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Plant traits, growth stage, and ash mass load control the vulnerability of potato, corn, and wheat crops to volcanic ashfall

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Abstract

Current predictive models of ash impact on crops use ash thickness (or mass load) as the explanatory variable but fail to account for other factors, such as plant traits and growth stage, which also influence impact. We conducted a plot experiment with three common crops (potatoes, corn, and wheat), exposing them to representative ash mass loads (0.5 to 9 kg m^{-2}). We recorded visual impacts on the plants at different intervals and estimated yield loss. Distinct impact mechanisms were identified for each crop, including premature flower abscission, irreversible leaf yellowing, desiccation and senescence, and stalk lodging. Exposure of potato, corn, and wheat plants to ash mass loads >1 kg m^{-2} significantly reduced yield, but production quality was largely unaffected. These results were used to develop new vulnerability functions for estimating yield loss in potatoes, corn, and wheat following exposure to an ashfall event.

Resumen

Los modelos actuales de predicción del impacto de las cenizas en los cultivos utilizan el espesor de las cenizas (o carga másica) como variable explicativa, pero no tienen en cuenta otros factores, como los rasgos de la planta y la fase de crecimiento, que también influyen en el impacto. Realizamos un experimento en parcela con tres cultivos comunes (patata, maíz y trigo), exponiéndolos a cargas de masa de ceniza representativas (de 0,5 a 9 kg m^{-2}). Registramos los impactos visuales en las plantas a diferentes intervalos y estimamos la pérdida de rendimiento. Se identificaron distintos mecanismos de impacto para cada cultivo, incluyendo la abscisión prematura de las flores, el amarilleamiento irreversible de las hojas, la desecación y senescencia, y el encamado de los tallos. La exposición de las plantas de patata, maíz y trigo a cargas de ceniza >1 kg m^{-2} redujo significativamente el rendimiento, pero la calidad de la producción no se vio afectada en gran medida. Estos resultados se utilizaron para desarrollar nuevas funciones de vulnerabilidad para estimar la pérdida de rendimiento en patata, maíz y trigo tras la exposición a un evento de caída de cenizas.

Keywords: Volcanic ash; Impact; Crops; Vulnerability functions.

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1 Introduction

Most volcanic soils formed from volcanic ash deposits are found in proximity to Pleistocene and Holocene volcanoes [Shoji et al. 1993]. These soils are usually highly fertile and offer excellent agronomic potential, providing food to hundreds of millions of people [Shoji and Takahashi 2002; Dahlgren et al. 2004; Delmelle et al. 2015]. However, their long-term fertility is contingent on the periodic inputs of fresh ash material from explosive volcanic eruptions. While beneficial for soil fertility in the long run, ashfall can damage crops, posing a direct hazard to agricultural production and the livelihoods of people who depends on it [FAO 20232]. Volcanoes that nurture agriculture also threaten it.

The most severe impacts of ash fallout on vegetation typically occur close to the volcano, where thick ash deposits cause burial and irreversible destruction of plants [Blong 1984]. Damage decreases as the ash deposit thins with distance downwind from the volcano. However, a millimetric to centimetric layer of ash can still harm crop plants by injuring foliage, hindering photosynthesis, destroying reproductive organs, and damaging fruits [Cook et al. 1981], overall resulting in lower yields and reduced product quality [Ligot et al. 2022; 2024b]. While crop production may be compromised for just one growing season, in some cases, the impact can persist for several years. For large explosive eruptions, thin ash deposits can blanket the land over a broad area, sometimes covering up to several thousand square kilometres downwind. Ash-induced damage to crops can then translate into significant economic losses for the region.

While the negative impact of volcanic ash on crops has long been recognized, the risk remains poorly understood, and effective strategies for mitigating it, such as early warning systems, preparedness planning, and pre- or post-event interventions, are still lacking. Quantifying this risk requires a comprehensive examination of crop vulnerability to ashfall, defined here as the potential loss in yield. In line with observations following the 1943–1952 eruption of Paricutin, Mexico [Eggler 1948], and the 1980 eruption of Mount St. Helens, USA [e.g. Mack 1981; Blong 1984; Antos and Zobel 1985], more recent post-eruption impact assessment studies highlight that ash deposit thickness is the primary variable influencing crop dam-

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age [Wilson and Kaye 2007; Craig et al. 2016; Ligot et al. 2022; 2024b]. Thus, ash accumulation on the ground, measured either as mass load or deposit thickness, is the hazard intensity metric most closely correlated with impact severity. Other characteristics of the ash deposit, including particle size distribution, presence of soluble salts on ash surfaces and/or hydrothermal minerals in the ash material, can also influence the capacity of ash to inflict damage to plants [Blong 1984; Ayris and Delmelle 2012; Ligot et al. 2023]. However, data paucity hinders our ability to quantitatively assess the contribution of these factors to crop impacts.

The ash mass load or deposit thickness is commonly used to develop so-called impact/damage state scales and vulnerability functions [Wilson and Kaye 2007; Jenkins et al. 2015; Craig et al. 2021]. These approaches link ash accumulation to the extent of damage across various crop categories [Bignami et al. 2012; Craig et al. 2021]. When combined with the spatial distribution of ash deposits over agricultural areas, impact/damage state scales and vulnerability functions allow for calculation of potential yield loss risks for different crops [Ligot et al. 2024a; b]. Such information is needed to inform the development of strategies to minimize the impact of eruptions on agriculture. Existing impact/damage state scales and vulnerability functions for crops, derived from field observations collected after eruptions, exhibit a higher degree of uncertainty for low ash mass loads (<10 $kg\,m^{-1}$) compared to heavier deposits [Wilson and Kaye 2007; Jenkins et al. 2015; Craig et al. 2016; Ligot et al. 2024b]. This suggests that other non-volcanic factors, such as plant-specific characteristics, rapid erosion of ash by rain or wind and—possibly—human intervention, modulate the impact at lower ash loads. However, their influence becomes minimal when ash mass loads are high enough to cause destruction or severe damage. Low confidence in the predicted vulnerability of crops to low ash mass loads undermines the reliability of yield loss estimates for thin ash deposits covering large areas in the case of large explosive eruptions (Volcanic Explosivity Index (VEI) ≥ 4), or smaller areas in the case of the less explosive but more frequent eruptions. This emphasizes the need for more comprehensive impact data to better understand the non-volcanic factors that influence crop vulnerability to ash.

Local farmers often report that ashfall impacts on crops vary not only by crop type but also by the timing of the eruption [Wilson et al. 2007; Ligot et al. 2022; 2024b]. This points to the critical role of plant traits and growth stages in determining crop vulnerability to ash at different mass loads [Blong 1984; Antos and Zobel 1985; Ayris and Delmelle 2012; Arnalds 2013]. Recent studies on several vegetable crops exposed to simulated ashfall under controlled greenhouse conditions [Ligot et al. 2023; 2024a] have confirmed this view. These experiments unambiguously demonstrated that crown architecture and leaf pubescence influence ashfall interception and retention, ultimately affecting crop vulnerability to ash. Similarly, temporal patterns of plant growth and development, particularly the onset and duration of specific life stages, play a key role in modulating the severity of ash-related damage to vegetable production. Therefore, the timing of ash deposition, combined with the crop calendars, determines the temporal dynamics of risk.

While the cited greenhouse studies have generated valuable insights, applying vulnerability data acquired in controlled settings to real-world field conditions requires caution. Various factors not accounted for in greenhouse experiments, such as inter- and intra-species competition, weather, and human mitigation efforts, also influence crop yields. This difficulty can be partly alleviated by assessing crop vulnerability to ash in experiments conducted at the plot level under near-field conditions. The primary objective of our study was to evaluate how plant traits, growth stage, and ash mass load collectively affect crop vulnerability to light ashfall in near-field conditions. To this end, we subjected potato, corn, and wheat plants to simulated ashfall within a high tunnel and assessed its impact on growth and production quantity and quality. These crops are globally significant and widely cultivated in volcanically active regions, including the Andean Cordillera, Central and North America, the Philippines, and Indonesia [FAO 2022], making them particularly vulnerable to ashfall hazards.

2 Material and Methods

2.1 Experimental site, plot management, and plant material

The crop vulnerability experiment took place in 2020 and 2021 at the Centre Alphonse de Marbaix, a farm owned by Université catholique de Louvain in Belgium. Potatoes (*Solanum tuberosum L.*) and corn (*Zea mays L.*) were planted in open-ended high tunnels in April and May 2020, respectively, and winter wheat (*Triticum Aestivum*) in November 2020. Potatoes and corn were grown on two 24 × 6 m plots (Figure 1A and 1B) under organic certificate. The same plots were subsequently reused for the cultivation of wheat (Figure 1C and 1D). We verified that soil fertility was adequate and distributed homogeneously across each plot (Supplementary Material 1; Table S1). The soil was ploughed and received fertilization (2 $t\,ha^{-1}$ of TM ORGANIC.B in April 2020 for potatoes and corn, and 1 $t\,ha^{-1}$ of TM ORGANIC.B and 0.1 $t\,ha^{-1}$ of TMS.B in March 2021 for wheat).

We used the 'Sevilla' potato cultivar, known for its low nitrogen requirements and excellent resistance to late blight disease [Vos 2015]. For corn, we selected the 'Asteroïd' cultivar, an early mixed corn variety suitable for forage and grain production, delivering high yields in the temperate maritime climate of Belgium [Euralis 2018]. The 'Alessio' wheat cultivar, characterized by its bearded and semi-late inflorescence emerging (heading), was chosen for its frost and disease tolerance and high yield [Lemaire Deffontaines 2019]. Potato tubers (35–50 mm) were planted in late April with a spacing of 25 cm between plants and 75 cm between rows, resulting in ~53,000 tubers ha^{-1}. Corn grains were sown in early May with a spacing of 15 cm between plants and 75 cm between rows, corresponding to a density of ~95,000 grains ha^{-1}. Wheat grains were seeded in November with row spacing of 15 cm, corresponding to a density of ~2,000,000 grains ha^{-1}. In comparison to yields obtained in Belgium or northern France for the same varieties (10.2, 6.3, and 44 t ha^{-1} for corn, wheat and potatoes, respectively [Euralis 2018; Abras et al. 2020; Dumont

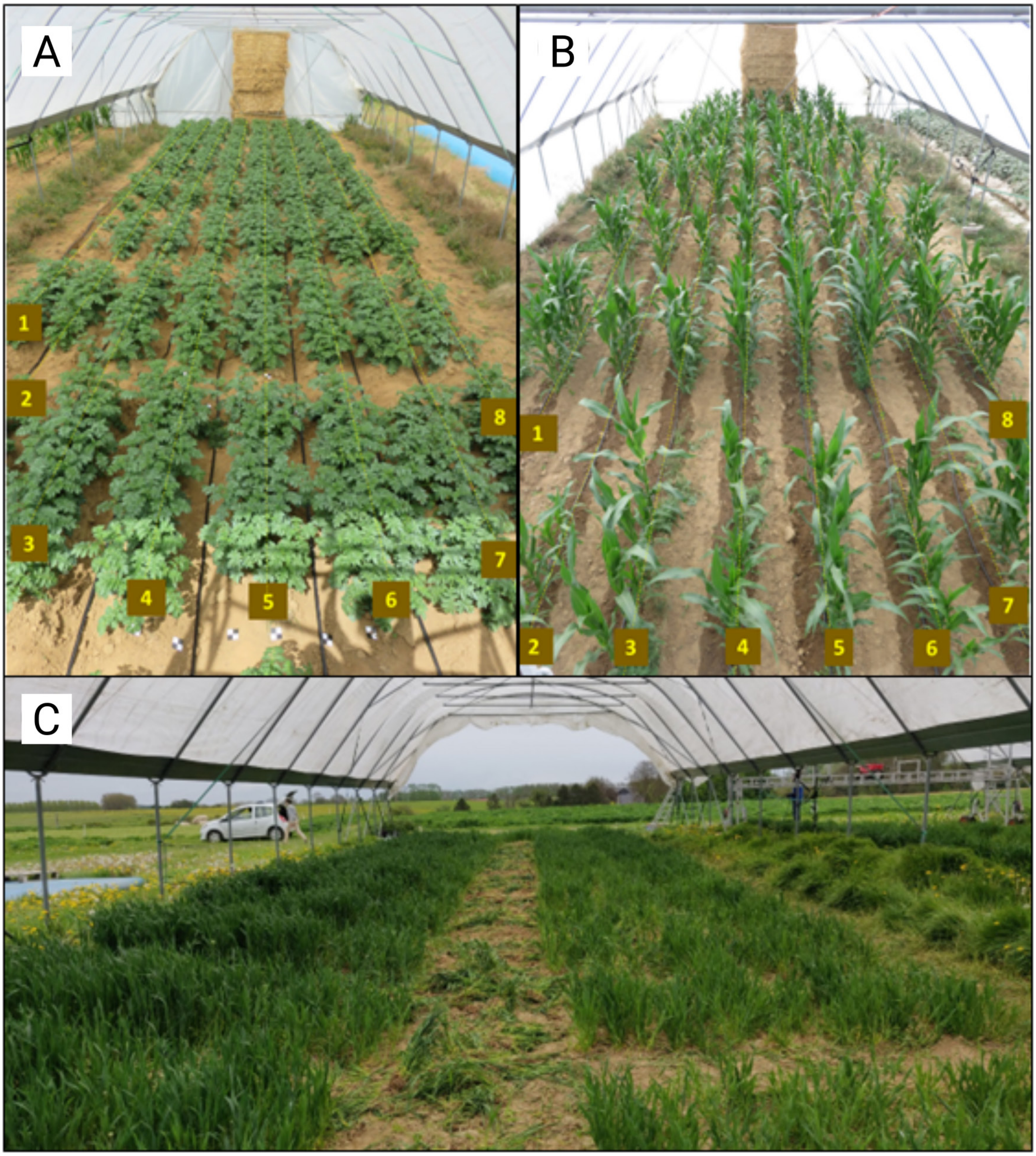

Figure 1: Photos of the experimental setup. Potato [A], corn [B], and wheat [C] were grown in subplots in open-ended high tunnels. Crop rows for potato and corn are numbered from 1 to 8 (left to right). Plants between the wheat subplots were removed to allow passage. Each crop received water through a drip irrigation system installed on the ground.

and Sinnaeve 2021]), the control plantations produced optimal yields (8.7, 7.2, and 42.3 t ha^{-1}, respectively).

Hourly air temperature, humidity, wind direction, wind speed, and solar radiation were recorded throughout the entire duration of the experiment (Supplementary Material 1; Figure S1) in one of the high tunnels using a weather station (METER Em50 data logger) installed ~2 m above the ground. The roof, north side, and west side of the high tunnel were closed off (in early July 2020 for potatoes and corn, and in May 2021 for wheat) and potato, corn, and wheat plants were exposed to relatively low wind speeds (0.5–1.5 m s^{-1} or 2 on the Beaufort scale). Following the covering of the high tunnels, the plots received regular irrigation using a drip system (Figure 1). Weed management for potatoes and corn was carried out in June

2020 during ridging and harrowing, respectively, and then manually in July and August 2020. The wheat plots were harrowed in March 2021. Around eight to ten weeks after planting, potatoes were sprayed with 2 kg ha^{-1} of Bordeaux mixture (Hydro-super 25 WG) to prevent blight disease. Before applying ash to potatoes, corn, and wheat, we ensured that plant growth was uniform across the subplots (Supplementary Material 1; Figures S2–S4, Tables S2 and S3). Wheat emergence was slightly uneven between subplots, but no outliers were identified in the grain production dataset.

2.2 Ash treatments

According to a post-eruption impact assessment study [Ligot et al. 2024b], potatoes, corn, and wheat exhibit the highest yield loss when they receive ash during the "flowering" stage. We subjected potato, corn, and wheat plots to simulated ashfall 84, 91, and 186 days after planting/sowing, respectively. This coincided with the second flowering stage in potatoes, the emergence of silks in corn, and heading in wheat. The available space in the wheat plot allowed for testing two additional growth stages: the first node becoming visible during stem elongation and the milk stage during grain ripening (occurring 174 and 221 days after sowing, respectively), which we will refer below to as "growth" and "maturation", respectively.

The ash material used in our experiments was prepared by crushing a fresh volcanic rock of phonolitic composition obtained from a quarry near the Laacher See (Ligot et al. [2023]; Supplementary Material 1 Table S4; Figures S5 and S6). To apply ash to the plants, we used a modified rolling salt spreader (Western WB-160D) retrofitted with a container (100 × 40 × 60 cm) and installed on a 7-m-long rail with an adjustable height (Figure 2). Prior to treating the potato, corn, and wheat plots with ash, we ensured that the ashfall generated with the spreader formed a uniform deposit on the ground (Supplementary Material 1 Table S5).

Potatoes, corn and wheat plants were exposed to three ash mass loads: 1, 2, and 5 kg m^{-2}; 1, 2, and 5 kg m^{-2}; and 0.5, 2, 5, and 9 kg m^{-2}, respectively. These are equivalent to ash deposit thicknesses of ~1, 2, and 5 mm; 1, 2, and 5 mm; and 0.5, 2, 5, and 9 mm, respectively (assuming a typical bulk density of 1 g cm^{-3} for the ash deposit [Eychenne et al. 2012]). Given that manually shaking the plants to remove ash that has accumulated on crop foliage is a mitigation strategy sometimes adopted by farmers [Wilson et al. 2007; Ligot et al. 2022; 2024b], we also assessed whether this method could partly mitigate impacts of ash on potato and corn plants. Subplots where plants were shaken manually one day after ash application are referred to as "with mitigation". For potatoes and corn, each treatment (six in total) was applied to a subplot comprising ~64 plants (covering an area of ~12 m^2) and 72 plants (covering an area of ~7.8 m^2), respectively. In addition, two subplots with pristine potato and corn plants were used as controls. In the case of wheat, the twelve treatments were spatially replicated four times within subplots of 0.9 × 2.5 m (area of 2.25 m^2) and eight subplots with pristine wheat plants were used as controls, with four in each high tunnel. The arrangement of the potato, corn, and wheat subplots within the high tunnels is depicted in Supplementary Material 1 Figure S7.

Figure 2: Photo of the ash spreader used to apply ash to the crop plants (here potatoes). The ash spreader consists of an ash box installed on a 7-m-long rail. The spreader is pulled manually with a rope allowing ash particles to exit the device through 20 holes located at the bottom of the ash box.

2.3 Data collection

2.4 Ash interception by and retention on plant canopy

Ash interception by potato, corn, and wheat foliage, as well as its retention over time, were described based on visual observations and photos. A quantitative estimate of ash accumulation on foliage was not feasible, as it could have disrupted the deposits, potentially compromising the experiment integrity. In some cases, ash application caused lodging of corn and wheat plants. We recorded the number of corn plants affected by lodging at 1, 5, 9, and 47 days after ash treatment, as well as the number of wheat subplots where lodging occurred. We also documented whether lodging resulted from corn stalk breakage (>45° angle with the vertical) or bending (<45° angle with the vertical) and noted the location of these occurrences and whether any recovery took place.

2.5 Harvest and crop yield

Mechanical potato haulm destruction took place in early September, and tubers were collected manually four weeks later (i.e. 22 weeks after planting). The tubers collected from each subplot were brushed to remove dirt and then weighed using a balance (precision ±10 g). For corn, plants were harvested manually in early October (i.e. 20 weeks after sowing), when the grains were still moist, and the leaves were green. Since corn is a mixed variety grown for both forage and grain, we determined by weighing both the total and grain productions. The harvest was split into two parts: one half consisted of all aerial plant parts (the whole plant), while the other half involved separating the ears from the stalk and leaves. Dry matter content was measured (in triplicate) for the whole corn plant, stalk+leaves, and grains after drying ~1 kg of the material at 105 °C for 72 hours. The fresh and dry biomass weights were highly correlated (R^2 = 0.95, 0.96, and 0.98

(data not shown), for the whole corn plant, stalk+leaves and grains, respectively), and we report here only the fresh weight measurements. Finally, we counted the grain-filled ears in the harvested corn plants and measured the total fertilized and unfertilized lengths of the ears. Wheat grain and straw were harvested separately in mid-August 2021 (i.e. 36 weeks after sowing) with a small combine harvester. The grain and straw productions were weighed to calculate the yield. Additionally, we measured the grain humidity for a 100 g sample of grains with a grain moisture meter. For both corn and wheat, plants that had lodged were included in the harvest.

For the different harvested plant parts (potato tubers, whole corn plants, stalk+leaves and grains, and wheat grains and straw), we quantified the yield (Y, t ha^{-1}) by dividing the production by the surface area. For corn and wheat grains, we also calculated the standardized grain yield (Y_{std}, t ha^{-1}) at 15 % of the fresh weight, which is a common yield indicator [Dumont and Sinnaeve 2021], using:

$$Y_{\text{std}} = \frac{GB}{SA} \times \left(\frac{100 - GH}{85}\right), \quad (1)$$

where GB (t) is the grain fresh biomass, SA (ha) the surface area and GH the grain moisture (%).

We estimated the yield and standardized grain yield loss (YL and YL_{std}, respectively; t ha^{-1}) of the ash-treated plants (*ash*) compared to the control treatment (*cont*) using:

$$YL = 100 \times \frac{Y_{\text{cont}} - Y_{\text{ash}}}{Y_{\text{cont}}}; \quad (2a)$$

$$YL_{\text{std}} = 100 \times \frac{Y_{\text{std-cont}} - Y_{\text{std-ash}}}{Y_{\text{std-cont}}}. \quad (2b)$$

The spatial repetitions of the wheat ash treatments and controls allowed us to compute a confidence interval of one standard deviation ($q_{34.1}$ and $q_{68.2}$, assuming a normal distribution) from the average straw and grain YL. In Equation 2, Y_{cont} and Y_{ash} are substituted by $\bar{Y}_{\text{cont}}$ and $\bar{Y}_{\text{ash}}$, two values generated based on 1,000,000 simulations for Y_{cont} and Y_{ash}, assuming a normal distribution and using the mean and standard deviation values calculated from our experimental datasets. A script written in R (version 3.6.2) was used for these calculations and is available on GitHub* [Ligot et al. 2024a].

2.6 Produce quality

Exposure of potato, corn, and wheat to ash may also reduce produce quality. We assessed the external quality of potato tubers based on size, shape, greening, presence of cracks, and damage due to scab, rot, insects, and/or rodents [Agriculture wallonie 2017]. Following Abras et al. [2020], five tuber size classes were used: <28 mm (I), 28–35 mm (II), 35–45 mm (III), 45–55 mm (IV), and >55 mm (V). Damage level was evaluated based on the percentage of the tuber's surface affected: 0–1 % (trace), 1–5 % (slight), 5–10 % (moderate), and >10 % (severe). The tuber external quality evaluation was performed for half of the production (plants harvested every two plot lines). For corn, we assessed the feed quality (i.e. total protein content, cellulose content, total mineral content, organic matter digestibility, and starch content) of fodders (i.e. shredded whole plant and stalk+leaves). The measurements were performed in triplicate on crushed (1 mm) samples using a near infrared spectrometer (FOSS NIRSystem Auto Cup Sampler [Minet et al. 2016]). Six analyses were carried out to check the bread-making quality of wheat grains: the hectoliter weight, the protein content, the sedimentation value according to Zeleny, the Hagberg falling number, the grain hardness, and the color of wheat flour. All analyses were performed on wheat flour according to protocols established by the Centre wallon de Recherches Agronomiques [Godin 2020].

2.7 Data statistical treatment

The plant yield dataset includes four spatial replicates for wheat, while no yield repetitions were generated for potato or corn. In the production quality data set, repetitions are included for potato tuber size (measurements on each tuber), corn feed quality (measurements on each ear, along with triplicate measurement on the ground fodder per treatment), and wheat grain quality (four spatial replicates per treatment). The effect of ash mass load was tested using a general ANOVA with the `aov` function in the stats package in R (version 3.6.2). When mean values showed significant differences, a post-hoc Dunnett's test was performed to compare them to the control group using the `DunnettTest` function from the `DescTools` package in R. For comparisons across all treatments, a Tukey HSD (honestly significant difference) test was performed using the `TukeyHSD` function from the `stats` package in R. We verified that the data within each group were normally distributed.

3 Results

3.1 Ash interception and retention on plant canopy, and impact of ash on plant growth

Interception of ash particles in potatoes exposed to simulated ash fall primarily occurred on the adaxial hairy leaf surface, forming a continuous coating. However, the stem and flowers were also affected (Figure 3A–3C). Immediately after ash application, leaves covered with ash curled upward and drooped, with this effect lasting for approximately one day. The weight of the ash deposit also caused leaves to bend, leading to some material falling to the ground (Figure 3A). Stem bending only occurred for ash mass loads ≥2 kg ash m^{-2} (Figure 3A and 3B). When potato flowers were opened, the corolla and reproductive organs became coated with ash particles (Figure 3A and 3C), which resulted in drying and abscission in the following days. The reproductive organs of flowers that were closed were not affected by ash deposition (Figure 3C). Six days after treatment, the basal leaves of potatoes exposed to ≥2 kg ash m^{-2} exhibited curling upward and the development of brownish-yellow spots, eventually leading to the drying out of these leaves. A similar phenomenon was observed ~15 days after treating the plants with 1 kg ash m^{-2} (Supplementary Material 1 Figure S8). Gentle manual shaking

*https://github.com/NoaLigot/R_script_total_crop_yield_loss/releases/tag/r_script of potato plants remobilized the ash deposit present on the leaf surfaces (Supplementary Material 1 Figure S9a), although a thin coating remained visible until destruction of the haulm. Direct erosion of ash by wind was minimal for the three crop types, with the primary mechanism for ash loss from plant foliage being organ expansion and swaying of plants exposed to wind gusts (<8 m s^{-1}). In general, ash seemed to be retained in greater quantities on potato foliage when applied at loads ≥2 kg ash m^{-2} (Supplementary Material 1 Figure S9b and Figure S10). Despite the ash covering crop foliage, potato plants were still able to produce new leaves and flowers as they continued to grow.

In corn plants, ash particles accumulated mainly in the leaf axil and on the adaxial hairy leaf blade (Figure 3D and 3F). Some ash settled on the panicle, ear spathes (the leaves surrounding the ear), and silks, as well as on the leaf surface surrounding the stalk (Figure 3D–3H). Silks covered with ash dried out after just one day (Figure 3G), while silks that appeared after ash application remained uncontaminated by ash (Figure 3H). Approximately 3 and 40 % of the corn plants exposed to 2 and 5 kg ash m^{-2}, respectively, underwent stalk lodging (Supplementary Material 1 Table S6). Lodging typically occurred at the base of the stalk or at the point of insertion of the first ear (Figure 4). Sixty days after ash application, all stalks affected by lodging fully recovered in the subplots that received 2 kg ash m^{-2}, whereas only ~50 % returned to a vertical position in the 5 kg ash m^{-2} treatment. In the subplots with the highest ash load, there was a ~5 % plant death rate. Gentle manual shaking of corn stalks remobilized some ash particles deposited on the foliage, leading to their accumulation at the leaf axil or their removal from the plant (Figure 3F; Supplementary Material 1 Figure S11). Similar to what was observed for potato haulm, ash was still adhering to corn foliage when harvest took place. Since the vegetative growth of corn plants was completed when they were exposed to ash, new leaves did not form after the treatment.

Ash was predominantly retained on the leaf axil and the adaxial leaf blade of wheat plants (Figure 3I). Younger leaves located on top of the stalk collected most of the ashfall. However, for ash loads ≥5 kg m^{-2}, these leaves deformed under the weight of the deposit, causing some of the ash to slide off and be retained by the older leaves located underneath (Figure 3K). After plant heading, significant amounts of ash accumulated between the grains of the wheat ears (Figure 3J). As a result of excessive ash loading on the ears, ~50 and 100 % of the wheat subplots exposed to 5 and 9 kg ash m^{-2}, respectively, underwent plant lodging (Figure 4). Regardless of the deposit load, ash was still present on the plant foliage one week after treatment. The higher the initial load, the more ash remained on foliage over time (Supplementary Material 1 Figure S12). At the time of harvest, wheat plants exposed to ash at "growth" and "flowering" were nearly free of ash, with the little remaining ash adhering to leaves due to crusting caused by morning dew. In contrast, plants treated with 5 and 9 kg ash m^{-2} at "maturation" still had ash particles covering the foliage, specifically the ears.

3.2 Crop yield

Potato Y ranged from 32 to 42 t ha^{-1} and was higher for the control group than for the ash-treated plants (Supplementary Material 1 Table S7). Potato subplots treated with 1, 2, and 5 kg ash m^{-2} produced 8, 20, and 25 % less than the control group, respectively (Figure 5). Ash cleaning by manual shaking the plants was inefficient in alleviating the detrimental effect since comparable YL values to those recorded in the absence of mitigation were measured (13, 24, and 18 %, respectively).

The corn total Y ranged from 43 to 59 t ha^{-1}, with the highest value observed in the control group. Compared to the control subplot, application of 1, 2, and 5 kg m^{-2} of ash to corn led to Y reductions of 3, 17, and 27 %, respectively. Subplots where corn plants were shaken manually following ash application had total YL of 6, 6, and 21 % for 1, 2, and 5 kg ash m^{-2}, respectively (Figure 5). A more pronounced impact of the 1, 2, and 5 kg m^{-2} ash treatments became evident when considering grain Y_{std}: without mitigation, YL_{std} reached 13, 34, and 41 %, respectively, whereas with mitigation, YL_{std} amounted to 16, 21, and 39 %, respectively. For the control corn plants, ~14 % (mean value) of the ear length remained unfertilized. The percentages of unfertilized ear length in the 1, 2, and 5 kg m^{-2} ash treatments were 13, 17, and 20 % (without mitigation) and 17, 19, and 21 % (with mitigation), respectively. A higher number of grain-filled ears was found for the control plants (44 ears) compared to the ash-treated plants (without mitigation: 39, 39, and 36 ears at 1, 2, and 5 kg ash m^{-2}, respectively; with mitigation: 41, 42, and 38 ears at 1, 2, and 5 kg ash m^{-2}, respectively).

None of the wheat treatments showed a significant difference in Y values compared to the controls, based on the two-way ANOVA (ash mass load: $F(2)$ = 0.009, p-value = 0.925; growth stage: $F(2)$ = 1.89, p-value = 0.143; Supplementary Material 1 Figure S13). Grain Y_{std} ranged from 5.6 to 8.1 t ha^{-1}. In general, Y_{std} was lower for the ash-treated plants compared to the control plants (7.2 t ha^{-1}), except for wheat plants treated with 0.5 and 2 kg ash m^{-2} at "growth", and with 0.5, 5, and 9 kg ash m^{-2} at "maturation", respectively (7.8, 7.4, 8.1, 7.5, and 7.4 t ha^{-1}, respectively). Plants exposed to 0.5, 2, 5, and 9 kg ash m^{-2} at "flowering" produced 1.3, 3, 11, and 22 % less grain than the control group, respectively (Figure 5; Supplementary Material 1 Table S8). In contrast, exposure of wheat at "growth" and "maturation" to a low ash mass load (0.5 kg m^{-2}) seemed to improve grain production (8.3 and 13.6 %, respectively). Wheat straw Y varied between 7.1 and 9.2 t ha^{-1}, with pristine plants producing an average of 8.9 t ha^{-1}. Irrespective of the applied ash load, exposure to ash reduced the Y by 0.6 to 20.1 % compared to control plants, except for plants treated with 5 and 9 kg ash m^{-2} at "maturation" (−2.5 and −4.4 %, respectively; Supplementary Material 1 Table S8).

3.3 Produce quality

The key results of the potato, corn, and wheat harvest quality analyses are summarized in Figure 6. Additional results are shown in Supplementary Material 1 Figures S14 (potato), S15

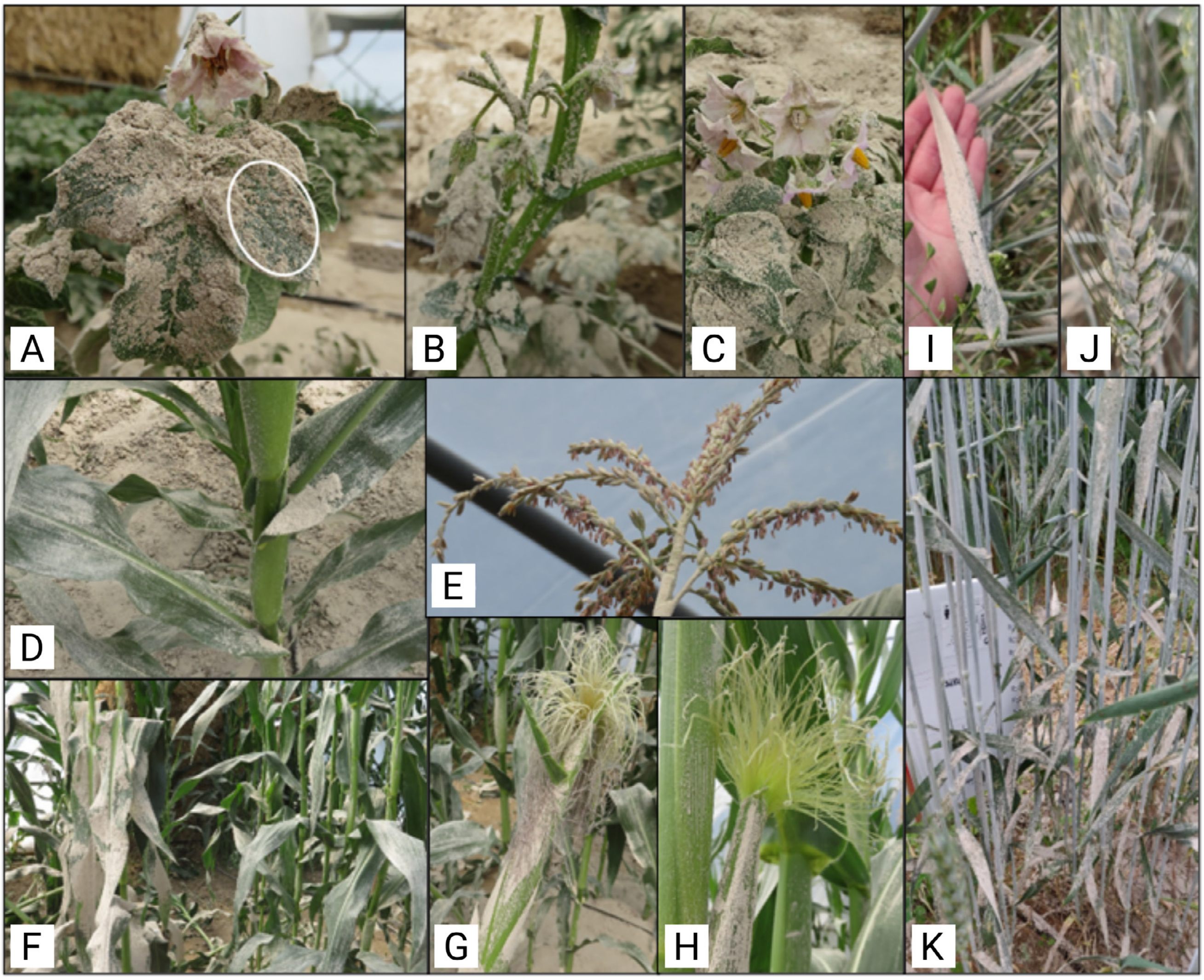

Figure 3: Photos of ash accumulation on potato [A]–[C], corn [D]–[H] and wheat [I]–[K] plant parts one day after exposure to simulated ashfall. Potato: adaxial leave blades and open flower; the white ellipse shows the area of the leaf surface where ash particles had slipped off [A], hairy stem and closed flowers [B], ash-coated and ash-free reproductive organs [C]. Corn: leaf axil [D], panicle [E], bended adaxial blades covered with ash after treatment with 5 kg ash m^{-2} (the plant shown on the right side of the photo was subjected to manual shaking, whereas that on the left side of the photo was not) [F], spathes and recently emerged silks covered with ash [G], silks free of ash emerged one day after exposure to ash [H]. Wheat: leaf axil and adaxial blade [I], ash accumulation between spikelet [J] and upper and lower leaves covered with ash after treatment with $\geq$5 kg ash m^{-2} [K].

(corn), and S16 (wheat). In all subplots, the size of the harvested potato tubers corresponded to class V (>55 mm) (Figure 6A). No significant difference in tuber size was observed between the control and treatments. In general, the tubers had a regular to very regular oblong shape and showed no signs of cracking or greening. In all but one subplot, less than 35 % of the produce had visual defects or disease symptoms, probably due to insect damage and scab. However, this proportion was higher (60 %) for tubers from plants treated with 2 kg ash m^{-2} and when mitigation was applied.

No ash contamination was observed in the corn grains. The results of the corn feed quality analyses are compiled in Figure 6C–6G. Only the results for the whole plant are described as those obtained for stalk+leaves feed exhibited similar trends. The protein content ranged from 7.4 ± 0.2 to 8.1 ± 0.1, with no significant difference between the control and treatment groups (p-value >0.05). The cellulose content in control plants was 15 ± 5 %. In the ash-treated subplots, cellulose content increased with the applied ash mass load, reaching its highest values at 5 kg m^{-2}: 18.4 ± 0.5 % (without mitigation) and 18.6 ± 1.3 % (with mitigation). Similarly, the total mineral content was significantly higher (0.4 % and 0.7 %, without and with mitigation, respectively) for corn subplots exposed to 5 kg ash m^{-2} than for the control subplot. Organic matter digestibility in control plants was 78 ± 1.8 %, whereas lower values were obtained for ash-treated corn, decreasing to 73 ± 0.6 % (without mitigation) and 74 ± 1.3 % (with mitigation) when exposed to 5 kg ash m^{-2}. The starch content also decreased, reaching 3.4 % (without mitigation) and 3.5 % (with mitigation) after exposure to 5 kg ash m^{-2}. Following

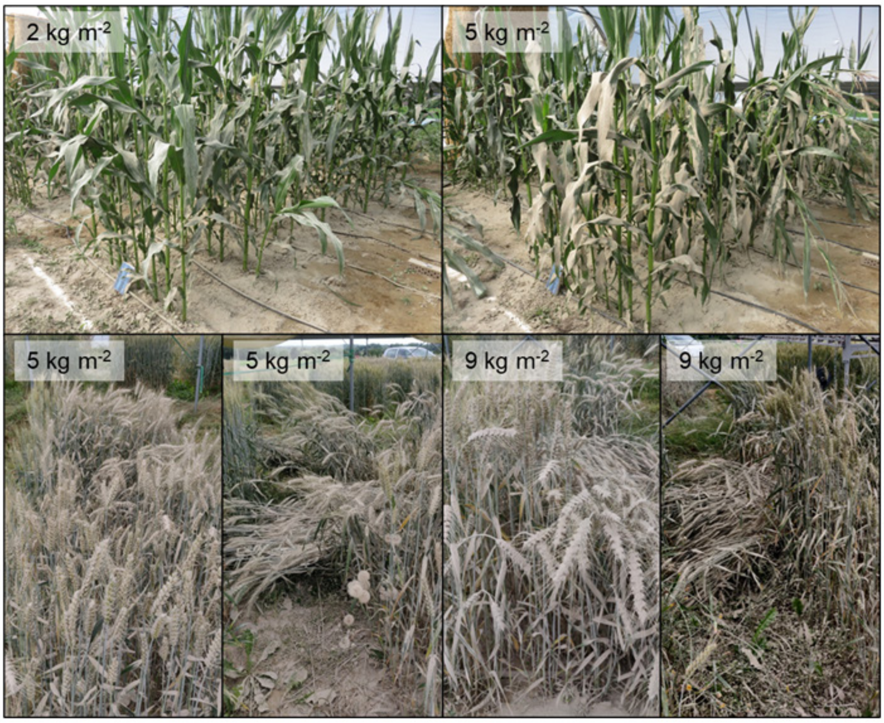

Figure 4: : Photos of lodged plants one day after ash treatment with 2 and 5 kg ash m^{-2} for corn (top row) and with 5 and 9 kg ash m^{-2} for wheat (bottom row).

harvest with the combine harvester, grains from wheat plants exposed to ash at "flowering" and "maturation" were found to be contaminated by ash. The grain hectoliter weight varied between 77 ± 1.3 and 82 ± 0.6 kg hL^{-1} and significantly lower values (between 2.2 and 4.4 %, p-value ≤ 0.05) were found for plants exposed to ≥ 2 kg ash m^{-2} at "maturation" compared to control plants (Figure 6B). The brightness and shine index of wheat flour showed a tendency to decrease (from 83.3 ± 0.2 to 82.6 ± 0.3 and from 79.4 ± 0.1 to 78.8 ± 0.1, respectively) with higher ash mass loads (ranging from 0.5 to 9 kg m^{-2}), although the difference from control plants was not statistically significant (p-value >0.05). Other quality parameters, including protein content, sedimentation value according to Zeleny, Hagberg falling number, grain hardness, and flour color, were not affected by ash significantly.

4 Discussion

4.1 Ash interception and retention by potato, corn, and wheat plants

Based on our visual observations, potato, corn, and wheat plants intercepted and retained ash efficiently (Figure 3; Supplementary Material 1 Figures S10–S12). Potato plants have compound oval leaves attached to numerous horizontal stems, while corn features long and wide spirally-arranged leaf blades on the stalk. Wheat, on the other hand, possesses narrow and upright leaves but can form a dense canopy after tillering. The ability of potato, corn, and wheat plants to intercept ash is attributed to a canopy structure which confers them a high leaf area index typically reaching ~6 in healthy plant populations [Herrmann et al. 2011; Hosseini et al. 2015; Yao et al. 2017]. Regardless of the crop type, ash tends to accumulate primarily on the central portions of leaves, which are stiffer and less inclined than the leaf blade edges. This confirms the importance of leaf angle in dictating ash interception and retention on plant foliage as already observed in the field for various crop types, including rose, black seed squash, cabbage, and lettuce [Cook et al. 1981; Ligot et al. 2023; 2024a]. Furthermore, leaf roughness favours ash retention as it can enable the formation of a thin deposit, even when the leaf angle is not horizontal. Potato, corn, and wheat plants exhibit rough surfaces allowing for ash interception, as also documented for tomato and chilli pepper plants exposed to simulated ashfall in a greenhouse [Ligot et al. 2023]. Hairy leaves in potato and corn, hairy sepal in potato, hairy spathes in corn, and the presence of beard in wheat ear enhance ash interception and retention. In the case of potatoes and corn exposed to ash, leaf roughness probably explains why manual shaking had a limited effect on ash remobilization (Supplementary Material 1 Figures S9–S11).

Giess et al. [1994] showed that a wind speed of 3 m s^{-1} can erode up to 35 % of silica spheres (1–10 µm) deposited on grass, while Auerbach [1970] concluded that 5 % of quartz particles (88–175 µm) present on oak and pine foliage were removed after exposure to ~0.5 m s^{-1} winds. Thus, we anticipate that in a natural environment, light winds (<3 m s^{-1}) will have relatively low potential for entirely eroding ash deposited on potato, corn, and wheat foliage.

4.2 Ash impacts on potato, corn, and wheat plants

The deposition of ash on potato plants resulted in irreversible damage, including yellowing, drying, and senescence

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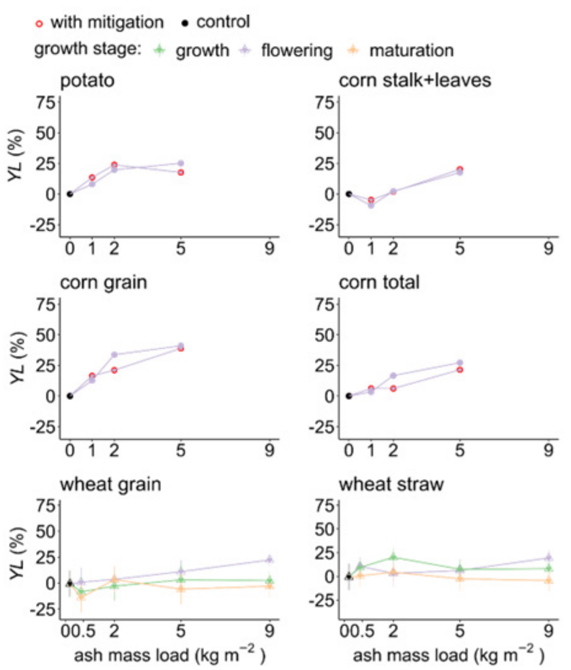

Figure 5: Vulnerability functions depicting the relationship between measured *YL* and ash mass load for potatoes (tuber), corn (stalk+leaves, grains, and total) and wheat (grains and straw) exposed to simulated ashfall at different growth stages ("growth," flowering," and "maturation"). The grain *YL* for potatoes and corn is the standardized grain yield loss (YL_{std}). For wheat, the vulnerability functions represent the mean *YL* and its standard deviation. The input parameters for estimating wheat mean *YL* are listed in Supplementary Material 1 Table S8. The effect of mitigation (manual shaking) on the *YL* of potatoes and corn is also shown.

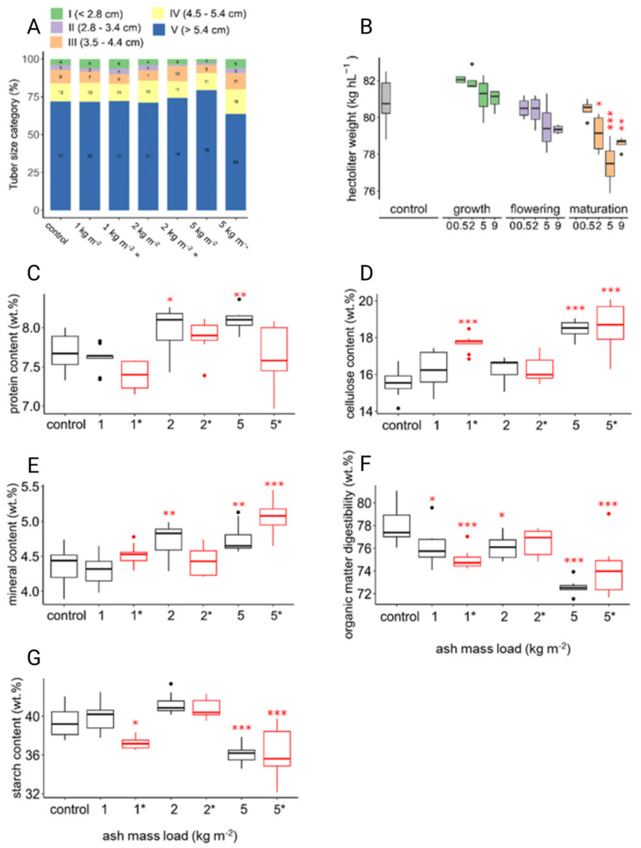

Figure 6: Harvest quality results for the control and ash treated potato (tuber size category [A]), wheat (hectolitre weight [B]) and corn (protein content, cellulose content, mineral content, organic matter digestibility and starch content [C]–[G]) plants. A post-hoc Dunnett's test was conducted to compare the treatments to the control group after confirming significant differences in the datasets using ANOVA. The Dunnett's test *p*-values for the 95 % family-wise confidence level are: (***) 0 <*p*-value <0.001, (**) 0.001 <*p*-value <0.01, (*) 0.01 <p- value <0.05, (.) 0.05 <*p*-value <0.1. The results are also presented in Supplementary Material 1 Tables S9 and S10.

of leaves—primarily basal leaves—as well as the abscission of flowers. The injuries appeared within 15 days in plants exposed to 1 kg ash m^{-2}, but within six days in plants treated with ≥2 kg ash m^{-2}, suggesting an increase in the detrimental effect with higher ash mass loads (Supplementary Material 1 Figure S8c). Changes in leaf coloration and other leaf damage, often documented in areas affected by ashfall, have been commonly attributed to the presence of elevated concentrations of soluble elements in ash [e.g. Miller 1966; Wilson et al. 2007; Stewart et al. 2020]. However, in our experiment, the artificially produced ash particles lacked soluble salts on their surfaces. Thus, we argue that yellowing, drying, and senescence observed for potato leaves covered with ash is not due to soluble salt-induced injuries, but the result of reduced light interception and subsequent lower photosynthetic activity [Weaver and Amasino 2001; Brouwer et al. 2012]. This interpretation is also supported by recent field and experimental data [Ligot et al. 2022; 2023; 2024b]. Flower abscission after exposure of vegetable crops (bean, pea, etc.) and fruit trees (apple, tree tomato, pear, etc.) was often reported by farmers affected by the eruptions of Tungurahua volcano, Ecuador [Ligot et al. 2022; 2024b].

Several observations [Blong 1984; Neild et al. 1998; Craig et al. 2021; Ligot et al. 2022; 2024b] suggest that the production of various crops is particularly susceptible to the impact of ash when the plants are in the flowering stage. Our measurements reveal the vulnerability of potato flowers to even relatively low ash mass loads, as low as 1 kg m^{-2} (or ~1 mm in thickness) (Figure 5). This may be attributed to the structural characteristics of potato flowers, where the stamens and pistil protrude slightly above the corolla. While tuber formation in potato is not contingent on flower fertilization [Jansky and Thompson 1990], production in other crops from the Solanaceae family (e.g. tomato, bell pepper, chilli pepper, and eggplant) which share a similar reproductive organ structure and rely on flower fertilization for fruit formation will be particularly at risk when exposed to ash during the flowering stage.

The exposure of corn silks to ash resulted in their drying out (Figure 3E). This could potentially hinder the transfer of pollen to the ovaries, leading to a limitation in ear fertilization and subsequent grain formation [Tollenaar and Dwyer 1999]. While our dataset did not permit a robust statistical analysis, we observed a ~4 ± 3 % decrease in ear fertilization across all subplots following ash application (Supplementary Material 1 Table S7). Additionally, corn plants covered with ash exhibited a lower number of ears filled with grains compared to the control plants (Supplementary Material 1 Table S7). Given the variation in the timing of pollen release and silk emergence among individual corn plants, flowering corn plants will likely remain vulnerable to ash for several days, the duration sufficient for the completion of fertilization at the crop field scale [Tollenaar and Dwyer 1999].

Stalk lodging affected corn and wheat plants exposed to ≥2 and ≥5 kg ash m^{-2}, respectively (Figure 4; Supplementary Material 1 Table S6). Wheat lodging due to ash accumulation was reported following the 1980 eruption of Mount St. Helens, USA [Cook et al. 1981]. It is attributed to overloading of the plants, leading to a surpassing of the stalk's mechanical resistance. In general, cereals belonging to the Poaceae family, such as corn, wheat, and rice, are prone to lodging, especially during the grain filling stage [Xue et al. 2017]. Lodging in cereal crops is influenced by a combination of plant traits and environmental conditions. It often results from factors like the crop's inadequate standing strength and adverse weather conditions, such as rain, wind, and/or hail. Lodging alters cereal growth and development, leading to reduced Y and compromised grain quality, along with additional harvest expenses [e.g. Pellerin et al. 1990; Berry et al. 2004]. Our observations strongly suggest that ash deposition increases the risk of lodging in various cereal crops (for instance, rice, millet, quinoa, barley), with the level of risk varying depending on the species and varieties.

4.3 Potato, corn, and wheat yield loss

Exposure to ash had a detrimental effect on the production of potatoes, corn, and wheat, and the impact on YL worsened as the ash mass load increased (Figure 4). Furthermore, there is no conclusive evidence that manual shaking of potato and corn plants covered with ash is a mitigation measure that can reduce impact effectively (Figure 4). Washing crops with water might be a potential effective mitigation, but farmers do not necessarily have easy access to this resource. Additionally, it is unclear whether washing would remove ash particles from cereal ears or worsen the issue by facilitating their cementing. In our study, the maximum loss in potato tuber production (~20 %) was observed for ash mass loads ≥2 kg ash m^{-2} (Figure 4), which departs from the assumption of Wilson and Kaye [2007] that root crops are resistant to ash loads of up to 20 kg m^{-2}. It also challenges a previous conclusion that there is a low probability (0.4, n = 4) that root vegetables exposed to 6 kg m^{-2} sustain a 30 % YL [Craig et al. 2021]. Based on 65 interviews with farmers near Tungurahua volcano, Ligot et al. [2024b] calculated a high YL of 63 ± 35 % for root vegetables (mainly potatoes) exposed to 4 kg ash m^{-2}. The comparatively low YL obtained in our experiments is most likely due to the ideal growth conditions provided to the plants, contrasting with the less favourable field situation. In line with other works that have explored the effect of dust on plant physiology [Hirano et al. 1990; 1991], we suspect that the presence of ash on the surface of potato leaves reduced photosynthetic activity, thereby affecting carbohydrate assimilation. This may have led to the remobilization of carbohydrates stored in other plant parts (stems and tubers) to facilitate growth of new leaves [Melis 2013]. In turn, this competition for carbohydrates could have impacted starch storage in the tubers and, ultimately, led to reduction in tuber Y.

Assuming that the loss in potato Y following ash deposition is primarily linked to the proportion of foliage surface area covered with ash [Ligot et al. 2023], we can draw a rough analogy from observations of the impact of defoliation on potato Y. In these studies [Cranshaw and Radcliffe 1980; Shields and Wyman 1984; Irigoyen et al. 2011], the outcome depends on factors such as plant variety, plant growth stage, defoliation intensity and defoliation distribution. For instance, Irigoyen et al. [2011] reported YL of 20 and 40 % in three potato varieties subjected to half and complete defoliation, respectively, at the "flowering" stage. This result suggests that a higher coverage of potato leaves by ash may result in a greater YL. Furthermore, we anticipate that YL will worsen if the ashfall coincides with the first flowering of potato plants, as this phase also corresponds to the initiation of tuber formation [Meier 2018].

Ash application to corn plants led to a reduction in both plant and grain Y; the loss increased with ash mass load, reaching a maximum of 24 ± 4 % and 34 ± 2 %, respectively, in the 5 kg ash m^{-2} treatment (Figure 4). For comparison, based on data (n = 57) collected during a post-eruption impact assessment study, Ligot et al. [2024b] predicted a higher YL of 58 ± 32 % for cereals (mainly corn) exposed to 2.9 kg m^{-2}. Similar to potato plants, the lower YL in corn grain observed in our experiment probably relates to the near-optimal growth conditions. Nonetheless, our findings cast doubt on the claim of Craig et al. [2021] that cereals subjected to 5 kg ash m^{-2} have a low probability (0.4) of sustaining a 30 % reduction in production. We contend that this evaluation, based on only four observations, represents an underestimation of the actual impact of ashfall on cereal production. The detrimental impact of ash on corn Y likely results from a combination of direct and indirect factors, including reduced ear fertilization, lodging (for ash loads ≥2 kg ash m^{-2}) and altered photosynthesis. We note that our YL estimates for corn plants exposed to 5 kg ash m^{-2} are compatible with values reported for plants that had suffered 50 % defoliation at flowering [Egharevba et al. 1976]. The magnitude of production loss in ash-affected corn plants will be influenced by factors such as variety, growth stage and the percentage of leaf surface area covered with ash. Based on Egharevba et al. [1976], we anticipate the greatest YL during the period extending from the onset of silking to ten days after reaching 50 % silking.

The severity of ash impact on the Y of wheat grain and straw depends on the ash load applied and the plant growth stage (Figure 4). In general, grain production decreased as the ash mass load increased, except for plants at "maturation" exposed to 9 kg ash m^{-2}. Wheat plants in the flowering stage were the most vulnerable, exhibiting the highest YL values, ranging from 1.3 to 22 % for ash loads between 0.5

and 9 kg ash m^{-2}. In contrast, exposure of wheat plants at "growth" to ash had Y similar to the control group, whereas those at "maturation" tended to produce more grains. The increased vulnerability of flowering wheat plants to ash probably relates to ash coverage of the ear and flag leaf (the last leaf on the stalk). Photosynthesis in both is responsible for up to 65 % of the grain's sugar content [Racz et al. 2022], but the presence of ash particles can reduce its efficiency. However, when these organs are covered with ash, they will likely perform photosynthesis less efficiently, potentially resulting in reduced grain production. Similarly, Shao et al. [2010] found that the heading stage is the most vulnerable period for winter wheat subjected to defoliation, with the severity of YL proportional to the extent of defoliation [Császár et al. 2021]. Additionally, lodging, which results from exposure to ≥5 kg ash m^{-2} and can affect cereal growth [Berry and Spink 2012], may have contributed to the reduction in grain Y in flowering plants exposed to ash. In our experiment, we harvested the corn and wheat affected by lodging; however, under real-world conditions, agricultural machinery does not harvest lodged crop plants. Thus, lodging of corn and wheat plants represents an additional potential YL in field conditions. In the field, the surface area of lodged cereal crops due to ash accumulation could be estimated using synthetic aperture radar data [Chauhan et al. 2020], offering a means for predicting the associated YL.

Exposure to ash of wheat plants at "growth" did not lead to a significant loss in grain production (Figure 4). This simply reflects that photosynthetic activity was adequate, probably because ash partially covered wheat foliage and the plants were capable of recovering a green canopy after ash deposition through the formation of new leaves. Similarly, grain production in wheat subjected to ash deposition at the "maturation" stage was on par with that of the control plants. Maturing wheat plants have their grains already being filled by sugar translocated from leaves to kernels [Acevedo et al. 2002], and thus ash will not directly affect production. We also anticipate that ashfall will not pose a threat to wheat ovary fertilization, and hence grain production, because pollination usually occurs before the opening of wheat flowers (i.e. cleistogamy, a form of automatic self-pollination [De Vries 1971; Ueno and Itoh 1997]).

4.4 Harvest quality

The ash treatments had no discernible effect on the quality of potato tubers (Figure 6A) but did induce slight alterations in the feed quality of corn (Figure 6C–6G). Although corn ears remained free of ash particles, they contained fewer grains compared to the control plants, suggesting reduced ear fertilization and grain filling (Supplementary Material 1 Table S7). The decrease in starch content and the proportional increase in cellulose content in the forage (stalk+leaves) from corn plants exposed to ash (Supplementary Material 1 Figure S15) may be due to reduced grain number. We suspect that the presence of ash particles adhering to the aerial parts of the plants artificially increased the mineral content in ash-treated corn. Compared to standard corn feed values [Chauveau 2019], no degradation in feed quality was observed after ash application. Nevertheless, it is worth noting that corn leaves were still contaminated with ash at the time of harvest, which could potentially pose a health hazard when used as animal feed. In the case of wheat, ears of plants exposed to ash at the "maturation" stage were covered with ash, and even after threshing, ash particles still contaminated the bare grains. Contamination of wheat grains by ash could have implications for the selling price. This was the case after the eruption of Mount St. Helens [Cook et al. 1981]. The presence of ash particles mixed with the grains may also cause damage to the harvesting equipment [Cook et al. 1981]. Similar to the Y, the hectoliter weight of wheat grain decreased with the ash mass load and is significantly lower for plants exposed to ash during "maturation" (Figure 6). This trend may be attributed to differences in grain size, shape, or the presence of impurities in the sample [Gegas et al. 2010] as reported at Mount St. Helens [Cook et al. 1981]. In our study, the wheat grains were cleaned before analysis and the quality of the harvest compared well with the reference for the Alessio wheat variety grown in Belgium [Dumont and Sinnaeve 2021]. At Mount St. Helens, Cook et al. [1981] reported a similar result, although in this case the grains from the ash-affected plants were not cleaned before analysis.

5 Conclusions

This study constitutes the first experimental assessment of the impact of ashfall on potato, corn, and wheat plants—three agriculturally important crops in volcanically active regions. Visual observations confirm that plant traits, notably canopy structure and leaf surface roughness, are key factors controlling the interception and retention of ash. Distinct impact mechanisms are identified for each of the three crops. Exposure to ash of potato plants at "flowering" led to premature flower abscission. Irreversible leaf yellowing, desiccation, and senescence occurred in potatoes covered by ash, likely due to disrupted leaf photosynthesis. In contrast, corn and wheat plants did not exhibit foliar symptoms following ash deposition. However, at ash mass loads ≥2 kg m^{-2}, corn and wheat were susceptible to stalk lodging. Additionally, the presence of ash particles on corn ear silks may have interfered with ear fertilization, likely reducing subsequent grain formation. Exposure of potato, corn, and wheat plants to ash mass loads >1 kg m^{-2} reduced their Y significantly, but the quality of the production was unaffected. We also showed that, in contrast to potato, wheat is most vulnerable to ash when at flowering, confirming that plant growth stage is a key parameter to consider when evaluating crop vulnerability to ash. Overall, our results provide novel insights into the potential adverse effects of relatively low ash mass loads (<10 kg m^{-2}) on three agriculturally significant crops. They strongly suggest that thin distal ash deposits can impact crop production over a large area downwind of an explosive volcano. Our study confirms that ash accumulation is a key hazard metric that determines the level of impact on crops, and we have generated new vulnerability functions for estimating potato, corn, and wheat YL following an ashfall event. Finally, we reiterate that controlled experiments improve the description of the influence of plant traits and growth stage in dictating crop vulnerability to ash, an aspect that field-based data have failed to address robustly.

We encourage further development of this approach to better understand the temporal variation in vulnerability of different crop types to ash exposure. This will improve our ability to analyse the dynamics of risk posed by ash emissions to agricultural crops in volcanically active regions.

Author Contributions

N.L., P.D., L.B. and H.F. conceptualised the experiments, and N.L. and L.B. conducted them. B.G. contributed the analyses of wheat quality. P.B. advised on the statistical treatment of the experimental results. N.L. analysed the data. N.L. and P.D. wrote the original draft. P.D. secured funding for this research and provided the resources.

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Data Availability

All data can be provided by the corresponding author upon request.

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