvest and during subsequent handling using artificial inoculation, simulating occurrences that might occur during actual harvest. Infection of tubers by *P. infestans* during the growing season renders them more susceptible to soft rotting caused by contaminating fungi and bacteria, and this is encouraged by high summer temperatures (Sicilia et al. 2002). Conspicuously rotten tubers are removed and destroyed during the selection stage prior to storage. Thus, tubers that were infected during the growth period appear to be uncommon in storage facilities. We hypothesize that the primary factor causing storage rot is tuber infection at harvest. We investigated whether storage rot was associated with both injury to potatoes during harvest and the presence of *P. infestans* sporangia in the soil. We hypothesized that injuries such as scratches, lacerations, and bruising inflicted to tubers during harvest or handling would facilitate contact with soil carrying *P. infestans* sporangia or blighted plant material. Thus, we artificially inoculated injured tubers with *P. infestans*.

Tubers (cv. Snowden, known as susceptible to leaf and tuber blight) manually harvested with every effort made to avoid injury were obtained from the Hokkaido Agricultural Research Center (HARC; Memuro, Hokkaido). The foliage of the potatoes had already died from late blight and the sample tubers were nearly mature and not rotted by *P. infestans* when they were harvested. In total, 360 tubers were harvested and divided into four groups: no injury/no inoculation, no injury/inoculation, injury/no inoculation, and injury/inoculation. Each group contained 30 tubers, with three replicates; the experiment was repeated in 2015 and 2016. Tubers in the injury/no inoculation and injury/inoculation groups were artificially injured by manual shaking in 45-L buckets (stroke width 30 cm; 30 strokes). The tubers filled 33% of the buckets and 10–15 mm of gravel (approximately 250 g in weight) were added. This inflicted surface wounds and bruises to tubers, considered to reflect injuries inflicted by careless harvesting. The strain of *P. infestans* employed was MR13235 isolated in 2013 in Memuro, Japan; it was identified as genotype JP-4, A1 mating type and sensitive to metalaxyl and has been dominant in Hokkaido since the early twenty-first century. Before the strain was used, its pathogenicity was verified by inoculating a total of 18 injured tuber surfaces at approximately 500 zoosporangia/cm^2, followed by incubation at room temperature; all inoculated tubers were rotted with typical

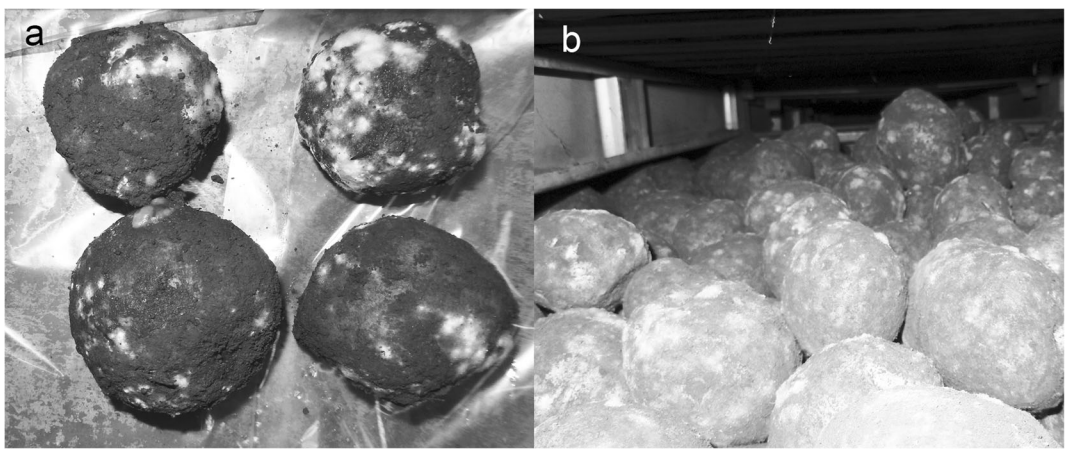

Fig. 1 Rotten tubers prepared in the present study (**a**) and naturally infected tubers in a storage facility (**b**)

hyphal masses and bacterial contamination within 3 weeks. Zoosporangia suspensions were prepared from colonies grown on pea agar media (Andrivon et al. 1994) at 15°C for 2 weeks, and were sprayed onto tuber surfaces at approximately 5000 zoosporangia/tuber. Non-inoculated tubers were sprayed with the same volume of distilled water. After spraying, all tubers were placed in plastic bags (30 tubers/bag) and mixed with uncontaminated soil from an HARC oats field; the soil covered almost all of the tuber surfaces. The soil moisture content was adjusted to approximately 35% with distilled water and the tubers were incubated at 18°C at 99% relative humidity in the dark. Inoculation was performed within 2 h after harvesting. The number of rotten tubers was counted weekly and the percentage of rotten tubers was calculated as follows: rotten tubers (%) = (the number of rotten tubers/the number of tested tubers) × 100. The percentages were then transformed to arcsine and two-way analyses of variance (ANOVA) were conducted with IBM SPSS software version 22.

P. infestans first grew on surface wounds and then gradually extended around the wounds. Vigorous growth of dome-shaped white hyphal masses, on which typical zoosporangia were generally observed, was also frequently evident at the lenticels. The infected tubers were similar to rotten potatoes found in commercial storage facilities (Fig. 1). Rotten tubers in the no inoculation groups did not exhibit hyphal masses; some soft rotting was observed due to fungal and bacterial contamination (besides *P. infestans*) from the uncontaminated soil. Thus, we regarded the rotten tubers in the no inoculation groups as the potential percentage of tuber rot caused by miscellaneous microorganisms besides *P. infestans*. Although the percentage of rotten tubers was somewhat higher in 2016 than in 2015, the results were similar, perhaps because the soil used in 2016 was moister than that used in 2015, due to continuous heavy rain during the growing season that facilitated *P. infestans* growth. The incidence of tuber blight differed significantly in 2015 and 2016 among treatments (Fig. 2). Rotten tubers were minimal, at 1% and 0% in 2015 and in 2016, respectively, if the tubers were not injured, as evidenced by the fact that tubers in the no injury/inoculation group exhibited an extremely low percentage of rotten tubers even when many zoosporangia were present on their surfaces. Similarly, the rotten tubers in the injury/inoculation group increased with incubation time, particularly in 2015.

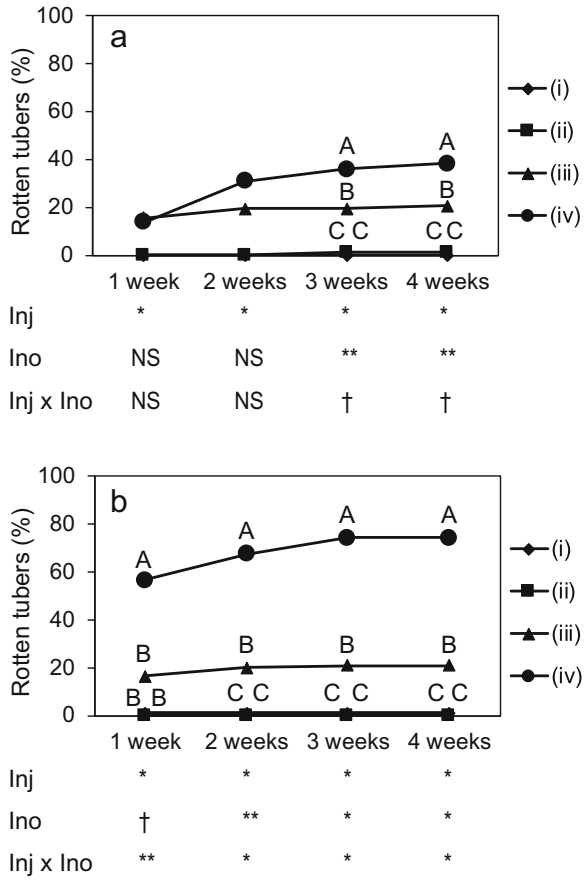

Fig. 2 Rotten tubers after injury and inoculation with *Phytophthora infestans* and the results of two-way ANOVA (Inj, injury; Ino, inoculation; Inj × Ino, interaction). (i–iv) refer to the no injury/no inoculation group, no injury/inoculation group, injury/no inoculation group, and injury/inoculation group, respectively. **a** Data from 2015 and (**b**) 2016. Rotten tubers (%) = (the number of rotten tubers/the number of whole tested tubers) × 100. The mean percentages of rotten tubers ($n = 3$) with different capital letters were significantly different in post hoc tests ($P \leq 0.05$ after Bonferroni correction). *, **, †, and NS indicate highly significant ($P \leq 0.01$), significant ($P \leq 0.05$), borderline significant ($0.05 < P \leq 0.10$), and not significant, respectively

Our results indicate that the development of potato rot during storage depends on whether tubers were injured during harvest. Uninjured tubers rarely rotted, even if there were numerous zoosporangia on the eyes and lenticels, which have been reported as invasion sites. The lack of infection of uninjured tubers by *P. infestans* in the present study might be associated with their maturity, as the tubers were not harvested until 2–3 weeks after the foliage was dead. However, in Japanese potato production, the foliage is usually killed before harvesting. Thus, the results reflect the rot of potatoes during storage in

Japan. Furthermore, uninjured tubers are minimally infected both before and after harvest (Osawa et al. 2016b). The rotten tubers increased with incubation time in the injury/inoculation group. However, the injury/no inoculation group exhibited only small increases in infection over 4 weeks of storage. Thus, percentage of rotten tubers is minimally affected by the presence of *P. infestans* during the first half of the storage period, even if serious surface injuries have been inflicted, because bacterial growth rates are faster than that of *P. infestans*. However, under such conditions, the infection percentage rises during the latter half of the storage period. Tubers harvested from infested fields should thus be shipped as soon as possible. Zoosporangia survived on uninjured tubers in soil for 8 weeks (Akino et al. 2016); this means that tubers that are handled roughly after harvest may rot even if they were carefully harvested. Moreover, removing soil from the tuber surface to keep harvested tubers dry is also assumed to be effective at preventing storage rot.

We conclude that surface injury at harvest and the presence of *P. infestans* sporangia or blighted plant material are important factors affecting the incidence of rotten tubers during storage and our results demonstrate that these factors are even more important than currently considered under Japanese commercial production. Blighted plant material can be reduced by a well-managed chemical protection of the foliage during the growing period. To prevent surface injury at harvest, it is recommended that producers remove pebbles and limit soil compaction through soil conditioning. However, it is impossible to entirely eliminate tuber injuries. Desiccating potato foliage, waiting for a period of time before harvesting (Hirst et al. 1965; Lacey 1965), and proper post-harvest handling conditions such as tuber skin drying before storage, are complementary actions that may reduce potato storage rot during commercial potato production.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Human and Animal Rights and Informed Consent Research involving Human Participants and/or Animals.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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