



# Effect of sap-feeding insects, plant characteristics, and weather parameters on sooty moulds in the temperate zone

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## Abstract

In this study, relevant variables were determined to predict the probability of sooty mould biofilm (SMB) occurrence on willow leaves in a multivariate model. Despite a large temporal gap between the main sap-feeding insect (SFI) season in spring (May to June) and the main season of SMBs in late summer and fall (August to September), trees infested with SFIs on four or more observation dates had significantly more SMBs (3.7-fold) toward the end of the growing season. In addition, a horizontal leaf position and recessed leaf veins, traits that may increase the wettability of the leaves, positively influenced SMB occurrence (27.8-fold). Among the weather parameters, those that lead to higher moisture on leaf surfaces, namely high morning and evening relative humidity, higher precipitation sums, and lower vapour pressure deficit values, also had the strongest positive effect. In addition to these parameters, higher wind speeds also had a strong positive effect on SMB occurrence.

**Keywords** Biofilm ecology · Host plant influence · Willow · Pest management · Climatic parameters

## Introduction

Leaves and stems of higher plants are regularly colonized by sooty mould biofilms (SMBs), which are characterized by a superficial dark mycelium (Schoulties 1980; Callan and Carris 2004; Agrios 2005; Chomnunti et al. 2014; Kim 2016; Kim and Kim 2017). Fungi forming these biofilms belong to diverse ascomycetous families (Chomnunti et al. 2014; Abdollahzadeh et al. 2020; Flessa et al. 2021), have a predominantly or temporarily saprotrophic life habit due to the absence of specific interbiotic cellular structures, such as haustorial protrusions, that are present in truly phytopathogenic fungi (An et al. 2006; Dekhuijzen and Scheer

1969), and they are not host plant specific (Callan and Carris 2004; Agrios 2005). Sooty moulds are not considered plant parasites; therefore, they do not penetrate the leaf surface (Hughes 1976; Agrios 2005; Chomnunti et al. 2014; Kim 2016; Kim and Kim 2017). Within phytopathology, SMB is considered a non-parasitic disease (Blancard 2012) due to its negative consequences for the host plant and economic damage, e.g., in tropical and subtropical crops, such as carambola, citrus, durian, durum wheat, guava, mango, and tomatoes (Swirski et al. 1997a, b; Ancisco et al. 2002; Siriphanich 2011; Warren and Sargent 2011; Blancard 2012; Fernandez and Knox 2012). SMBs reduce respiration, cause yellowing of leaves (Blancard 2012), and increase the water costs for each CO<sub>2</sub> molecule fixed during photosynthesis (Insausti and Ploschuk 2018). The black coating acts as a light filter, which leads to a reduction in the incident light by physical obstruction (de Filho and Paiva 2006; Nelson 2008), resulting in an increase of leaf temperature at least in the regions covered by SMBs (Wood et al. 1988; Kim and Kim 2017) and a decrease of water content in covered leaves (Santos et al. 2013). The negative impact on photosynthesis of the affected plants, however, is controversial (Wood et al. 1988; de Filho and Paiva 2006; Insausti and Ploschuk 2018). At a minimum, the plant needs to compensate for this disadvantage with more chlorophyll (Insausti et al. 2015)

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and changes in the morphology of cell organelles (Kim and Kim 2017).

In general, it is postulated, that SMB is strongly linked to the occurrence of members of the sap-feeding insect guild (SFI), such as aphids, scale insects, whiteflies and psyllids, which produce honeydew, a highly concentrated sugar dilution that may function as a nutritional resource for fungal species forming the SMB (Hughes 1976; Parbery and Brown 1986; Callan and Carris 2004; Perez et al. 2009; Kirk et al. 2010; Dhimi et al. 2013; Chomnunti et al. 2014). Therefore, it is recommended to reduce SMB accumulation indirectly by controlling SFIs with insecticides (Agrios 2005). The correlation between SFIs and SMBs has thus far only been studied for evergreen plants, foremost in the tropics and subtropics. Most studies on SMBs examined variables that alter the composition of the fungal community but not which variables lead to an SMB on host plants in the first place. Studies on multitrophic interactions in the phyllosphere, concerning SMB and sap-feedings insects, include usually just one (Stadler et al. 1998; Mühlberg and Stadler 2005; Perez et al. 2009; Shukla and Gundappa 2017) or a few host plant species (Dhimi et al. 2013) and do not provide conclusions about SMB-promoting host plant characteristics. The occurrence, structure, and succession of epifoliar fungal communities are known to underlie seasonal variations (Cabral 1985; Lee and Hyde 2002; Osono 2008), but data on SMBs were usually sampled during a very short time period and, therefore, disregard seasonal variations in SFI dynamics (Perez et al. 2009; Dhimi et al. 2013). In some studies on symptomless leaves without visible SMBs, variations in fungal communities were investigated and mainly interpreted as directly linked with climatic weather conditions, such as temperature, precipitation, relative humidity, and wind speed (Lee and Hyde 2002; Talley et al. 2002; Gomes et al. 2018) without a link to SFI occurrence. There was one long-term study in mango orchards that confirmed a strong correlation between SFIs and SMBs (Shukla and Gundappa 2017) in combination with weather parameters. However, since this study was carried out on a single evergreen host plant species in the tropics, no conclusions can be drawn about the influence of host plant characteristics, especially on deciduous leaves in the temperate zone. While host plants of SMBs in tropical habitats are usually perennial and have durable leaves, they also provide a continuous habitat for sooty moulds. This continuity does not exist in deciduous host plant leaves. The development of the fungal community stops in autumn and restarts every spring with the leaves sprouting (Flessa et al. 2012); therefore, it is uncertain whether the causal relationship between SFIs and SMBs also applies here. As SMBs are a more subtropical or tropical (Callan and Carris 2004; Kirk et al. 2010) than a temperate climatic zone phenomenon, the present study is the first on deciduous host plants that includes a broad range of species of one genus of host plants, i.e., *Salix* (willows), and examines

the effects of SFI occurrence on SMB development in combination with leaf traits and weather parameters. Willows are widely distributed in the northern hemisphere, mainly in the temperate climatic zone, i.e., in the northern parts of Europe and North America, as well as Asia, with the diversity center located in China. Willows are uncommon in subtropical and tropical regions, and only a few species have been reported in Africa and South America (Argus 1986; Zhen-Fu 1987; Ghahremaninejad et al. 2012; Zhao et al. 2019). Willows are suitable as study objects, as they are known host plants of SMBs (Hughes 1976; Flessa et al. 2012; Khodaparast et al. 2015) and aphids (Blackman and Eastop 2000) and differ considerably in their interspecific leaf characteristics. The main saprotrophic fungi within the SMB on leaves of willows in the studied area are *Aureobasidium pullulans*, *Cladosporium cladosporioides*, and *Phoma* sp., with *A. pullulans* being the most dominant species (Flessa et al. 2012).

The aim of our study was to identify, as a first step, those variables that have a significant impact on the development of SMBs. In a second step, our goal was to develop a multivariate model based on the relevant variables that would allow predictions of SMB occurrence on the leaves of willows.

The following hypotheses were tested:

SFI occurrence promotes the occurrence of SMB. However, the probability of SMB occurrence does not depend on SFI occurrence alone, but is additionally increased by favourable plant characteristics. The growth of the fungi is dependent on favourable weather parameters, which is why only the combination of SFI occurrence, favourable plant characteristics and weather variables increase the probability for SMB occurrence on potential host plants.

## Material and methods

### Location of the host plants

Data sampling took place during one vegetation season from May to September 2010 in the *Salix* collection (Salicetum) of the Bayreuth University Ecological-Botanical Garden (49°55'31.5" N, 11°34'58.6" E, 352 m alt.). The area of the study site measured 4010 m<sup>2</sup>. All plants were grown without manipulation, i.e., application of pesticides or fertilizers or truncation.

### Observation in the field and data collection

This study included 147 host plants, belonging to 75 different taxa and hybrids within the plant genus *Salix*, which were all exposed to the same conditions (geographical location, treatment).

Data sampling was performed at bi-weekly intervals from the calendar weeks CW 18 until CW 36. On each date, for each plant, the presence of SMB, SFIs, and evidence of ants visiting SFIs were registered.

The following characteristics of host plant leaves were recorded in August: summer leaf position, summer leaf structure, leaf appearance, adaxial leaf vein type, adaxial midrib type (Mantovani et al. 2009), adaxial midrib pubescence, and visible adaxial surface gloss. The plant characteristics from surveys were supplemented with further data from the literature, i.e., leaf length and form, leaf glands, surface waxes, shape of the leaf, from the literature (Rechinger 1962; Stelfox 1965; Chmelar and Meusel 1976; Walters 1984; Lautenschlager-Fleury and Lautenschlager-Fleury 1988; Lautenschlager 1989; Uchytel 1992; Böhlmann 2012; Isebrands and Richardson 2014; Roloff and Bärtels 2018; Mastel 2019; Züllig-Morf 2019) and online resources (arbolapp.es, lhprism.org, rhs.org, gobotany.nativeplanttrust.org, treesandshrubsonline.org, eFloras.org). Categories per factor are given in Table 1.

## Climatic data

Climate data were provided by the Micrometeorology group at the University of Bayreuth and derived from a weather station in the Ecological-Botanical Garden of the University of Bayreuth, at a distance of about 250 m to the middle of the *Salix* collection area (49°55'45" N., 11°35'10" E., 350 m. alt.). The data we used to analyze the impact of different climatic factors on SMBs were daily precipitation sum (mm), mean air temperature (°C), daily air temperature minimum and maximum (°C), global radiation (MJ-m<sup>2</sup>), sunshine duration in hours, mean vapour pressure (hPa), daily relative humidity minimum (%), instantaneous 10 min average of

relative humidity at 8, 12, 16, and 20 MEZ (%), daily mean wind speed (m-s), vapour pressure deficit (hPa), daily sum of potential evaporation rates (Ep, Priestley-Taylor, mm) and actual evaporation rate (ET, Penman-Monteith, mm). For each variable, we calculated mean values or totals over the 14, 7, and 3 days preceding the collection date.

Evaporation rates over the meadow at the climate station were derived from 10 min observations. Potential evaporation rates were calculated after Priestley and Taylor (1972). Actual evapotranspiration was derived according to the Penman-Monteith approach using the formulas given in Foken (2017). More details on climate variables, including used instruments are given in Table 2.

## Statistical analyses

Analyses were conducted using the packages 'lme4' (Bates et al. 2015), 'ggeffects' (Lüdecke 2018), and 'oddsratio' (Schratz 2017) of the statistical software R v. 4.0.3 (R Core Team 2020). Logistic mixed effect models were used for the analysis. The influence of SFI observations, ant presence, and different plant characteristics on the occurrence of SMB were initially evaluated univariately. For the multivariate model, in a first step, variables that were significant ( $p < 0.05$ ) or almost significant ( $p < 0.1$ ) were selected. We had to restrict our considerations to multivariate logistic mixed-effects models with few variables (4–5, depending on the variables), since the fitting algorithm became unstable leading to convergence problems for higher numbers of variables. Univariate testing was also initially performed on the weather variables. Due to the limited number of variables, only one weather variable could be included in the multivariate model at a time. The selection was based on

**Table 1** Plant characteristics and categories per factor

Factors	Categories
SMB presence	Yes/no
SFI presence	Yes/no; sporadic, at least 10 individuals, heavy infestation of the whole plant, i.e., about 50% of leaves/shoots are infested
Ants visiting SFIs	Yes/no
Summer leaf position	Upwards, horizontally, downwards
Summer leaf structure	Smooth or rugose
Leaf appearance	Glabrous leaf blade, light-haired, dense-haired, glaucous
Adaxial leaf vein type	Flat, concave, convex
Adaxial midrib type	Flat, U-shaped
Adaxial midrib pubescence	Yes/no
Visible adaxial surface gloss	Yes/no
Leaf length	1–4.9 cm, 5–6.9 cm, 7–8.9 cm, > 8 cm
Leaf glands	Yes/no; size small, medium, large
Surface waxes	Yes/no
Shape of the leaf	Narrow, narrow-broad, broad, elongated, round

**Table 2** Selected variables from meteorological observations and instrumentation

Variable (Measurement height)	Instrument/source	Used statistics
Precipitation (1 m)	Pluvio, OTT Messtechnik, Kempten, Germany	Daily sum (mm)
Air temperature (2 m)	Frankenberger psychrometer, Th. Friedrichs, Hamburg, Germany, actively ventilated	Daily mean, minimum, maximum (°C)
Global radiation (2 m)	CM14, Kipp & Zonen, Delft, Netherlands	Daily sum (MJ m <sup>-2</sup> )
Sunshine duration (2 m)	SDE 9.1, Thies, Göttingen, Germany	Daily sum in hours
Relative humidity (2 m)	HMP45a, Vaisala, Finland, corrected with summertime Frankenberger psychrometer measurements	Daily minimum, daily instantaneous 10 min average at 8, 12, 16, 20 MEZ (%)
Vapour pressure (2 m)	Derived from air temperature and humidity	Daily mean (hPa)
Vapour pressure deficit (2 m)	Derived from air temperature and humidity	Daily mean (hPa)
Wind speed (17 m)	2D Ultrasonic, Thies, Göttingen, Germany	Daily mean (m s <sup>-1</sup> )
Net radiation (2 m)	CM14 (shortwave components) and CG2 (longwave components), Kipp&Zonen, Delft, Netherlands	For evaporation calculation only
Air pressure (1 m)	AB60, Ammonit Measurement, Berlin Germany	For evaporation calculation only
Volumetric soil moisture	TDR TRIME-EZ, IMKO, Ettlingen, Germany	For actual evaporation calculation only
Potential evaporation (-)	Priestley and Taylor (1972)	Daily sum (mm)
Actual evaporation (-)	Penman–Monteith, after Foken (2017), Jarvis-Stewart scheme for stomatal resistance (Vilà-Guerau de Arellano et al. 2015)	Daily sum (mm)

biological relevance in comparable studies, significance of the corresponding p-value, and a low AIC value.

## Results

The main occurrence of SMBs, as well as the main occurrence of SFIs on willows, was highly seasonal. The SFI main season started with a peak in mid-May and lasted until mid-June. The curve for the SMBs showed a shifted pattern with an increase from mid-August to September, when SFIs were rarely found (Fig. 1). There was a large time gap between the end of the SFI main season in June and the sudden increase of SMB records in August.

On 35% of the 147 willow individuals in this study, SMB was observed at least at one collection date, and 86% were infested with SFI at one or multiple observation dates. Among the willow species, subspecies, and hybrids that were represented by at least 3 individuals in the experimental design, SMB was observed on more than half of the individuals, i.e., *S. helvetica* Vill., *S. appendiculata* Vill., *S. x hegetschweileri* Heer, *S. caprea* L., and *S. cinerea* L., but on one-third, SMB was never observed, i.e., *S. apennina* Skvortsov, *S. caesia* Vill., *S. glabra* Scop., *S. mielichhoferi* Saut, and *S. repens* L.

SMBs recorded without previous or simultaneous SFIs were observed in only 2% of host plants. However, the occurrence of SFIs did not necessarily result in SMBs later in the season; half of the host plants on which SFIs were detected never showed SMBs during the study period. While the occasional occurrence of SFIs had no significant effect on SMBs, SFI presence on four or more observation dates

significantly increased the probability of SMB occurrence ( $\beta = 1.515$ ,  $z = 2.86$ ,  $p = 0.004$ ,  $AIC = 715.3$ ) (ESM 2). The probability of developing an SMB was 3.7-fold higher on trees with  $\geq 4$  SFIs than on trees with less SFI observations. Of the hosts listed above, with at least three individuals without SMBs, only a single individual of *S. glabra* was observed with SFIs four times, all others belonged to the willows with less than four SFI observations.

Whether SFIs were visited by ants or not had no significant impact on SMBs. Of the plant characteristics examined, a horizontal leaf position ( $\beta = 1.968$ ,  $z = 2.56$ ,  $p = 0.011$ ,  $AIC = 704.8$ ) and rugose leaves ( $\beta = 0.842$ ,  $z = 2.05$ ,  $p = 0.04$ ,  $AIC = 711.1$ ) had a positive significant effect; recessed leaf veins had a positive effect, but it was only almost significant ( $\beta = 0.903$ ,  $z = 1.89$ ,  $p = 0.058$ ,  $AIC = 665$ ). Longer leaves also had a positive effect, which increased with leaf length, but was also only almost significant (category with the longest leaves of 10–15 cm:  $\beta = 1.257$ ,  $z = 1.93$ ,  $p = 0.054$ ,  $AIC = 676.2$ ). While most leaf shapes had no significant effect, wide leaves had a negative effect ( $\beta = -1.528$ ,  $z = -2.3$ ,  $p = 0.021$ ,  $AIC = 653.1$ ). All other plant characteristics had no significant effect (ESM 2). With the significant and almost significant variables, we first built a multivariate model. We then successively removed the variable with the lowest p-value from the model, resulting in a model with SFI observations on four or more dates, horizontal leaf position, and concave leaf veins (Table 3). The relative abundance of SMBs on trees with an SFI  $\geq 4$ , horizontal leaf position, and recessed veins was 30%, and the relative abundance predicted by the model was 36% (CI 15–63%). In comparison, the observed relative frequency of SMBs on trees with an

SFI < 4, without horizontal leaf position and recessed leaf veins was 2.5%; the relative frequency predicted by the model was 1% (CI 1–3%).

In the next step, we added weather variables to this model. Due to convergence problems with the fitting algorithm, we could only add one variable at a time. Therefore, we built different models by adding the weather variables individually (ESM 3). Weather parameters that, in combination with the plant model (SFI  $\geq$  4, horizontal leaf position, and recessed veins), led to the highest (> 80%) predicted relative abundances of the SMBs were mean VPD of 3 hPa at 8:00 am over the last three days (90%, CI 65–98%), increased wind speed of 2.1 m-s over the last three days (89%, CI 64–97%), high relative humidity at 8:00 AM of 90% over the last 14 days (87%, CI 56–97%), high precipitation sum over the last 14 days of 85–90 mm (89%, CI 52–97%), and high relative humidity at 8:00 PM of 91% over the last 7 days (82%, CI 48–95%).

Favourable weather conditions only led to an increased probability of SMB occurrence when they occurred in combination with prolonged or repeated SFI presence and favourable plant characteristics. Based on the multivariate model, the predicted probability of SMB occurrence at a morning relative humidity of 90% over the past 14 days was 26-fold higher for trees with  $\geq$  4 SFI observations, horizontal leaf position, and recessed leaf veins than for trees with < 4 SFI observations, a non-horizontal leaf position, and non-recessed leaf veins. This occurrence was still 9.9-fold higher for trees with favourable plant traits but without SFI  $\geq$  4 (Table 4).

Among the other weather variables that were univariately significant, with lower predicted probabilities on SMB occurrence by the multivariate model compared to the parameters mentioned above, lower average values of ETp (2.1 mm), lower average values of GLB (12 MJ-m<sup>2</sup>), a medium to shorter mean sunshine duration (3.8 to 6 h), and medium averages of the maximum daily temperature (21 °C) appeared beneficial (data not shown).

## Discussion

The aim of this study was to investigate to what extent the presence of SFI promotes the occurrence of SMBs on deciduous host plants and to evaluate which other factors (different plant characteristics and weather variables) additionally influence the probability of SMBs occurrence. We therefore present for the first time multivariate models that include these three levels (SFI, host plant characteristics, weather).

## Applied methods

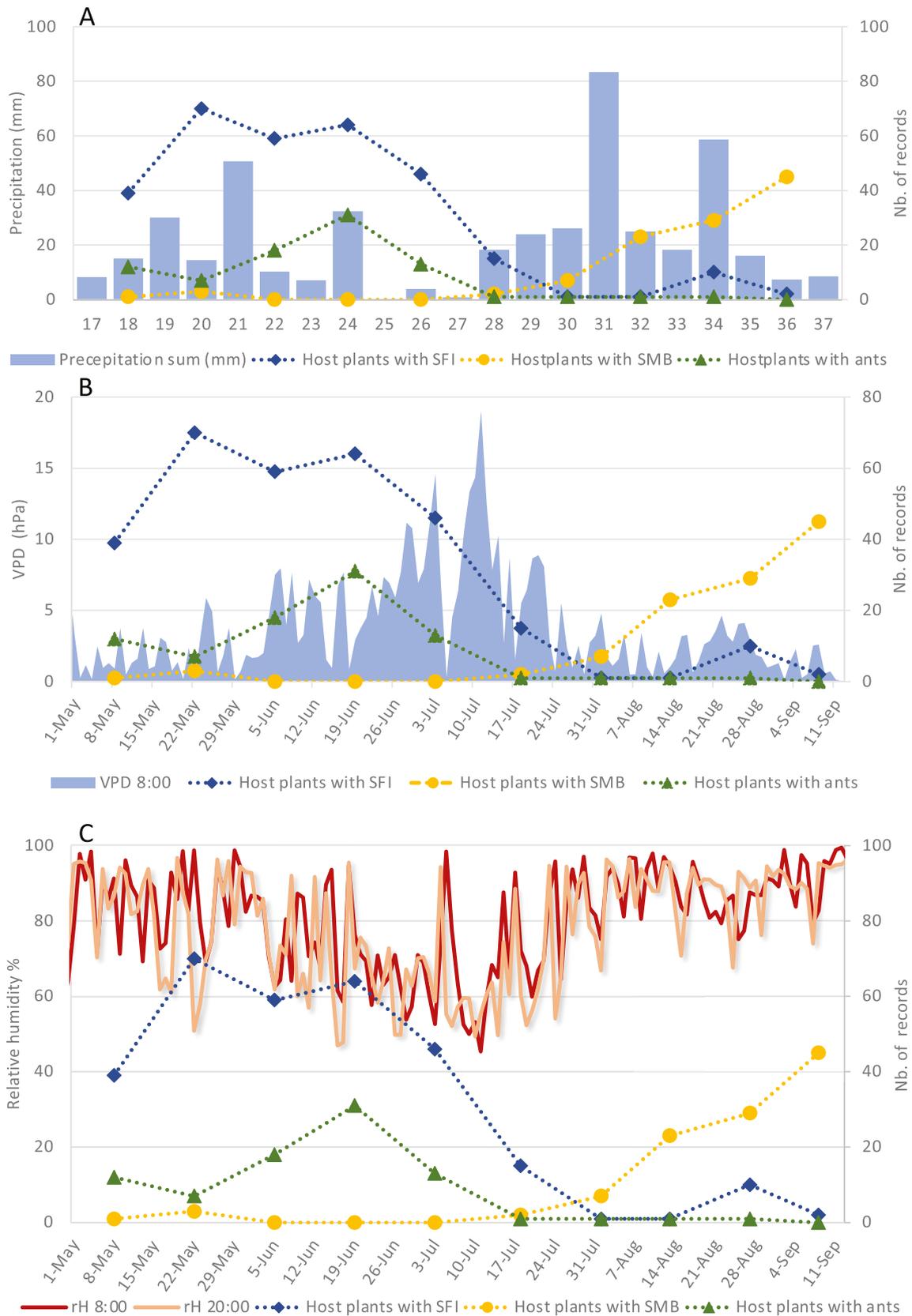
Due to the study design, in which it was important for us to compare plants under similar conditions, the number of

plant individuals was limited. We examined all plant individuals available on the plot and found that on two-thirds, no sooty mould occurred. Nevertheless, we could identify variables that lead to a higher probability for the occurrence of SMB. In addition, it was possible to derive a multivariate model in which all plant-related variables relevant for SMB were included. The observed relative abundance corresponds quite well with the relative abundance predicted by the model.

Unfortunately, it was not possible to include more than one weather parameter in this model because of convergence problems with the fitting algorithm.

## Influence of SFI occurrence and host plant traits

In the tropics, SMB occurs throughout the year on evergreen host plant leaves (Shukla and Gundappa 2017), while in the temperate region, SMB can only be observed on host plants with deciduous leaves toward the end of the growing season. However, many weather parameters are similar in spring and fall and, therefore, cannot be the main reason for the late occurrence of SMB. SMBs were found on slightly more than one-third of the experimental plants, and most individuals remained symptom-free during the observation season in our study. Since SMBs can occur on almost all surfaces as soon as conditions are favourable and, in addition to honeydew, leachates from leaves can also serve as a nutritional source, it is possible that individual host plant species have further traits that may prevent SMBs, in addition to the variables examined in this study. One possible reason may be salicylates, common secondary metabolites of willows, which at high doses (2.0–5.0 mM) can have a negative effect on the growth of individual fungal species (Strobel and Porter 2005). That effect of salicylates was confirmed in an in vivo experiment with *Aspergillus* (Panahirad et al. 2014) in *Pistacia vera* fruits. Conversely, *Epichloë festucae*, which is a symbiotic fungal endophyte of *Festuca rubra*, expresses a salicylate hydroxylase and is, therefore, able to bypass that host plant mechanism (Ambrose et al. 2015). Whether fungi of the core community of SMB in the experimental area, i.e., *Aureobasidium pullulans* and *Cladosporium cladosporioides* (Flessa et al. 2012), are affected by salicylates needs to be examined in future studies. Since SMB in this study was found on *S. pentandra*, and *S. purpurea*, which are willows with verified medium to high salicylate content (Förster et al. 2008; Volf et al. 2015), it can be presumed that salicylates cannot prevent SMBs. Salicylate content in willows is highest at the beginning of the vegetative season in March and continues to decrease throughout the season (Förster et al. 2008), representing an inverse pattern with SMB occurrence, which could be a reason for the appearance of SMB towards the end of the season. No SMBs were found on *S. daphnoides*, which could be related to the significantly higher salicylate



**Fig. 1** Seasonality of appearance of sooty mould biofilms (SMB), sap-feeding insects (SFI), and ants during the sampling period in relation to climatic data. **A** Weekly sum of precipitation, **B** daily means of maxima and minima of air temperature, **C** daily means of relative morning and evening humidity

content compared to the other two willows. However, this remains highly speculative, as the salicylate content was determined in the bark and not in leaves by Förster et al. (2008), and only two individuals of *S. daphnoides* were present in our experimental design.

Another reason for the late occurrence of SMBs could be related to changes in surface structures during leaf aging. One of the most important ageing-related factors is the roughness of surfaces, which is much higher in older leaves (Mechaber et al. 1996). The process of getting rougher alters the surface topography, which has impact on key factors for epifoliar communities. It affects the surface wettability, temperature, humidity, and wind speed and may affect the localization of plant compounds released from cells on the leaf surface (Ford and Salt 1987; Derridj et al. 1989). If the wettability of a leaf changes during the aging process, this affects the fungal growth because it facilitates the germination and growth of germ tubes (Dickinson 1981, 1986; Cabral 1985). Horizontal leaf position, rugose leaf surfaces, and concave veins are plant traits that had significant

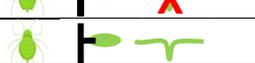
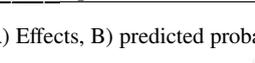
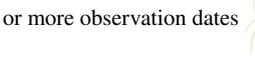
or almost significant effects on SMB in univariate models. Those traits may lead to higher water availability and more available nutrients on leaves through the accumulation of honeydew or leachates.

While sooty mould fungi may also be associated with extrafloral nectaries (Ji-Hyun et al. 2015; Choi et al. 2015) or leaf glands (Flessa and Rambold 2013), we did not detect a significant effect of leaf glands on SMBs. This is in agreement with the results on *Juglans regia*, where SMBs were associated with honeydew of aphids but not with the presence of glandular trichomes (Kim 2016).

In tropical SMBs on mango, SFI incidence significantly influenced SMB incidence up to 45% (Shukla and Gundappa 2017), and SFIs often occurred simultaneously with the SMB (Dhami et al. 2013; Shukla and Gundappa 2017), which could not be confirmed in this current study for the temperate region on host plants with deciduous leaves. However, despite the large time gap between the main season of SFIs in spring and the main season of SMB in late summer and fall, trees infested by SFIs on four or more observation dates had significantly more SMBs (3.7-fold). On evergreen conifers in the temperate region, there were significantly more filamentous fungi found in the time when the aphids were most abundant as well (Stadler et al. 1998). In the month before (May), when aphid abundance was low, the abundance of microorganisms was low as well, but fungi were still more abundant on previous aphid-invested twigs than on the

**Table 3** Multivariate model with the relevant tree-based variables

A)	Estimate	SE	Z	p-value		CI 95%
Intercept	-4.342	0.459	-9.47	<0.0001	***	-5.24, -3.44
SFI ≥ 4 	1.848	0.522	3.54	0.0004	***	0.83, 2.87
Horizontal leaf position 	1.151	0.408	2.82	0.0048	**	0.35, 1.95
Concave leaf veins 	0.748	0.42	1.78	0.0751	.	-0.08, 1.57

B)	Predicted	2.5%	97.5%
	0.01	0.01	0.03
	0.08	0.03	0.20
	0.04	0.02	0.07
	0.21	0.09	0.41
	0.03	0.01	0.07
	0.15	0.05	0.36
	0.08	0.04	0.16
	0.36	0.15	0.63

A) Effects, B) predicted probabilities based on the logistic mixed effect model in table 3A. SFI ≥ 4: trees with sap-feeding insect observations at

4 or more observation dates  , LP: horizontal leaf position  , LV: recessed leaf veins  , factor excluded 

**Table 4** Multivariate model with the relevant tree-based variables and relative morning humidity

A)	Estimate	SE	Z	p-value		CI 95%
Intercept	-6.3907	0.7307	-8.746	<0.0001	***	-7.82, -4.96
SFI $\geq$ 4 	2.6298	0.7563	3.477	0.000507	***	1.15, 4.11
Horizontal leaf position 	1.5259	0.5473	2.788	0.005298	**	0.45, 2.60
Concave leaf veins 	1.1269	0.5828	1.934	0.053154	.	-0.02, 2.27
poly(rH 8h mean14d perc, 2)1	74.923	15.9575	4.695	2.66E-06	***	43.65, 106.20
poly(rH 8h mean14d perc, 2)2	12.5631	9.4049	1.336	0.181614		-5.87, 31.00

B)	rH 64%	CI 2.5%	CI 97.5%	rH 70%	CI 2.5%	CI 97.5%	rH 77%	CI 2.5%	CI 97.5%	rH 83%	CI 2.5%	CI 97.5%	rH 90%	CI 2.5%	CI 97.5%
  	<0.001	<0.001	0.001	<0.001	<0.001	0.001	0.001	<0.001	0.003	0.003	0.001	0.012	0.033	0.010	0.103
  	<0.001	<0.001	0.004	<0.001	<0.001	0.003	0.002	<0.001	0.008	0.010	0.002	0.037	0.096	0.029	0.274
  	<0.001	<0.001	0.005	0.001	<0.001	0.004	0.003	0.001	0.009	0.014	0.005	0.038	0.137	0.063	0.273
  	0.001	<0.001	0.016	0.002	<0.001	0.012	0.008	0.002	0.030	0.043	0.014	0.122	0.328	0.141	0.593
  	0.001	<0.001	0.019	0.002	<0.001	0.016	0.008	0.002	0.043	0.042	0.009	0.177	0.323	0.091	0.696
  	0.003	<0.001	0.059	0.006	0.001	0.048	0.025	0.005	0.127	0.118	0.025	0.415	0.596	0.214	0.889
  	0.004	<0.001	0.077	0.009	0.001	0.060	0.037	0.008	0.148	0.166	0.045	0.457	0.687	0.338	0.904
  	0.012	0.001	0.218	0.027	0.004	0.179	0.106	0.022	0.382	0.381	0.110	0.754	0.872	0.557	0.973

A) Effects, B) predicted probabilities based on the logistic mixed effect model in Table 4A. SFI  $\geq$  4: trees with sap-feeding insect observations at 4 or more observation dates , LP: horizontal leaf position , LV: recessed leaf veins , factor excluded 

control twigs without aphids in September, which is consistent with the observations in our study. This influence partially be due to the honeydew produced by SFIs. Many SFIs on willows are phloem-feeders and belong to the aphids (Charles et al. 2014). Many of them are known to decrease plant health (Dixon 1998), particularly in temperate regions (Blackman and Eastop 2000). Aphids secrete saliva when they pierce and feed on host plant tissue. This saliva contains effectors that are secreted into the host and manipulate cell processes in plant tissue. Aphid damage in plants can result in water stress, reduced growth, and wilting (Jaouannet et al. 2014) and could be an explanation for the increased SMB occurrence of these trees. In this study, willow species (with at least 3 individuals) without SMBs also had fewer than 4 SFI observations, which was an indication that SMBs were more dependent on prolonged or repeated infestation by SFIs than on host plant species. One reason that less frequent SFI feedings (<4 observation dates) did not have a significant effect on SMB occurrence could be that the chemical composition of honeydew differs between SFI species (Fischer et al. 2005; Shaaban et al. 2020), which could also have an influence on SMB growth. Another reason might be that honeydew produced by insects is, to a major proportion, consumed by other insects (Stadler and Müller 1996). About one-quarter to one-third of all aphids are myrmecophiles (Bristow 1991; Stadler 1997), and ants alone may consume more than two-thirds of the available honeydew

(Müller 1956, 1960). However, no significant negative effect of ant visitation to SFIs could be detected on SMB occurrence in this study. This might need to be investigated in more detail in a future study, as a shorter observation interval is most likely required for adequate monitoring of ant presence.

### Influence of weather

In the multivariate plant model combined with individual weather parameters, the highest probabilities of SMB occurrence were predicted at low VPD, higher but not maximal precipitation sums, and the highest values of morning and evening relative humidity. In tropical SMBs on mango, a positive relationship was found only for precipitation, while morning and evening relative humidity had no effect (Shukla and Gundappa 2017). Increased precipitation also led to significantly higher infestations of leaves by biotrophic fungi that cause grapevine leaf disease (Serra et al. 2018). However, a positive effect of morning and evening relative humidity is known for the biotrophic fungus *Mycosphaerella berkeleyi*, which causes late leaf spot disease in groundnuts (Pappachan et al. 2015). In a study of cultivable fungi growing asymptotically on leaf surfaces from a temperate region, low VPD and a daily relative humidity of > 90% and higher monthly precipitation averages also had a positive

effect on fungal abundance (Talley et al. 2002). These values all relate to water availability for fungi, which is an important factor for fungal growth (Ruinen 1961). This also applies to SMB as seasonal variations in *C. cladosporioides*, a fungal species belonging to the core community of SMBs on willows (Flessa et al. 2012), are directly positively linked to relative humidity (Cabral 1985). Growth and survival of fungal spores germinating on leaves depends not only on the amount of moisture available but also on the length of time the leaf is wet. Although the duration of leaf wetness was not measured, the positive effects of horizontal leaf position and incised leaf veins on SMBs indicate that, in addition to higher nutritional availability through SFI, available moisture plays a major role in the growth of sooty moulds on leaves. Rainfall and night dew form thicker water films on leaf surfaces (Burkhardt and Hunsche 2013), which enables chemical reactions between compounds dissolved in the rain or dew water and leachates from the leaf, impacting phyllosphere microorganisms by altering the water pH and availability of nutrients (Morris 2002). Honeydew becomes desiccated at a relative humidity of <95% (Lievens et al. 2015). As honeydew is water soluble, rainfall washes it to underlying plant parts as a nutrition source for SMB fungi (Beggs et al. 2005), where it will persist for long periods during dry periods (Batista and Ciferri 1963). High prediction probabilities for SMBs also resulted from higher mean wind speeds 3 days before the observation date, in combination with the multivariate plant model. Although wind causes desiccation and, thus, a negative effect was expected, fungi belonging to the SMB core community, i.e., *A. pul-lulans*, *C. cladosporioides*, and *Phoma* sp., were regularly found in the spectrum of airborne fungal spores (Ogulana 1974; Górny et al. 2002; Horner et al. 2004). The influence of higher wind speed on the abundance and diversity of epiphytic microorganisms is consistent with other studies (Vacher et al. 2016; Gomes et al. 2018).

## Conclusion

Even if SFIs and SMBs do not occur at the same time, SFIs have a significant impact on SMBs. If intervention is needed to prevent SMBs, it should be performed as early as possible in the case of SFI infestation, since a prolonged SFI presence will lead to increased SMB prevalence weeks after the SFIs have disappeared. However, the approach of simply reducing SFIs to reduce SMBs may fall short. In a greenhouse, good moisture management that prevents sooty mould growth is essential. In addition, when possible, care should be taken in breeding to obtain plants with leaf characteristics that are less conducive for SMBs.

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## Declarations

**Ethics approval** Not applicable.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Conflicts of interest/Competing interests** The authors declare that they have no conflict of interest.

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