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RAPID COMMUNICATION

Effect of potato tuber greening on blackleg development by *Dickeya solani* and *Pectobacterium brasiliense*

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Abstract

Potato (*Solanum tuberosum*) is a globally important crop, but its production is often threatened by pectinolytic bacteria of genus *Pectobacterium* and *Dickeya*, including *Pectobacterium brasiliense* (Pcb), and *Dickeya solani* (Ds), which cause two diseases, soft rot of potato tubers and blackleg of potato plants. These pathogens cause a reduction of potato yield, and significant yield losses due to tuber rot in storage. Currently, there are no effective chemical solutions to control these bacterial pathogens. This study aimed to investigate the effect of tuber greening, a process that significantly increases the content of glycoalkaloids (GAs), on the susceptibility of the potato cultivar Tajfun to infection by Pcb and Ds. Tubers were exposed to continuous artificial light for 2 weeks to induce greening. Control tubers were kept in the dark under the same environmental conditions. Then, tubers were infiltrated with Pcb and Ds under low pressure to ensure efficient bacterial penetration and planted in pots under controlled conditions. After 3 weeks phenotypic symptoms of bacterial infection such as wilting, overall plant vitality and stem necrosis were determined. Results showed a significant reduction in Ds infection in greened tubers compared to non-greened controls, supporting the hypothesis that greening which increases GAs levels, enhances resistance to bacterial pathogens. The response to Pcb was more variable, with some plants grown from greened tubers still exhibiting high levels of infection, suggesting that while greening may reduce susceptibility, the greater aggressiveness of Pcb may limit the protective effects of greening. In conclusion, the present study showed that tuber greening could be an effective non-chemical method for controlling blackleg, particularly against Ds. However, the variable response to Pcb indicates that additional strategies are needed. Future research should focus on integrating GAs-based defenses with potato cultivars that exhibit stronger resistance to pectinolytic bacteria for improved management of blackleg.

Keywords: bacterial pathogens, glycoalkaloids, pectinolytic bacteria, plant protection, resistance, *Solanum tuberosum*

Introduction

Potato (*Solanum tuberosum*) is one of the most important crops worldwide, both in terms of its nutritional value and economic importance (Nahirñak *et al.* 2022). However, potato production is often challenged by bacterial diseases such as soft rot and blackleg, caused by pectinolytic bacteria from the genera *Dickeya* and *Pectobacterium* (van Gijsegem *et al.* 2021). Of these, *Dickeya solani* (Ds) and *Pectobacterium brasiliense* (Pcb) have emerged as particularly aggressive pathogens, causing significant losses in potato production. Latently infected seed tubers are the main source of infection. Plants grown from these tubers, under conditions favorable to the development of the disease (wet and warm weather), may show symptoms of blackleg. Otherwise, the plants may not show any visible symptoms. However, the mother tuber may rot, and bacteria spreading in the soil may infect offspring tubers. Bacteria can enter the tuber through wounds, lenticels, roots, and stolons. They can survive the winter as latent infections in seed tubers and be transmitted to the next generation, or if storage conditions are not appropriate (high humidity and warmth), tuber rot can occur. (Czajkowski *et al.* 2011; Lebecka *et al.* 2019; Motyka-Pomagruk *et al.* 2023). In Europe, for example, the total loss in the potato sector due to pectinolytic bacteria is estimated to be around €46 million per year, with the downgrading of seed potato plantations accounting for 32% of these losses, the ware potato sector for 43% and the processing potato sector for 25% (Dupuis *et al.* 2021). There are currently no effective commercial solutions for managing these bacterial pathogens in seed potato production, either during field cultivation or in storage facilities (Czajkowski *et al.* 2011; van der Wolf *et al.* 2021). Blackleg pathogens are difficult to control due to their presence in the vascular system of potatoes, rendering traditional treatments ineffective (Dupuis *et al.* 2021; Toth *et al.* 2021). The inheritance of resistance to pectinolytic bacteria is a complex trait and breeding potato cultivars with high levels of resistance is difficult (Charkowski *et al.* 2020).

Potato naturally produces toxic steroidal alkaloids – glycoalkaloids (GAs). In cultivated potato two major GAs such as α-solanine and α-chaconine comprise 95% of recognized GAs. They play an essential role in plant defense mechanisms (Friedman 1997). Their synthesis and concentration significantly increase during pathogen and herbivore attacks. They also pose a feeding deterrent for potato aphids, leafhoppers, and snails. The group of GAs called leptines, acetylated forms of α-chaconine and α-solanine, are responsible for foliar resistance to the Colorado Potato Beetle (Rangarajan *et al*. 2000). In potato tubers, GAs are unevenly distributed in the tissues, where the highest concentrations are under the tuber skin in the phelloderm (Ginzberg *et al*. 2009). Several abiotic factors can increase GA concentration in tubers including damage by machinery in the field, low temperature, and exposure to sunlight (Percival and Dixon 1996). These compounds have been shown to have significant antimicrobial properties. While much of the research has focused on their antifungal effects and antibacterial properties against Gram-positive bacteria, recent evidence suggests that GAs may also have bactericidal or bacteriostatic effects against plant pathogens such as *Pectobacterium* and *Dickeya,* Gram-negative bacteria (Fewell and Roddick 1993; Grunenfelder *et al.* 2006; Lelario *et al.* 2018; Al Kabee 2019; Sołtys-Kalina *et al.* 2023). Potato tubers contain many starch-storing amyloplasts. When exposed to light, they develop into chloroplasts in the peripheral cell layers (Muraja-Fras *et al.* 1994). In particular, blue and red wavelengths increase the synthesis and accumulation of both, chlorophyll and GAs in tubers (Okamoto *et al.* 2020). Thus, long-term exposure of potato tubers to light stimulates two independent responses: greening and GAs synthesis.

The aim of the study was to evaluate if the greening of potato seed tubers which increases the content of GAs, alters the severity of blackleg symptoms in plants cultivated from seeds that were vacuum inoculated with bacteria.

This study provides new insights into the potential of greening as a natural, sustainable method of increasing blackleg resistance.

Materials and Methods

Two bacterial strains, known for their high aggressiveness towards potato, were used in this study: *Pectobacterium brasiliense* Pcb3M16 from the collection of Plant Breeding and Acclimatization Institute – National Research Institute, Division at Młochów (Lebecka and Michalak 2020) and *Dickeya solani* IFB0099, kindly provided by Prof. Ewa Lojkowska (see the Acknowledgments), synonymous with IPO2276 (Plant Research International collection in Wageningen, The Netherlands) (Golanowska *et al.* 2015).

Potato tubers (cv. Tajfun) from the Pomeranian-Masurian Potato Breeding Company in Strzekęcino were greened by exposure to artificial light in a phytotron for 2 weeks (24 hours day, 19°C, 2000 lux). The absolute light density received by the seed tubers was about 26 µmol $m^{-2} \cdot s^{-1}$ (Light spectrum: from 400 to 700 nm).

One batch of tubers was kept under identical conditions but without light exposure and used as a control. A total of 160 tubers were prepared for two independent experiments. In each experiment, 40 greened and 40 non-greened tubers were used, out of which 20 were inoculated with Pcb and 20 with Ds. The inoculation process was carried out according to a modified method of Hélias (2000). Bacterial cultures of Ds and Pcb (stored at −70°C) were grown on Luria Bertani (LB) agar plates in an incubator at 30ºC for 24 h. They were collected in sterile deionized water and adjusted to a final concentration of 10^9 CFU ml^{-1}, equivalent to an optical density (OD_{600}) of 1.0. The concentration was checked using a spectrophotometer (Hitachi U-1900). In the first experiment, the bacterial suspensions were diluted to the concentration of 10^6 CFU ml^{-1}, and in the second experiment to the concentration of 10^3 CFU ml^{-1}.

Potato tubers were pre-soaked in water for 17 hours prior to inoculation at 20°C to promote lenticel opening and facilitate bacterial entry. Tubers were immersed in bacterial suspensions and subjected to vacuum infiltration at 0.05 MPa for 20 minutes to ensure efficient bacterial penetration. After inoculation, the tubers were allowed to air dry for 2 hours before being planted in pots. They were then placed in a phytotron (16 hours day/8 hours night at 24°C). Three weeks post emergence, plants were assigned a score based on phenotypic symptoms such as wilting, overall plant vitality and stem necrosis. Potato plants were observed for disease symptoms and scored on a scale 0 to 5, where 0 indicated no visible symptoms of infection and 5 indicated lethal infection with complete plant collapse or no emergence. Plants were assigned a score based on several factors, including the extent of visible wilting and overall plant vitality. Differences in stem infection severity were visualized under UV light. The Mann-Whitney U test was used to determine if the two tested groups (greened vs. control) differed significantly.

In addition, infection with bacteria was confirmed by their isolation from the stems of green plants. Stem pieces were kept in LB liquid medium and then, after 48 hours of incubation at 28°C, the suspension was centrifuged, and the pellet was used for stab inoculation of semi-selective Crystal Violet Pectate medium (CVP). The presence of cavities was observed after 48 hours of incubation at 30°C.

Results and Discussion

The greening process, induced by continuous light exposure for 2 weeks, was visible in greened tubers, which exhibited a characteristic yellowish-green coloration compared to the non-greened controls (Fig. 1A).

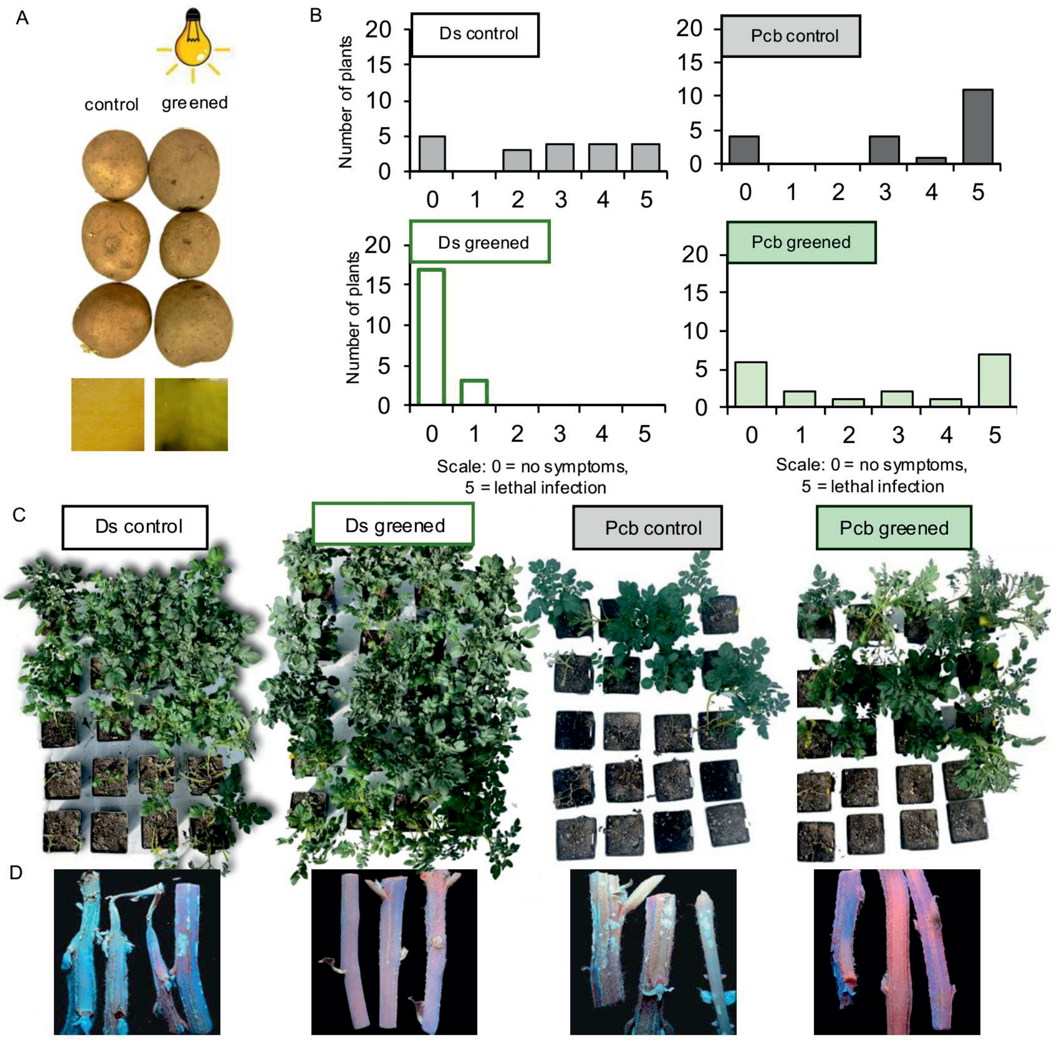

Fig. 1. Disease severity in 3-week-old potato plants (*Solanum tuberosum* cv. Tajfun) grown from greened and non-greened tubers inoculated with *Dickeya solani* (Ds) and *Pectobacterium brasiliense* (Pcb). Each experimental group contained 20 tubers: greened and non-greened (control). A – visual comparison of non-greened (control) and greened potato tubers after 2 weeks of light treatment. B – histograms of frequency distributions of disease severity expressed on a scale from 0 to 5, where 0 meant no symptoms and 5 meant lethal infection. C – the appearance of the plants due to the treatment: Ds control, Ds greened, Pcb control and Pcb greened. D – symptoms of stem infection observed under UV light, showing more severe symptoms in control plants than in plants grown from greened tubers

In the tuber skin of cv. Tajfun the concentration of GAs in the tuber skin increased fivefold compared to non-greened tubers 14 days after exposure to light (data not shown). This agrees with Rymuza *et al.* (2020) who observed that the maximum increase of GAs in tubers of several potato cultivars was observed after 14 days of light exposure. In this experiment, the blackleg symptoms in pot plants obtained from vacuum-infiltrated tubers with bacteria Ds and Pcb were investigated. When tubers were soaked in a bacterial suspension, in the first experiment, a higher inoculum concentration of 10^6 CFU ml^{-1} was used for tuber inoculation, the level of infection in the two groups, greened and non-greened control for each bacterial strain, did not differ significantly according to the Mann-Whitney U test (data not shown). There was a difference in the severity of symptoms between the two bacterial strains, plants inoculated with Pcb showed more severe symptoms of infection (mean 2.15 in control and 3.45 in greened tubers), whereas plants inoculated with Ds showed very weak symptoms (mean 0.60 in control and 0.25 in greened tubers). The differences between the two independent groups (control vs. greened) for each bacterial strain were not statistically significant according to the Mann-Whitney U test. Therefore, in the second experiment, the inoculum concentration was reduced to 10^3 CFU · ml^{-1}.

In the second experiment, in the control group of plants developed from non-greened tubers soaked in Ds suspension, only five out of 20 plants showed no symptoms of infection (Fig. 1B, C) and the mean score was 2.7. In contrast, 17 out of 20 plants grown from greened tubers showed no symptoms of infection (Fig. 1B, C) and the mean score was 0.15. A significant difference was observed when comparing these two groups according to the Mann-Whiney test U test ($p = 0.000$). In plants grown from control tubers inoculated with Ds, necrotic spots were observed along the stem under UV light, in addition to the typical blackleg symptoms observed (Fig. 1D). In contrast, plants grown from greened tubers had significantly lower infection levels (Fig. 1B).

The response of plants developed from tubers soaked in Pcb suspension was more variable, with a mean score for control plants of 3.55 and 2.45 for greened tuber plants. There was a difference between the two groups, but it was not statistically significant ($p = 0.163$) (Fig. 1B, C). In addition, necrotic spots on the stem were occasionally observed and were much less frequent than in control plants (Fig. 1D).

Potato tuber greening in the field and during storage is an undesirable phenomenon in tubers intended for consumption due to light-induced accumulation of GAs. GAs have been shown to have neurotoxic properties and interfere with the mammalian digestive system (Friedman 2006). However, GAs have antimicrobial properties against bacterial and fungal pathogens of potato (Andrivon *et al.* 2003; Fewell and Roddick 1993). These compounds exert their antimicrobial effects primarily by disrupting the integrity of pathogen cell membranes through interaction with membrane sterols. This interaction compromises the structural stability of the cell walls, leading to cellular damage and pathogen death (Keukens *et al.* 1995; Wolters *et al.* 2023). As demonstrated by Dahlin *et al.* (2017) GAs may also act indirectly on *Phytophthora infestans* by forming complexes with sterols in a liquid medium. This process reduces the availability of exogenous sterols, which are essential for the growth of this oomycete. It has recently been demonstrated that GAs affected the mitochondrial structure and tricarboxylic acid cycle enzyme activity of *Fusarium* (Zhang *et al.* 2024). However, there is a significant gap in the available data concerning the direct effects of GAs on bacterial cells. Thus, practices such as greening tubers under artificial light that increase GAs concentration, and planting them as seed tubers in the field can reduce the incidence of blackleg (Sołtys-Kalina *et al.* 2023). Infection of plants developed from inoculated potato tubers with pectinolytic bacteria was confirmed by the isolation of bacteria from stems of plants on a selective medium. The most common medium for the isolation of bacteria is the CVP, on which bacteria cause characteristic cavities as a result of pectin degradation. It contains crystal violet, which inhibits the growth of Gram-positive bacteria (Hélias *et al.* 2012).

In view of previous research on the antimicrobial activity of GAs derived from potato cultivars, cv. Tajfun was selected for the current experiments. The GAs isolated from this cultivar (α-solanine and α-chaconine at a 4:4 ratio) were shown to have the highest antibacterial activity, as evidenced by their ability to significantly inhibit bacterial growth and induce high levels of cell death, as compared to other cultivars studied (Sołtys--Kalina *et al.* 2023). In the present study the greened tubers of cv. Tajfun artificially wounded and inoculated with bacteria at 10^6 CFU · ml^{-1} showed a higher level of resistance than non-greened tubers measured as the weight of macerated tissue after 72 hours of incubation with bacteria (unpublished).

This variability may be related to the aggressiveness of the Pcb strain (Pcb3M16), which is an even more aggressive strain to potato tubers than the highly aggressive strain Ds (IFB0099) (Lebecka and Michalak 2020; Golanowska *et al.* 2015). The rapid spread of the pathogen and its high aggressiveness, especially under favorable environmental conditions, probably contribute to its ability to overcome the GA-based defenses observed in greened tubers. It is very difficult to create natural test conditions. The results of this study suggest that although greening provides some protection against Pcb, the greater aggressiveness of this pathogen, as well as severe infection by bacterial infiltration under pressure, may limit the effectiveness of GAs alone. In studies by Dubois Gill *et al.* (2014), evapotranspiration and soil moisture were shown to be the most critical factors for the number of days to blackleg outbreak. These factors accounted for 50% of the total variance observed, while the total number of diseased plants was influenced by the susceptibility of the potato variety and the aggressiveness of the isolate. The effect of GAs may delay the bacteria from reaching the critical level required for the quorum sensing signal to switch on the synthesis of cell wall degrading enzymes. This delay gives the plant more time to grow and become stronger to defend itself. Plants obtained from greened tubers showed improved growth and reduced stem infection, as indicated by visual assessment and UV light analysis (Fig. 1C, D). This finding suggests that the benefits of greening extend beyond the tuber, potentially providing broader protection to the plant and improving its resistance to bacterial infection. The inhibitory effects of GAs, whose concentration increases during greening, may play a crucial role in the early stages of infection, especially during the multiplication of the bacteria after they have entered the tuber tissues. As previously shown, there was a significant inhibition of the bacterial multiplication factor (by about 75%) in the presence of GAs isolated from leaves of potato cv. Tajfun (Sołtys-Kalina *et al.* 2023). Consequently, a reduced number of bacteria in the tuber can move up the stem and down the stem, reducing the number of infected progeny tubers. The improved plant health observed in plants obtained from greened tubers may reflect the systemic effect of the protective effects of GAs, which have been shown to accumulate in various plant tissues and contribute to overall disease resistance (Friedman 2006; Friedman 1997; Sołtys-Kalina *et al.* 2023).

This study demonstrated the potential of tuber greening as a natural method of blackleg control in potatoes. The significant reduction in Ds infection in plants obtained from greened tubers supports utilization of this method as a non-chemical control strategy. However, the variable responses to Pcb, a more aggressive pathogen, suggest that additional control measures are needed. Future research should focus on combining GA-based defenses with other practices, such as using potato cultivars expressing higher levels of resistance to pectinolytic bacteria, to more effectively manage blackleg. In addition to expanding these results, there are plans to determine the impact of the greening process on the susceptibility of the potato cultivars and breeding clones to be infected by Pcb and Ds and the transmission of bacteria from seed tubers to progeny tubers.

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