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SYMPOSIUM

Rain-induced Ejection of Pathogens from Leaves: Revisiting the Hypothesis of Splash-on-Film using High-speed Visualization

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Synopsis Plant diseases are a major cause of losses of crops worldwide. Although rainfalls and foliar disease outbreaks are correlated, the detailed mechanism explaining their link remains poorly understood. The common assumption from phytopathology for such link is that a splash is generated upon impact of raindrops on contaminated liquid films coating sick leaves. We examine this assumption using direct high-speed visualizations of the interactions of raindrops and leaves over a range of plants. We show that films are seldom found on the surface of common leaves. We quantify the leaf-surface's wetting properties, showing that sessile droplets instead of films are predominant on the surfaces of leaves. We find that the presence of sessile drops rather than that of films has important implications when coupled with the compliance of a leaf: it leads to a new physical picture consisting of *two* dominant rain-induced mechanisms of ejection of pathogens. The first involves a direct interaction between the fluids of the raindrop and the sessile drops via an off-centered splash. The second involves the indirect action of the raindrop that leads to the inertial detachment of the sessile drop via the leaf's motion imparted by the impact of the raindrop. Both mechanisms are distinct from the commonly assumed scenario of splash-on-film in terms of outcome: they result in different fragmentation processes induced by surface tension, and, thus, different size-distributions of droplets ejected. This is the first time that modern direct high-speed visualizations of impacts on leaves are used to examine rain-induced ejection of pathogens at the level of a leaf and identify the inertial detachment and off-center splash ejections as alternatives to the classically assumed splash-on-film ejections of foliar pathogens.

Rain and foliar diseases

Fungal and bacterial pathogens inducing foliar disease cause rust and lesions that can dramatically decrease agricultural yield (Fitt and Mcartney 1986; Campbell and Madden 1990; Madden et al. 2007). Leaf and strip rusts alone can cause up to 60% of the annual loss of wheat worldwide (Park 2007; AHDB 2012). A third of all wheat crops could be lost by re-emerging strains of rust in the coming years (Kona 2010; Dubin and Brennan 2009; Schnepf 2005; The Economist 2010). Besides pesticide-spraying and bioengineered crops, strategies of managing diseases more recently included the introduction of *warning* systems (Gleason et al. 2008; West et al. 2008; Gordon et al. 2014). Similarly to calendar-based spraying, these warning systems rely on past empirical correlations between weather and outbreaks. Specifically, temperature, moisture, and precipitation are some of the many parameters examined for correlation with early appearance of foliar lesions (Fitt 1989; Cooke et al. 2006). The quantification and discussion of rain intensity, defined as the volume of rainwater per unit of time and unit of area, and the splash processes in relation to transport of foliar pathogens have been important endeavors in phytopathology (e.g., Reynolds et al. 1989; Walklate 1989; Walklate et al. 1989; Madden, 1992; Madden et al. 1990, 1996; Yang et al. 1990a, 1990b, 1992; Ntahimpera et al. 1997; Huber et al. 1997, 2006; Williams et al. 1998; Hoberg 2002; Saint-Jean et al. 2006; Travadon et al. 2007; to cite a few). The recent review by Horberg (2002) compiles a summary of the key experimental setups examined during the discussions of splash of raindrops on

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plants. In all such discussions, large droplets resulting from impacts are the focus as they are considered of greater importance for the transport of larger quantities of spores and because of their localized deposition on neighboring plants. Moreover, one can see that the focus remains on the splash of raindrop on a film coating various surfaces (Fitt and Lysandrou 1984; Brennan et al. 1985; Fitt et al. 1988).

Indeed, the physical picture purported to explain rain-induced spreading of pathogens is that of a splash-on-film, where a raindrop impacts a thin film of contaminated fluid coating leaves (see Fitt et al. 1989; Yang et al. 1990a, 1990b, 1992; Dunkerley 2009 for example). The coating is considered to be a suspension of pathogens. This film is formed, for example, from condensation during the moist ambient conditions preceding rainfalls (e.g., Fitt et al. 1989; Walklate 1989; Walklate et al. 1989). The effects of the intensity of rainfall are rationalized with this physical picture in mind, as discussed more extensively in ''The intensity of rainfall and splash-dynamics: the missing link'' section (e.g., Carisse et al. 2006). However, despite numerous studies examining simulated rainfall and dispersal on real (see above references) and artificial leaves (e.g., Horberg 2002), the efforts remained focused on empirical links between simulated rainfalls and outcomes of contamination around the targeted plant or leaf (e.g., Madden and Ellis 1990; Yang et al. 1990a, 1990b, 1992; Madden et al. 1996; Ntahimpera et al. 1997). Little has been done to understand the mechanism of raindrop-leaf interaction governing the detachment that ultimately shapes the patterns of dispersion typically observed macroscopically around the contaminated plant or leaf. For example, Huber et al. (2006) described the splash process, commonly discussed in phytopathology, as a black box in which the details of the impact are ignored. Only the cumulative variables and correlations are used to link input (e.g., rainfalls) and output (patterns of transmission) at the macroscopic level surrounding the infected targets.

The above scenario leaves us with little understanding of the fundamental physics governing epidemiological outcomes (e.g., Yang et al. 1991; Fitt and McCartney 1986). In other words, the splash-on-film scenario as a main mechanism governing the dynamics in the *black box* (Dunkerley 2009) remains conjectural. In the present article, we zoom into the details of the raindrop-plant interaction and examine whether the impacts at the level of the leaf are indeed dominated by splash-on-film events.

Plant targets used in the macroscopic studies discussed above typically focused on rigid artificial surfaces or leaves deposited on rigid surfaces (e.g., Walklate et al. 1989; Fitt et al. 1992; Huber et al. 2006). Although evoked, flexibility of the leaves in shaping the outcome of the dispersion and possibly changing the nature of the impact-on-film scenario was not examined previously. We discuss the qualitative effect introduced by compliance of the foliage and, in an experiment on a population at a larger scale, link such an effect to the expected outcomes of ejection of droplets.

In the spirit of the symposium linking surface tension and biology, our short article is intended to accomplish the following: (1) review the concept of intensity of rainfall discussed in the literature on phytopathology in light of the physical concept of interfacial dynamics and surface tension; (2) review the conjecture that predominance of splash-on-film constitutes a link between intensity of rainfall and ejection of pathogen-bearing droplets. Namely, we discuss the underlying assumptions of the wettability of leaves and the presence of a film. We show that leaves usually cannot support films, as most common foliage is not fully wetting. Closer examination shows that such foliage can only support distinct sessile drops rather than a coating film; (3) provide detailed high-speed visualizations demonstrating the dynamics between droplet and leaf and report two dominant alternative modes of ejection of rain-induced pathogens. These modes both are likely to happen and to be efficient at dispersing pathogens. The first is a drop-on-drop interaction with offset, introducing diverse behaviors that can be related to the physics of splash-on-film to some extent, but with clear distinctions of outcome in ejecta. The second is the result of the motion imparted by the raindrop to compliant leaves, leading to an inertial mode of detachment and ejection that is a different mechanism altogether from that of splash. It is the first time that the inertial-detachment scenario is reported within the context of interactions between contaminated leaves and raindrops and of the spread of foliar disease.

In ''The intensity of rainfall and splash-dynamics: the missing link'' section, we revisit the discussion of the intensity of rain in more detail and discuss the discrepancies in the literature; we offer possible explanations related to the interfacial dynamics at the level of the leaf. In ''Foliar wetting properties: the absence of a coating film'' section, we revisit the wetting properties of common leaves of various sizes and compliances. In ''Fragmentation of the fluid on a leaf: one drop at a time'' section, we discuss the implications of the results in the previous section and present detailed observations of the impacts of drops on leaves supporting contaminated fluid.

In "Discussion and conclusions" section, we discuss the implications of the above results and consider the next steps to be taken. Although in this article we could not cite the full body of the extensive literature on rain-induced transmission of disease, we do cite numerous key reviews and books as a guide to wider literature.

The intensity of rainfall and splash-dynamics: the missing link

Background discussion of the intensity of rainfall and its relation to the spread of foliar diseases

Despite various studies reporting that simulated rainfall induces contamination of the surroundings of an infected plant or fruit (Reynolds et al. 1989; Walklate 1989; Walklate et al. 1989; Madden et al. 1990, 1996; Yang et al. 1990a, 1990b, 1992; Madden, 1992; Huber et al. 1997, 2006; Ntahimpera et al. 1997; Williams et al. 1998; Geagea et al. 1999; Lovell et al. 2002; Hoberg 2002; Saint-Jean et al. 2006; Travadon et al. 2007, to cite a few), it is still debated whether the intensity of rainfall actually affects the dispersal of pathogens (Yang et al. 1991; Madden 1992; Lovell et al. 2002). In the present paper, intensity refers to the volume of rain that passes a fixed area in a fixed amount of time.

Yang et al. (1990a, 1990b) used two different spray-nozzles to create artificial rains that differed in intensity. The authors infected strawberry fruit and placed these fruits under the spray nozzles. They noticed that increasing the intensity increased the number of colonies they collected at almost all distances from the source-fruit. Yang et al. (1990a, 1990b) used two different intensities and a linear relationship of increasing dispersal of spores with increasing intensity of rainfall did not seem to confirm preceding data. Ultimately no simple relationship between simulated or actual intensity of rainfall and resulting final levels of dispersal emerged (Madden and Ellist 1990; Yang et al. 1990a, 1990b). Ground cover, the plant canopy, or subsequent impacts of spore-bearing droplets were mentioned as possible reasons for the discrepancies. Madden et al. (1996) investigated intensity of rainfall further; they discovered a nonlinear relationship between dispersal and intensity. Instead of only using petri plates in their study, they also included healthy, uninfected strawberry plants. This would allow them to distinguish the relationship between the number of colonies dispersed and the number of fruits that actually became infected. The spray-nozzles were changed to obtain a number of different intensities. The authors determined that both the rate of wash off and the rate of removal of spores from the source-fruit increased with increasing intensity, but also subsequently reported that the latter increased more than the former. Thus, the incidence of disease in previously healthy fruit increased with increasing intensity; however, beyond a threshold intensity, incidence of disease dropped. This puzzling phenomenon occurred across multiple distances from the initial source and after different simulated durations of rain. They postulated that these results were due to the washing off of spores that splashed onto healthy fruit. Ntahimpera et al. (1997) used the same experimental setup as Madden et al. (1996); however, they placed a mesh frame under the spray nozzle in some experiments. This frame kept the volume of falling water and the intensity of rainfall approximately constant, but changed the size of the falling drops. By comparing the dispersal of spores and incidence of disease between each nozzle alone and each nozzle with a mesh frame, the study found that experiments that differed in size of raindrops, but had only slightly different intensities, had great disparities in dispersal of spores. Larger sizes of drops corresponded to more dispersal, but changing intensity alone, without a corresponding change in drop-size, had an insignificant effect on dispersal. The authors cited this as a reason for discrepancies in the preceding literature and for the complex nonlinear relationships deduced from correlations among all the variables. Furthermore, the results showing that although the standard nozzle without the mesh resulted in significantly lower dispersal of spores than did the standard nozzle with the mesh frame, the difference in incidence of disease between the two was not statistically significant. The complexity of the influence of rainfall-intensity is at the heart of our motivation to revisit the physical understanding of how splashes influence the interaction between leaves and droplets.

Indeed, predicting the incidence of disease and the dispersal of pathogens by splash, using only macro-level data is difficult. In particular, even accurate macro-level statistical results do not provide sufficient insight into how pathogens are detached and emitted at the level of the leaf and how the surface and compliance of the leaf fundamentally affects such dispersal. Following, we discuss the notions of surface tension and nondimensional numbers that shed light on the role of intensity of rainfall.

Droplet-dynamics at the level of the leaf

Rainfall intensity is a coarse quantity that does not encompass the physics of splash and dispersal, nor does it account for the nature of the leaf's surface and its mechanical properties. Storms with distinct distributions of sizes of raindrops can have the same average volume of rainwater falling per unit of time and unit area (Villermaux and Bossa 2009). Thus, rain-intensity is blind to the variations in size and speed of the impacting raindrops.

Size and speed of incoming drops, however, are critical determinants of the properties of their splash. Given that prior studies on the role of rain intensity in the dispersal of pathogens typically did not report the size-distributions of raindrops used, it is impossible to explain previous results in terms of splash-dynamics. The size or speed of an impacting drop alone is not sufficient to determine the nature of its breakup upon impact. What matters most is the ratio of its kinetic energy to surface energy, referred to as the Weber number

$$We = \frac{\rho D V^2}{\sigma}$$

where D is the drop's diameter, V is the impact velocity, ρ is the density and σ is the fluid's surface tension (Yarin 2006). Note that among the numerous studies of the impact of raindrops on plants discussed in the first section, only the recent study by Saint-Jean et al. (2006) mentioned the Weber number as a possible parameter to use in the macroscopic statistical correlations linking range of deposition in incoming raindrops. In that article, We was used in addition to the diameters of drops, or velocity or product of the two as another variable with which correlations could be investigated.

More generally, the process of droplet formation from the breakup of a fluid bulk is referred to as fluid-fragmentation. The particular physical processes initiating such breakup select the steps of the cascade from a fluid-volume to sheets to ligaments to droplets (Villermaux 2007). The timescale of a raindrop's impact is on the order of a few milliseconds. This can be obtained by considering a raindrop of diameter D—typically limited to a few millimeters—and of velocity typically limited to a few meters per second; leading to an impact time:

$$\tau_i = \frac{D}{V}$$

The breakup or fragmentation of the drop into sheets is usually slower; however, still occurring on a timescale on the order of a hundred milliseconds. Hence, high-speed imaging tools are critical in the capture of dynamics of raindrop impacts on leafs.

Splashes on thin films of fluid, deep liquid layers, or solid surfaces lead to quite distinct processes of the breakup of fluid; thus resulting into distinct final sizes of droplets (Vander Wal et al. 2005; Yarin 2006; Deegan et al. 2008). On thin films (films of much smaller thickness than the diameter of the impacting droplet), a sheet or film of liquid, usually called corona, is typically observed to emerge and break up into secondary droplets. It is reported that such a splash-regime is possible when the dimensionless group

$$K = We\left(\frac{\mu}{\sqrt{\rho\sigma D}}\right)^{-2/5}$$

is larger than about 2100. Here μ is the fluid viscosity. K is a measure of the relative importance of the surface energy and kinetic energy to the viscous dissipation of such energies. Millimetric raindrops satisfy $K > 10000$ and thus are fully in the splashing regime in which fragmentation via formation of a corona occurs. Although analog criteria are reported for splashes on a dry surface, attempts to understand how to incorporate additional parameters of wettability, or roughness of the substrate, remain active areas of research (e.g., Latka et al. 2012). Raindrops have a broad distribution of sizes that strongly depends on the type of storm. Nevertheless, there is a maximum size of ~5–6 mm in diameter above which drops spontaneously fragment during their free fall. A drop of 5 mm achieves a terminal velocity of ~10 m/s, which corresponds to a Weber number We ~6000 and an impact parameter K ~80,000.

Foliar wetting properties: the absence of a coating film

Our first approach was to directly observe the impact of simulated raindrops on various leaves using high-speed videography (Phantom, from Vision Research) at 1000 frames per second (fps). A front lighting was used to allow for the capture of the dynamics on the leaves' surfaces. Placing a container at ~3 m above the foliage generated artificial rain. The container was tapped at the bottom with closely spaced sub-millimeter holes through which raindrops dripped at various time-intervals. The choice of 3 m was made to allow for all raindrops to reach at least 60% of their terminal velocity during fall.

These preliminary experiments revealed how rich and dynamically complex the interaction between rain and leaves can be. Droplets are ejected from the foliage in a multitude of different ways, classified, and then described. Nevertheless, one key systematic observation was that no thin film of liquid could reside on regular plant leaves. Instead, we observed residual fluid in the shape of sessile drops (Fig. 1). The size of such residual drops was never found to be larger than a few millimeters. To confirm this first systematic observation, we proceeded to measure the wetting properties of 13 different types of common foliage readily found in the botanic gardens (e.g., English Ivy, lucky bamboo) and agricultural plants (e.g., coffee and banana). A goniometer (Dataphysics) was used for accurate estimation of contact angles. The results of the measurements of wettability are reported in Table 1.

Interfaces between solids and fluids are associated to a certain interfacial energy per unit area. Solid surfaces that are wetting are energetically stabilized by the presence of the fluid coating; while those that are hydrophobic, are energetically destabilized by the interaction with the fluid coating. Most plant surfaces we examined were found to be partially wetting. In such configurations, the fluid residing on the leaf takes the geometrical form of a droplet with a finite base angle of contact with the interface—or contact angle (Figs. 1 and 2A). If a surface and its sessile drop are inclined, the contact angle of the drop's front-end with the leaf increases progressively until reaching a critical value, θ_A, at which the contact line defining the edge of the droplet begins to advance or the droplet starts to slide (Fig. 2B). The back-end's contact angle, on the other hand, decreases until it reaches a critical value, θ_R, at which the contact line defining the back edge of the droplet recedes or detaches from its pinned end. θ_A is called the advancing contact angle while θ_R is called the receding contact angle (Fig. 2B). For a given fluid and substrate, the apparent contact angle θ^* can take any value between the two: $\theta_R \leq \theta^* \leq \theta_A$.

A substrate is considered hydrophobic when the average contact angle of a drop of fluid deposited on it is larger than 90°, while it is considered hydrophilic otherwise. Thin films are observed after splashing when θ_R becomes very small (closer and closer to zero). Our measurements of advancing and receding contact angles of the foliage we examined indicate that common leaves are usually slightly hydrophilic, with θ_A up to 130° and θ_R not smaller than 40° (Table 1). So the formation of a thin film of water on common agricultural leaves would not be energetically favorable, and therefore unlikely.

As already mentioned, at the onset of a sliding motion, a drop on an inclined substrate shows values of θ_A and θ_R at its leading and trailing edges, respectively (Fig. 2B). The existence of a

Fig. 1 Simulated rainfall on a Peppermint leaf. The residual water takes the shape of sessile drops. The scale bar is 1 cm.

Table 1 Foliage advancing θ_A and receding θ_R contact angles for 13 species of plants

Plant species	θ_A	θ_R
Peace Lily Spathyphyllum wallisli	75°	40°
Pothos Epiprenmum	101°	79°
Lucky Bamboo	76°	54°
Heartleaf Philodendron Cardatum	74°	47°
Dwarf rubber plant	73°	50°
Croton codiaeum variegatum	85°	75°
Areca Palm Plant	90°	74°
English Ivy	90°	64°
Chlorophytum comosum	56°	46°
Red-veined prayer plant	127°	92°
Coffee leaf	84°	69°
Banana leaf	131°	110°
Strawberry leaf	77°	56°

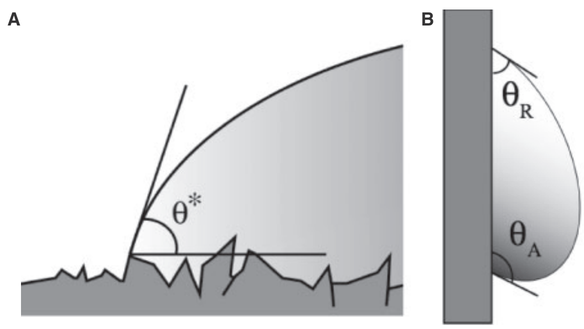

Fig. 2 (**A**) Apparent contact angle θ^* of a drop on a rough horizontal surface, such as a leaf. (**B**) The apparent contact angle of a drop on a vertical surface resides between the advancing contact angle θ_A and the receding contact angle θ_R: $\theta_R \leq \theta^* \leq \theta_A$. The difference between the advancing and receding contact angles allow for a drop to resist gravitational pull. It can thus stick to surfaces such as leaves (Bourouiba and Bush 2013).

difference between the advancing and receding contact angles is referred to as hysteresis: $\Delta\theta = \theta_A - \theta_R$. Hysteresis originates from the finite roughness of the substrate. Sliding occurs as soon as the capillary force induced by the contact angle's hysteresis no longer balances the pull of gravity. Compliance of the leaf magnifies this gravitational pull by providing additional inclination under loading, or during impact of a raindrop. The maximum size of drop that capillary forces can retain is of the order of the capillary's length λ_σ:

$$\lambda_\sigma = \sqrt{\frac{\sigma}{\rho g}}$$

where $g = 9.81\,\mathrm{m/s^2}$ is the acceleration of gravity. This length is about a few millimeters for water, which is consistent with our systematic observations of the limited size of the residual drops we found on leaves in the course of our experiments (e.g., Fig. 1).

The observations in this section support the fact that seldom will the surface of leaves be fully wetted during rainfall, as also argued in some prior works (e.g., Herwitz 1987 and discussed by Dunkerley 2009). Moreover, the implication is that the conjectured splash-on-film dynamics at the level of the leaf needs revisiting. This is the subject of the next section. Finally, note that partial wetting behavior could be rationalized as it is thought to minimize disturbance to plants' breathing and structural stability, while also possibly reducing detrimental parasitic colonization of the leaf's surface (Vogel 2012).

Fragmentation of the fluid on a leaf: one drop at a time

Set up and direct observations

Our next approach was to examine the impact of an analog raindrop on a leaf bearing the weight of an analog contaminated fluid. Based on our prior findings, we focused on a contaminated-fluid analog in the form of a colored drop of fluid (rather than a film) residing on the leaf-surfaces examined. This drop is made of liquid food dye (McCormick) diluted in at least twice the volume of pure water. At such concentration, the dye does not significantly modify the surface tension or the viscosity of water. Our goal was to directly examine the dynamics of a raindrop's impact leading to the detachment and ejection of the analog contaminated drop from the leaf (Fig. 3). We aimed at identifying scenarios that were both the most likely, and the most efficient, at dispersing contaminated fluid away from the leaves.

Indeed, only such scenarios can shape significantly the dynamics of rain-induced dispersal of pathogens and onset of an epidemic. We specifically examined the dynamic coupling between an impacting raindrop and the motion of the leaf and its payload, one impact at a time. Between each raindrop's analog impact, the leaf was cleaned and a new colored analog-contaminated drop of the same size was deposited at the same location. Leaves were still attached to the plant. Indeed, detached leaves experience a loss in turgor pressure that affects their bending stiffness. Two dominant mechanisms were identified as leading to the majority of ejections of droplets from the leaves. One required the direct contact between the raindrop and the sessile drop; while the other did not.

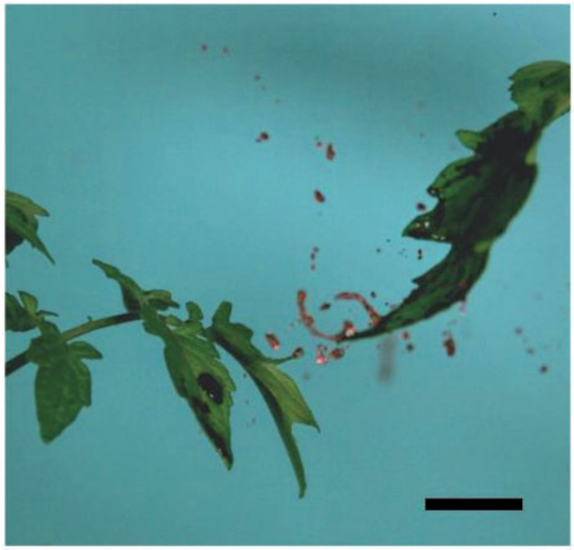

Fig. 3 Ejection of contaminated droplets resulting from the impact of a raindrop in the vicinity of a contaminated fluid drop residing on a tomato leaf. Scale bar is 2 cm.

"Crescent moon" detachment

One of the two dominant mechanisms of ejecting droplets observed throughout our experiments was labeled the "crescent moon detachment". It relies on the direct contact between the impacting drop and the colored sessile drop (Fig. 4). For uniform distribution of impact points, which is expected for rainfalls, off-centered impacts between the two drops would be likely to occur at a much higher probability than that of a centered impact. Upon an off-centered impact, a raindrop impacting in the vicinity of the sessile drop expands in the form of a sheet until direct contact between the two fluids can occur (Fig. 4). Upon occurrence of such contact, the impacting raindrop pushes the sessile drop, forcing it to stretch and expand into a liquid sheet. Progressively, the sheet fragments into filaments and then into droplets via hydrodynamic instabilities,

Fig. 4 Splash by raindrop (diameter 5.0 mm, speed 7 m/s) and fragmentation of a contaminated sessile drop on an Areca Palm leaf. We = 3500 and K = 45,000. The first snapshot is taken at 2 milliseconds prior to the raindrop's impact. Subsequent snapshots at 2, 4, 7, and 11 ms after impact are then displayed. The largest ejected droplet is 1.6 mm in diameter. Scale bar is 1 cm.

such as Rayleigh-Taylor and Rayleigh-Plateau. A similar process of sheet-fragmentation is observed when a raindrop splashes on a thin film of liquid; however, the difference is the important change of symmetry. In particular, in the case of an impact on a thin film, the impact leads to the stretch of the film in the vertical direction, and a resulting transfer of momentum to the ejected droplets, again mostly in the vertical direction (Yarin 2006). On the contrary, the impact next to a sessile drop breaks the symmetry of the ejection of the sheet, leading to a significant transfer of momentum to the stretched film and ejected droplets in the horizontal direction. This transfer enhances the potential dispersal of contaminants to nearby plants. The shape of the sheet, reminiscent of a crescent moon, constituted the origin of the name we chose for this recurrent mechanism of ejection.

"Inertial detachment"

We named the second dominant mechanism of formation and ejection of droplets "inertial detachment". This mechanism does not require direct contact between the fluids of the raindrop and the contaminated sessile drop (Fig. 5A). Upon impact, part of the incoming momentum is transferred to the leaf and to the droplets on its surface. The mechanical properties of the leaf play a critical role in shaping the outcome of such transfer of momentum. For example, a lightweight and compliant leaf will respond to the impact of the raindrop by a motion of large amplitude. The sessile drop may then deform sufficiently to fragment and to detach from the moving leaf in the form of small droplets. We note that the ejected droplets appear to inherit the leaf's velocity at the time of detachment. On such foliage, detachment could occur during two phases.

First, the sudden downward acceleration of the leaf can stretch the sessile drop into a vertical filament that fragments into droplets (Fig. 5B). Given that the leaf is at rest prior to such sudden motion, these ejected droplets have negligible components of horizontal velocity and thus fall back onto the leaf. Second, the contaminated drops can also detach in a similar way when the leaf is in an upward motion during its spring-back (Fig. 5C). In this phase of the motion, the ejected droplets are catapulted away, owing to the strong horizontal component of the motion of the leaf. This latter mechanism has a great potential for dispersing pathogen-bearing droplets. In particular, it potentially can eject larger droplets further away than could the splash-dynamics discussed in the previous section.

The crescent-moon and inertial-ejection mechanics both are expected to be frequent in a rainfall event; they may even coexist in a single impact (e.g., Fig. 6). There, the raindrop first impacts the sessile drop in the form of a crescent moon; nevertheless, when significant, bending reduces the efficiency of this mechanism of ejection. In particular, the asymmetric crown-sheet is inclined downward, leading to the ejection of contaminated droplets downward with little horizontal range. However, during such bending, a mixture both of the impacting raindrop and the contaminated fluid drifts to the tip of the leaf by centrifugal acceleration. At the tip, the mixed fluid is then catapulted away during the upward motion of the leaf.

In summary, although inertial and crescent-moon ejections both can occur in one type of plant, the flexibility of the leaf visibly determines which regime

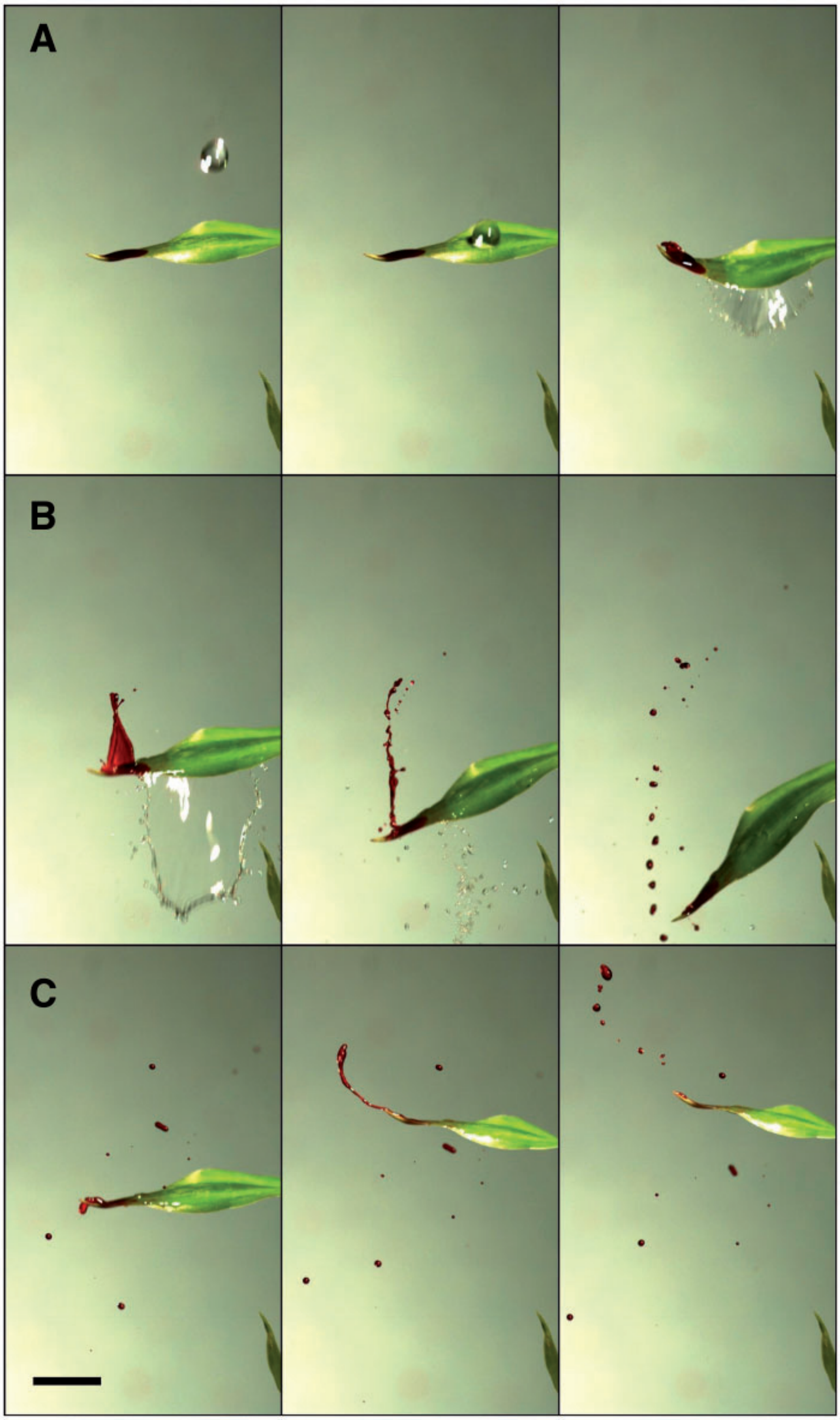

Fig. 5 Inertial detachment of a sessile drop in response to the motion of a bamboo leaf induced by an impacting raindrop (diameter 4.2 mm, speed 6 m/s). We = 2160 and K = 27,000. Snapshots are taken at 2 ms before impact, at impact, then at 2, 5, 10, 20, 60, 75, and 85 ms after impact. Scale bar is 1 cm. Row A indicates that there is no direct interaction between incoming and sessile drops. Row B shows the droplets ejected by the initial downward motion of the leaf. The ejection during spring-back is shown in row C. The largest droplet ejected by inertial detachment was 1.8 mm in diameter.

Fig. 6 Coexistence of splash, dripping and catapult during a single impact of a raindrop (diameter 4.6 mm, speed 6.5 m/s) on an English Ivy leaf. We = 2780 and K = 35,000. Snapshots are taken at impact, then 3, 25, 35, and 45 ms later. The largest droplet ejected by splash and detachment are 0.68 and 0.84 mm in diameter, respectively. Scale bar is 1 cm.

is most efficient at propelling pathogen-bearing droplets away from the leaf. The type of ejection that a leaf can produce affects both the range and the size of droplets emitted.

Discussion and conclusions

Plant diseases are a major cause of the loss of crops worldwide. Although rainfalls are observed to correlate with outbreaks of foliar disease, the mechanisms explaining their link remain poorly understood. A scenario of the splash of a raindrop on a thin film residing on the leaves is usually invoked to explain such correlation.

As recently shown in the context of the transmission of diseases among humans (Bourouiba et al. 2014), it is critical to characterize the size-distribution of the contaminated droplets emitted during an ejection from an infected host (e.g., violent expirations). Indeed, such information directly shapes the pathogen's footprint surrounding a host, which in turn, determines the dynamics of the spread of disease within the population.

In this article, we started by revisiting the discussions linking the average intensity of rainfall to the dynamics of the interaction of leaf and rain at the scale of the leaf. Indeed, in the context of rain-induced transmission of foliar disease, the dynamics of pathogen-plant interaction and the mechanisms of creating and ejecting pathogen-bearing droplets during rainfalls remain seldom examined and little understood; effectively being treated as a black box. We started by revisiting the concepts of surface tension and presented new measurements of wettability of leaf-surfaces relevant to the problem of rain-induced spread of foliar pathogens. We intended to examine leaves of various compliances as well as a range of surface-properties, while remaining focused on very common plants. We showed that such common leaves are unlikely to become fully wetted during rainfalls. Instead they can support sessile, contaminated droplets instead of contaminated thin films. As a result, the scenario of splash-on-film usually conjectured as a dominant mechanism required revisiting.

We then presented the results of direct high-speed videography of interactions of raindrops and leaves. We reported observing systematically two dominant mechanisms of ejecting droplets. One is the "crescent-moon" ejection, relying on the direct interaction of the impacting raindrop with the contaminated sessile drop on the leaves. The other is the inertial-detachment mechanism, solely facilitated by the compliance of the leaf. The flexibility of the plant plays a key role in the selection of the dominant scenarios of ejections and their efficacy in projecting contaminants to neighboring plants. Both scenarios are clearly distinct from the splash-on-film dynamics. The inertial detachment involves a very different physics from that of either the splash-on-film or crescent-moon mechanisms. This opening study only starts to highlight the rich fluid dynamics hidden at leaf-level during rainfalls. Our ongoing work consists of characterizing the physical picture governing both drop-on-drop and inertial detachments. We hope that the present paper, within this interdisciplinary symposium, will open the road to numerous follow-up studies that can shed new light on what has so far remained a critical missing link between statistical macroscopic studies of the spread of foliar pathogens and the detailed phenomenology of the interfacial dynamics at the level of a leaf.

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