Journal of Plant Pathology (2024) 106:1537–1548
https://doi.org/10.1007/s42161-024-01775-0

ORIGINAL ARTICLE

Gone-wild grapevines in forests host phytoplasma genotypes linked to grapevine's flavescence dorée epidemics in cultivated vineyards and competent vectors

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Received: 17 May 2024 / Accepted: 24 September 2024 / Published online: 7 October 2024

Abstract

"Flavescence dorée" (FD) is a quarantine grapevine disease associated with FD phytoplasmas (FDp). In Switzerland, FD was identified in 2004 in the southernmost part of Canton Ticino (TI) and then rapidly propagated throughout the entire regional winegrowing area despite the mandatory control measures. The reported widespread distribution of gone-wild grapevines (GWGV) in TI raised the hypothesis of a potential role of GWGV as an FDp reservoir and as a habitat for FDp vectors. To test this assumption, GWGV and FDp vectors were sampled in 13 plots to attest their infection status and compare the FDp genetic profiles. The primary (*Scaphoideus titanus*) and best-candidate alternative (*Orientus ishidae*) vectors were collected throughout the season and were found in moderate to high abundance in all the study area. The infection rate of both GWGV and *S. titanus* followed the historical gradient of *S. titanus* arrival and dispersal in TI with a clear geographic distinction between the southern and northern part of TI. Interestingly, the rate measured for *S. titanus* was similar to that observed in highly FD-infested cultivated vineyards. Moreover, the genetic profiles of the infected GWGV and *S. titanus* samples were identical to those commonly observed in cultivated vineyards (*map* M54). Importantly, four specimens of *O. ishidae* were also found harboring the same genotype. This study emphasizes the importance of GWGV (and abandoned vineyards) and alternative vectors for the FD epidemics in FD-infested regions, as well as a potential origin for FD outbreaks in areas currently designated as FDp-free.

Keywords Genotyping · Grapevine Yellows · *Orientus ishidae* · *Scaphoideus titanus* · Switzerland

Introduction

"Flavescence dorée" (FD) is a quarantine grapevine disease associated with FD phytoplasmas (FDp, taxonomic subgroups 16SrV-C and 16SrV-D) responsible for severe production losses to European viticulture (Lee et al. 2004; Jeger et al. 2016). Its first observation on grapevines dates back to the 1950s in south-western France (Caudwell 1957). A decade later, the Nearctic leafhopper *Scaphoideus titanus* (Ball, 1932) was identified as the vector responsible for the epidemic spread in vineyards (Schvester et al. 1961; Chuche and Thiéry 2014). Despite mandatory control measures, which consist of the application of insecticides against the main FDp vector *S. titanus*, the removal of FDp-infected grapevines, and the use of certified propagation material only (Chuche and Thiéry 2014; Jeger et al. 2016), the disease is resilient and even spreads to new regions (Tramontini et al. 2020).

In Switzerland, *S. titanus* was first reported in 1967 in the Sottoceneri, which corresponds to the southernmost part of Canton Ticino (Baggiolini et al. 1968), while in the Sopraceneri (central and northern part of Ticino), it was detected only three decades later in 1998 (Linder and Jermini 2007). In the North of the Alps, the first reports of *S. titanus* date back to 1996, 2007, and 2016 for the Cantons of Geneva, Vaud, and Valais, respectively (Linder et al. 2019). FDp

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followed a similar spreading history, being detected for the first time *in planta* in 2004 in the Canton of Ticino and more precisely in the Sottoceneri, and in 2006 in the Sopraceneri, respectively (Schaerer et al. 2007; Jermini et al. 2014). The first detection in the Northern Alps occurred in the western Cantons of Vaud, Valais, and Geneva in 2015, 2020, and 2021, respectively (Schaerer et al. 2017; Canton of Valais 2022).

Besides the introduction of FDp contaminated plant material (Jeger et al. 2016), the European and Swiss diffusion history of the FD epidemics suggests that two additional factors may play a role in the maintenance and expansion of the disease. Firstly, abandoned vineyards and gone-wild grapevines (GWGVs) may represent an undetected source of FDp inoculum and a habitat for uncontrolled vector populations in the areas surrounding cultivated vineyards (Pavan et al. 2012; Lessio et al. 2014; Ripamonti et al. 2020; Oggier et al. 2023). Secondly, the existence of different and parallel FDp epidemiological cycles consisting of alternative and putative FDp vectors and host plant species may maintain FDp in the landscape and trigger FD outbreaks in cultivated vineyards (Filippin et al. 2009; Lessio et al. 2016; Casati et al. 2017; Strauss and Reisenzein 2018; Belgeri et al. 2021; Rizzoli et al. 2021; Jarausch et al. 2023). Of great interest for the particular case of Canton Ticino is the alternative epidemiological cycle consisting of the East Palearctic leafhopper *Orientus ishidae* (Matsumura, 1902) and related host plant species (e.g., *Alnus glutinosa* and *Corylus avellana*), which are known to harbor FDp strains compatible with grapevine and *S. titanus* (Casati et al. 2017; Mehle et al. 2019; Malembic-Maher et al. 2020; Rizzoli et al. 2021; Kogej Zwitter et al. 2023).

The vineyard area of Southern Switzerland and of Canton Ticino, in particular, is emblematic in this respect. The fragmented landscape hosts a significant presence of GWGVs in the forests as a result of a long-lasting abandonment process of the formerly cultivated vineyards on steep slopes or terraced terrain which cannot be mechanized and are thus very difficult to manage (Krebs and Bertogliati 2017; Oggier et al. 2023; Wyler et al. 2023). As a result, cultivated vineyards usually border or are even surrounded with forest area (Wyler et al. 2021), which makes considering the potential epidemiological impact of both GWGVs and other plants species in forested areas crucial for effectively controlling the FD epidemics and ensure eradication.

The aim of this work was to deepen the understanding of the epidemiological risk represented by areas colonized by GWGVs in the forests of Canton Ticino in the context of the FD epidemics. In particular, we aimed at (i) testing if GWGVs are a suitable habitat for juvenile forms and imagoes of *S. titanus* and *O. ishidae* and harbor FDp genotypes compatible with FD epidemics; (ii) comparing the genetic profiles of FDp-infected GWGVs and insect vectors found in the wild compartment with those infesting cultivated vineyards; iii) verifying possible geographical patterns in the FDp frequency and genotype distribution in Canton Ticino.

The implementation of the acquired knowledge for either eradicating or containing FD in areas already affected by the disease or conducting risk assessments in regions that have not yet experienced FD outbreaks are then discussed.

Materials and methods

Study area and experimental design

The study area is located in the Swiss southern Alps (Canton Ticino) and consists of forest plots hosting GWGVs originating from formerly cultivated vineyards which experienced a forest transition after management abandonment (Oggier et al. 2023). The initial plot selection consisted of intersections of the vineyard and forest signatures on historical and contemporary Swiss national topographic maps freely available to the public (see https://map.geo.admin.ch, accessed on 06 March 2024). The resulting intersections delineate former winegrowing areas that transitioned into forested landscapes, thus, potentially still hosting GWGVs. After attesting the presence of GWGVs during field visits, the most promising plots were selected and characterized in terms of location, mean slope, distance from the nearest cultivated vineyard and last time registered as a vineyard on official topographic maps (see Oggier et al. (2023) for a complete description of the methodology).

Following this procedure, 13 forest plots hosting GWGVs distributed across the whole cultivated vineyard area of Canton Ticino were selected for the experiment, trying to balance the design between the southern part of Ticino characterized by an earlier arrival of the main vector (Sottoceneri with seven plots) and the central part which was colonized significantly later by the vector (Sopraceneri with six plots, Fig. 1). Subsequently, the plots were internally further subdivided into three to 13 distinct sampling units, based on the abundance and distribution of GWGVs across the plot.

Leafhoppers collection and processing

Nymphs of *S. titanus* and *O. ishidae* were collected with a beating tray, while imagoes were captured with chromotropic sticky traps. The sampling of juvenile forms was conducted between weeks 24 and 26 of 2022. Ten GWGV shoots per sampling unit were shaken for ten seconds each, taking note of the number of available leaves for each shaken

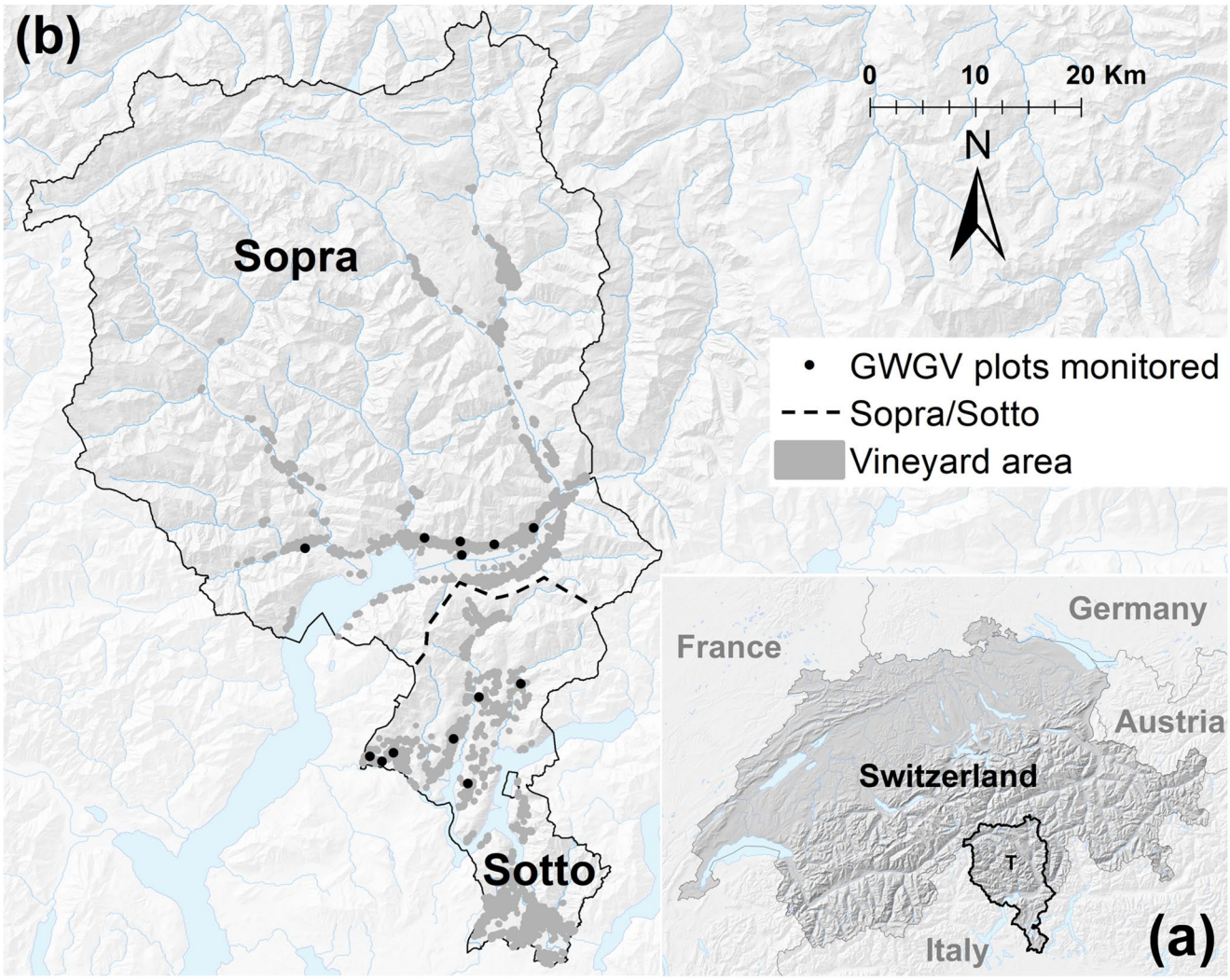

Fig. 1 Location of the experimental plots in Canton Ticino. **a** Location of the study area within Switzerland; T = Ticino. **b** Black dots: plots hosting GWGVs monitored for the presence of FDp-infected insect and plant samples. Sopra = Sopraceneri (Ticino); Sotto = Sottoceneri (Ticino). Grey areas = cultivated vineyard area

shoot. Insects were collected into labelled plastic bags and preserved in a cooling container for transportation to the laboratory facilities, where they were stored at −20 °C for conservation prior to further processing.

Adult insect specimens were captured by the mean of yellow sticky traps (Rebell Giallo, Andermatt Biocontrol AG; hereinafter referred to as YST) positioned on GWGV shoots where leaves were abundant. The number of YST per plot ranged from three to eleven, depending on plot size and accessibility. YST were replaced every other week between August and October 2022 and transported to the laboratory facilities and stored for a maximum of 2 days at 5 °C before determination and further processing. YSTs and plastic bags were checked with a stereo microscope (Olympus SZX16 with SDF PLAPO 1XPF objective lenses) and by consulting the determination keys by Della Giustina et al. (1992) and Günthart and and Mühlethaler (2002). Target nymphs were directly collected into tubes with 99% Ethanol (v/v). Target specimens glued on YST were detached using Glurex forte (50–100% D-Limonene [v/v], Andermatt Biocontrol AG), washed in 70% Ethanol (v/v) and transferred into tubes with 99% Ethanol (v/v). Finally, tubes were frozen at −20 °C until molecular analysis.

Grapevine sampling and processing

In September 2022, all GWGVs showing symptoms associated with Grapevine Yellows were identified and a minimum amount of twelve representative leaves was systematically collected for molecular analysis from each location. Considering that rootstocks might host FDp even in the absence of discernible external symptoms (Caudwell et al. 1994; Eveillard et al. 2016), for each YST position, at least twelve representative asymptomatic and healthy leaves

were additionally sampled from the available GWGVs. Leaf samples were stored in a portable fridge at 5–7 °C and transported to the lab facilities. Petioles and midribs were excised from the sampled leaves no later than the next day and promptly frozen at −20 °C to ensure preservation before undergoing nucleic acid extraction.

Nucleic acid extraction and molecular analysis

Leaf samples

Petioles and midribs taken from 3 to 4 different leaves per sample, corresponding to 0.5 to 1 g of plant material were ground in 6 mL of extraction buffer (3% Cetyltrimethylammonium bromide CTAB, 1.4 M NaCl, 25 mM EDTA, 100 mM Tris, pH 8.0) using a Homex grinder (Bioreba). Afterwards, 2 mL of this homogenate were centrifuged for 10 min at 1000× g. 900 µL of the supernatant were mixed with 2 µL of β-Mercaptoethanol and shaken for 30 min at 600 rpm and at 65 °C. Chloroform/Isoamylalcohol (900 µL) was added, homogenized by vortexing for 5 s, and centrifuged for 5 min at 3000× g. The resulting aqueous layer was transferred to a new tube, mixed with an equal volume of cold isopropanol, and incubated for 30 min at −20 °C for DNA precipitation. Precipitated material was recovered by 2 min of centrifugation at 10,000× g and washed with 1 mL of 70% Ethanol. Finally, the DNA pellets were dried overnight at room temperature and resuspended into 100 µL of PCR-grade water.

Insect samples

Nucleic acids were extracted separately for each adult specimen caught in plots hosting FDp-infected GWGVs. For adult insects caught in plots hosting FDp-negative GWGVs, nucleic acids were extracted from pools of 3 to 5 specimens. In particular, insects were homogenized in 900 µL of extraction buffer (3% Cetyltrimethylammonium bromide CTAB, 1.4 M NaCl, 25 mM EDTA, 100 mM Tris-HCl, 2% β-Mercaptoethanol, pH 8.0) and shaken for 30 min at 600 rpm and 65 °C. From here on, the same procedure applied to the leaf material was used for the insects.

FDp detection

For the leaf samples, FDp detection was accomplished with a triplex qPCR method according to Pelletier et al. (2009) with a final volume of 15 µL using a GoTaq Probe qPCR kit (Promega) and CFX96 thermocycler (Bio-Rad). The thermal cycle was composed by a denaturation phase of 5 min at 95 °C for Hot Start Taq DNA polymerase activation, followed by 40 cycles of 15 s at 94 °C and 30 s at 60 °C. All leaf samples were also analyzed for the presence of '*Candidatus* Phytoplasma solani', the pathogenic agent associated with "Bois noir" (BN). For the insect samples, a duplex qPCR method was used, as in Oggier et al. (2023). This allowed for the simultaneous detection of FDp and the Cytochrome Oxydase I (COI) of the insects applied with a final volume of 15 µL using a GoTaq Probe qPCR kit (Promega) and CFX96 thermocycler (Bio-Rad) and the same cycling conditions used for the leaf samples. All FDp-infected GWGV and insect samples had a Cq value between 18 and 35. Cq values obtained for COI ranged from 15 to 25.

Sequencing

The *map* and *vmpA* genes loci were amplified by nested PCR according to Arnaud et al. (2007) and Malembic-Maher et al. (2020), respectively. Nested PCR amplifications were carried out in 25 µL reactions using 20 pmol of forward and reverse primer, 1–2 µL of DNA template, with GoTaq G2 Flexi DNA polymerase (Promega) following manufacturer's instructions. For *malG*, PCR amplifications were carried out in 25 µL reactions with Q5 High-Fidelity DNA Polymerase (New England Biolabs) using 50 pmol of *malG_F* and *malG_R* primers from Rossi et al. (2019), 1 µL DNA template, and 0.5 U of Q5 polymerase with cycling as follows: 30 s at 98 °C, 35×(10 s at 98 °C, 20 s at 67 °C, 15 s at 72 °C), 2 min at 72 °C, hold at 8 °C. PCR products were controlled by electrophoresis on a 1% agarose gel and purified by ultrafiltration with NucleoFast 96 PCR plates (Macherey-Nagel). Products were sent to Fasteris (Plan-les-Ouates, Switzerland) for forward and reverse sequencing using Sanger technology.

Data analysis

Descriptive statistics were performed using the software R (version 4.2.2; R Core Team 2024). ArcGIS (release 10.6.1; ESRI, 2011) was used for spatial analysis and mapping renditions. Phylogenetic trees were inferred by maximum likelihood method in MEGA using the General Time Reversible model and bootstrapping with 500 replicates. All trees were visualized with iTOL (https://itol.embl.de, accessed on 21 February 2024; Letunic and Bork 2021).

Results

Leafhopper captures

Scaphoideus titanus nymphs were present across all investigated plots, while *O. ishidae* nymphs were observed in nine out of 13 plots (69%) for a total of 244 *S. titanus* and

27 *O. ishidae* collected nymphs, respectively. The capture rate (i.e., number of insects per hundred leaves) ranged from 0.39 to 10.02 for *S. titanus*. For *O. ishidae*, the capture rate ranged between 0.22 and 0.64 specimens per hundred leaves (Table 1). Imagoes of both vector species were collected in all investigated plots for a total of 1088 *S. titanus* and 324 *O. ishidae* specimens, respectively. The captures per YST ranged from 1.67 to 39.33 for *S. titanus* and from 0.17 to 19.67 for *O. ishidae*, respectively (Table 1).

Molecular analysis

Insect samples

All analyzed *S. titanus* specimens sampled in the Sopraceneri region resulted FDp-free. In contrast, specimens captured in the Sottoceneri region were consistently found harboring FDp, with infection rates ranging from 14.9 to 49.6% (Table 2; Fig. 2a). In-depth insights pursued by sequencing the *map*, *vmpA* and *malG* genes revealed that all sequenced samples were infected by the profile M54—*vmpA*-II—*malG*1/*G*3.

Regarding the alternative FDp vector *O. ishidae*, four individuals were found to be FDp-infected. Two specimens caught in Losone (Sopraceneri region) harbored the profile M50—*vmpA*-III—*malG* (mixed infection), while the other two, captured in Sessa (Sottoceneri), exhibited distinct profiles: one specimen infected by M50—*vmpA*-III, *malG*18, whereas the second one harbored the same profile found in the main FDp vector *S. titanus*, i.e., M54—*vmpA*-II—*malG*1/*G*3. Given the exceptionality of the finding, a follow-up targeted monitoring was conducted in the plot of Sessa in 2023 to confirm the potential acquisition of the M54 genotype by *O. ishidae*. Six YSTs were placed on the GWGV canopy where FDp-infected *O. ishidae* were collected in 2022 (same conditions as reported in the Materials and Methods). Four *O. ishidae* specimens resulted FDp-infected. Among these, three harbored the M54 genotype, while one M50 (Table 2).

Map sequences had 100% identity with the reference sequences LT221949 (M54) and LT221945 (M50) (Fig. 3a). Two different types of *vmpA*-III were evidenced, one with 100% similarity to LR585140 (*O. ishidae* from Losone) and the other with 100% similarity to LR585130 (*O. ishidae* from Sessa). All *vmpA*-II profiles were equivalent and had a 100% match with LR585083 (from FD92 reference strain).

Leaf samples

Symptomatic GWGVs usually showed a mild down-curling and yellowing of the leaf lamina and lack of shoot lignification, as commonly observed for symptomatic cultivated grapevines. Among the 120 analyzed leaf samples, 36 were collected from symptomatic GWGVs, while 84 came from the routine collection of asymptomatic GWGVs. The molecular analysis confirmed FDp infection in 91.7% and 7.1% of the symptomatic and asymptomatic probes, respectively. Subsequent sequencing of a subset of symptomatic GWGVs confirmed infection by the *map*-type M54 genotype (Table 3). All FDp positive GWGVs (symptomatic and asymptomatic) were exclusively found in the Sottoceneri region (Fig. 2b; Table 3). All tested samples were free from BN phytoplasma.

Discussion

GWGVs as habitat for FDp vectors

Building upon the findings reported in Oggier et al. (2023), the current study further extends the investigation into the role of GWGVs in the Swiss southern Alps forests in FDp epidemiology. The results confirmed that in the study area GWGVs within forest ecosystems serve as habitat for all life stages (i.e., egg, nymph, and imago) of both the main FDp vector, *S. titanus*, and the alternative vector, *O. ishidae* (Lessio et al. 2016; Jarausch et al. 2023). The consistent presence of nymphs and imagoes of *S. titanus* attested across all thirteen plots of this study further supports the fact that the vector populations can be sustained in the forests where GWGVs are present in spite of the mandatory treatments applied in the neighboring cultivated plots. This aligns with previous findings showing that both leafhopper species are capable of laying eggs in GWGVs bark (Oggier et al. 2023).

When forests grow in the surroundings and in proximity of vineyards as it is the case for the Swiss southern Alps (Wyler et al. 2021), vector movements between cultivated and wild compartments are most likely facilitated (Pavan et al. 2012; Lessio et al. 2014; Ripamonti et al. 2020). Lessio et al. (2014) showed that *S. titanus* typically travels distances of up to 30 m from GWGVs on the forest edge to cultivated vineyards, but few specimens were found up to 330 m from the point of origin. In this study, 70% of the GWGV plots are located within 26 m from the nearest cultivated vineyard, making an active displacement between the wild and the cultivated compartment very likely. When looking at the abandonment history of the studied plots, in the Sopraceneri region the presence of GWGVs predominantly results from recent vineyard management abandonments (i.e., post 2007), with the exception of Gerra Piano_1 and Gudo_1, both abandoned in the late 1960s (Table 1). Since the first record of *S. titanus* in the Sopraceneri dates back to 1998 only (Linder and Jermini 2007), its presence in the plots of Gerra Piano_1 and Gudo_1 may originate from

Table 1 Plot characteristics and collected insect specimens in terms of coordinates, region, mean slope, closest distance from nearest cultivated vineyard (DV), distance range between yellow sticky trap and nearest forest edge (DF), last time registered as cultivated vineyard (Last_T); absolute captures (*N*) and mean captures per hundred leaves (mean/100 leaves ± SE) during nymph collection for *Scaphoideus titanus* and *Orientus ishidae*, absolute captures (*N*) and mean captures per single yellow sticky trap (mean/trap ± SE)

Plot ID	Coordinates WGS 84	Region	Mean slope [degrees]	DV [m]	DF [m]	Last_T [y]	Leafhopper species	Nymph collection		YST	
								N	mean/100 leaves ± SE	*N*	mean/trap ± SE
Gerra Piano_1	46°10'34.3"N 8°54'10.9"E	Sopraceneri	37.7	3	0–9	1969	*S. titanus*	2	0.39 ± 0.25	28	5.60 ± 2.54
							O. ishidae	2	0.39 ± 0.25	23	4.60 ± 2.56
Gordola_2	46°11'03.2"N 8°52'09.9"E	Sopraceneri	30.3	24	0–12	2007	*S. titanus*	20	10.02 ± 8.11	118	39.33 ± 12.77
							O. ishidae	2	0.64 ± 0.32	59	19.67 ± 10.81
Gudo_1	46°10'39.7"N 8°57'17.8"E	Sopraceneri	24.2	8	0–4	1969	*S. titanus*	5	3.21 ± 3.21	8	2.67 ± 0.67
							O. ishidae	0	0.00	36	12.00 ± 9.54
Losone_1	46°10'39.1"N 8°43'22.5"E	Sopraceneri	29.2	270	0–10	2007	*S. titanus*	5	0.53 ± 0.42	60	8.57 ± 1.56
							O. ishidae	2	0.22 ± 0.14	61	8.71 ± 5.67
Monte Carasso_1	46°11'28.0"N 9°00'12.7"E	Sopraceneri	36.9	3	0–6	2007	*S. titanus*	9	1.33 ± 0.52	10	1.67 ± 1.12
							O. ishidae	0	0.00	1	0.17 ± 0.17
Medoscio_1	46°10'52.7"N 8°54'13.2"E	Sopraceneri	30.2	26	0–11	2007	*S. titanus*	9	1.36 ± 0.18	51	8.50 ± 3.33
							O. ishidae	4	0.55 ± 0.27	12	2.00 ± 0.93
Bioggio_3	46°00'44.0"N 8°54'01.1"E	Sottoceneri	29.8	35	0–7	1934	*S. titanus*	19	2.18 ± 1.57	107	13.38 ± 3.29
							O. ishidae	2	0.23 ± 0.23	7	0.88 ± 0.40
Collina D'Oro_1	45°58'27.7"N 8°54'59.5"E	Sottoceneri	16.3	140	0–22	1934	*S. titanus*	6	0.87 ± 0.39	113	14.12 ± 5.08
							O. ishidae	0	0.00	13	1.62 ± 0.62
Lamone_1	46°02'54.3"N 8°55'59.2"E	Sottoceneri	29.7	5	0–9	1969	*S. titanus*	8	0.80 ± 0.36	64	9.14 ± 4.27
							O. ishidae	0	0.00	10	1.43 ± 0.87
Monteggio_3	45°59'51.9"N 8°47'31.8"E	Sottoceneri	26.0	63	0–45	1934	*S. titanus*	91	4.91 ± 1.00	146	13.27 ± 2.08
							O. ishidae	6	0.31 ± 0.12	58	5.27 ± 1.24
Monteggio_4	45°59'36.3"N 8°48'16.0"E	Sottoceneri	25.4	9	0–12	1934	*S. titanus*	10	1.75 ± 0.73	32	8.00 ± 2.74
							O. ishidae	1	0.17 ± 0.17	3	0.75 ± 0.48
Sessa_1	46°00'00.9"N 8°49'18.2"E	Sottoceneri	28.7	8	0–25	1969	*S. titanus*	31	3.24 ± 0.96	39	5.57 ± 3.35
							O. ishidae	3	0.32 ± 0.15	8	1.14 ± 0.83
Sonvico_1	46°03'30.6"N 8°59'03.7"E	Sottoceneri	23.7	6	0–32	1934	*S. titanus*	29	2.17 ± 0.67	312	34.67 ± 12.98
							O. ishidae	5	0.39 ± 0.26	33	3.67 ± 1.91

Table 2 Molecular characterization of the Flavescence dorée phytoplasmas detected in *Scaphoideus titanus* and *Orientus ishidae* specimens collected on gone-wild grapevines; number of analyzed and infected insect specimens and genotype profile for the *map*, *vmpA* and *malG* genes

Region	Plot ID	*Scaphoideus titanus*		*Orientus ishidae*	
		Analyzed/infected	Genetic profile	Analyzed/infected	Genetic profile (sequenced specimens)
Sopraceneri	Gerra Piano_1	27/0	–	20/0	–
	Gordola_2	112/0	–	32/0	–
	Gudo_1	8/0	–	20/0	–
	Losone_1	59/0	–	51/2	M50 *vmpA*-III *malG* mix (1) M50 *malG* mix[a] (1)
	Monte Carasso_1	10/0	–	1/0	–
	Medoscio_1	51/0	–	10/0	–
Sottoceneri	Bioggio_3	96/45	M54 *vmpA*-II *malG*1/*G*3[b]	7/0	–
	Collina D'Oro_1	94/14	M54 *vmpA*-II *malG*1/*G*3[b]	13/0	–
	Lamone_1	61/17	M54 *vmpA*-II *malG*1/*G*3[b]	9/0	–
	Monteggio_3	141/70	M54 *vmpA*-II *malG*1/*G*3[b]	57/0	–
	Monteggio_4	27/5	M54 *vmpA*-II *malG*1/*G*3[b]	3/0	–
	Sessa_1	33/16	M54 *vmpA*-II *malG*1/*G*3[b]	8/2	M50 *vmpA*-III *malG*18 (1) M54 *vmpA*-II *malG*1/*G*3 (1)
		20/4[c]	-	43/4[d]	M54 (3) M50 (1)
	Sonvico_1	154/59	M54 *vmpA*-II *malG*1/*G*3[b]	30/0	–

[a]Sequencing of *vmpA* not possible due to amplification issues

[b]Gene sequencing conducted on a subset of the available *S. titanus* specimens ($N = 3$)

[c]Referred to *S. titanus* specimens collected in targeted monitoring 2023 and no genotyping

[d]Referred to *O. ishidae* specimens collected in targeted monitoring 2023 and sequencing on *map* gene only

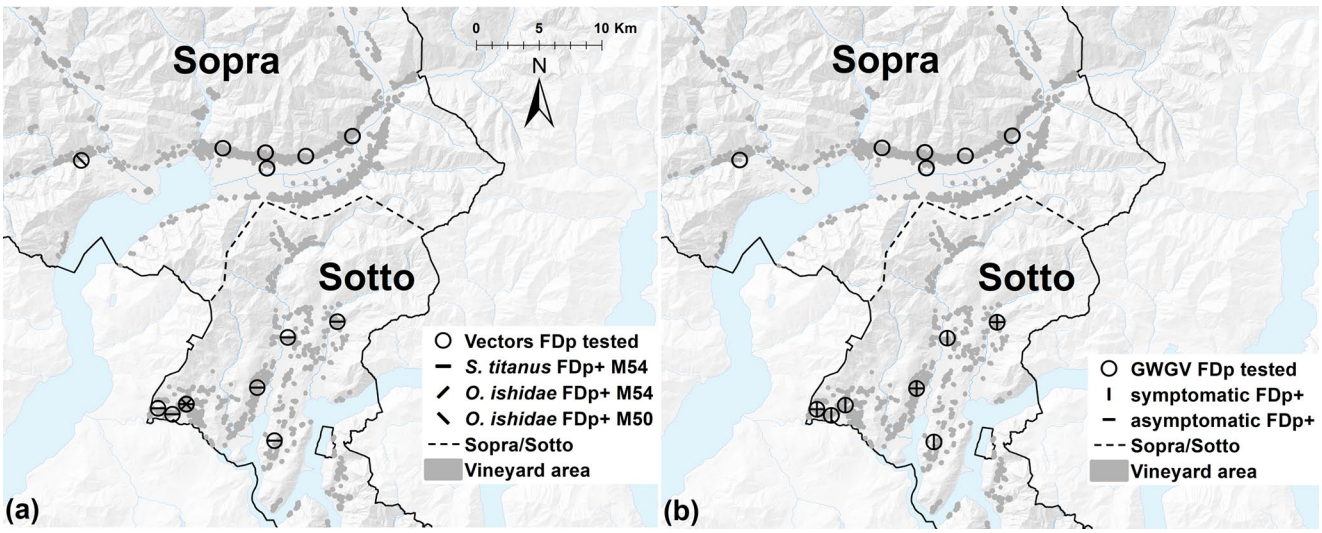

Fig. 2 Flavescence dorée detection on the analyzed insect (**a**) and gone-wild grapevine (**b**) samples. **a** Circles: location with insect vectors tested for Flavescence dorée phytoplasma; horizontal bar: *S. titanus* FDp-infected with *map*-genotype M54; diagonal line top right to bottom left: *O. ishidae* FDp-infected with *map*-genotype M54; diagonal line top left to bottom right: *O. ishidae* FDp-infected with *map*-genotype M50. **b** Circles: Gone-wild grapevines (GWGV) tested for FDp; vertical bar: symptomatic and FDp-infected samples; horizontal bar: asymptomatic and FDp-infected samples. Sopra = Sopraceneri (Ticino); Sotto = Sottoceneri (Ticino). Grey areas = cultivated vineyard area

active migration from nearby cultivated vineyards (Lessio et al. 2014), whereas in the most recently abandoned plots, a portion of the observed populations of *S. titanus* may have persisted throughout the transition from cultivated vineyard to forested area. On the other hand, in the Sottoceneri region the investigated plots hosting GWGVs exclusively originate from long-abandoned vineyards (Table 1). Considering that in this region *S. titanus* was already identified in 1967 (Baggiolini et al. 1968), it is assumable that most of the established *S. titanus* populations in GWGV plots could

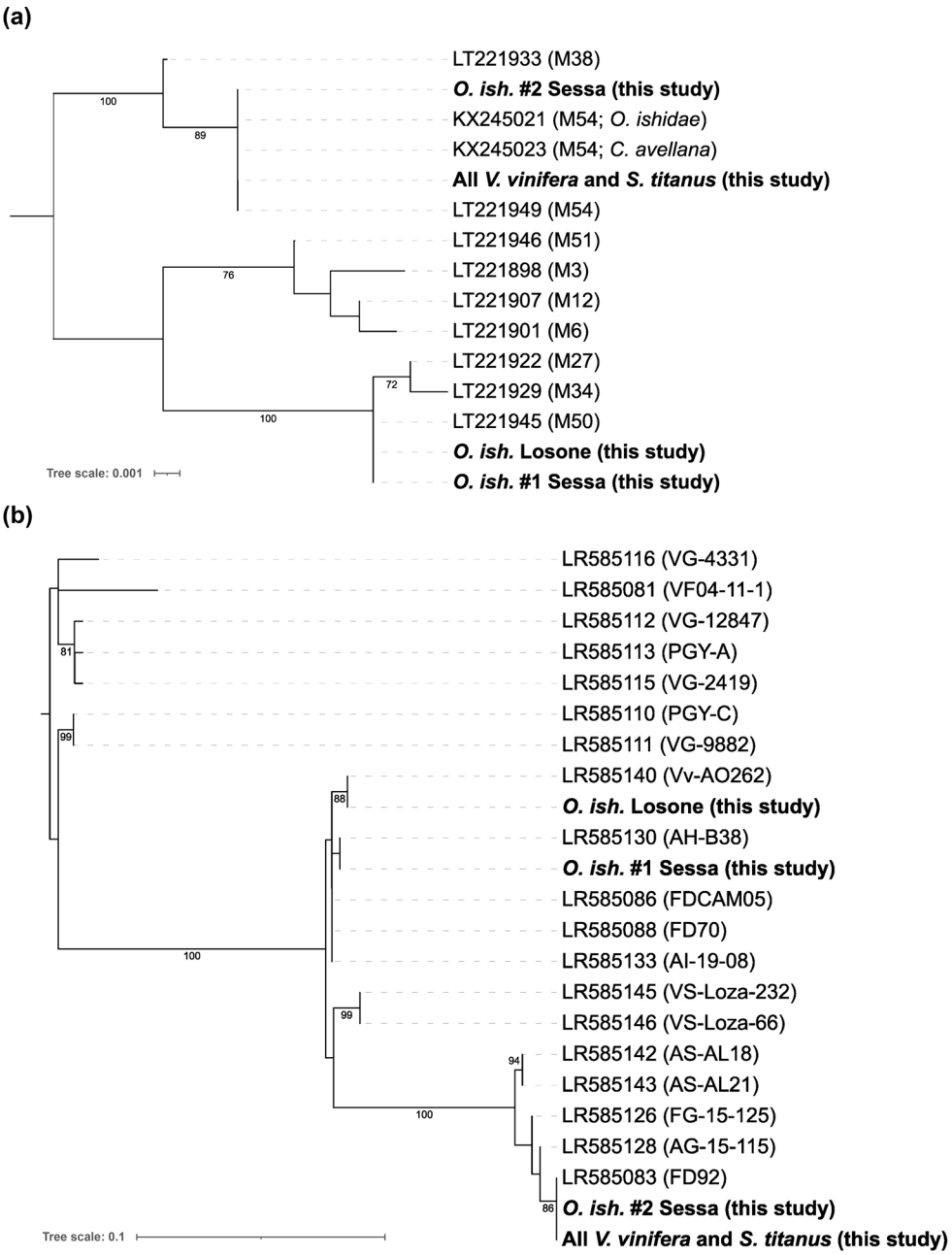

Fig. 3 Phylogenetic tree of the *map* (**a**; partial) and *vmpA* (**b**) genes sequences from *Scaphoideus titanus*, *Orientus ishidae* and gone-wild grapevines obtained in this work and reference strains from Genbank (see Online Resource 1). Maximum likelihood phylogeny based on nucleotide sequences of **a** *map* (543 bp) and **b** *vmpA* (465 bp) genes. The numbers on branches indicate the level of bootstrap support (500 replicates). Support values above 70% are labeled. The scale bar shows the number of substitutions per site

have already been present before vineyards abandonment. Nevertheless, the proximity to cultivated vineyards might have further contributed to ensure a steady input of additional specimens in both regions.

Regarding the best-candidate alternative FDp vector *O. ishidae*, both juvenile forms and imagoes were captured on GWGVs in the whole study area, despite the fact that grapevine is not one of its main hosts (Nickel 2010; Lessio et al. 2016). The proximity to better suited and preferential host plant species such as *C. avellana* may indeed have masked the actual population abundance of *O. ishidae* observed on YST (Hamilton 1985; Nickel 2010), since the latter were placed in the GWGV canopy. Nevertheless, once again, it is confirmed that *O. ishidae* does visit grapevine and has the potential to oviposit on it (Lessio et al. 2019; Oggier et al. 2023). Considering that *O. ishidae* favors plant species that naturally occur in European forests such as *C. avellana*, *Carpinus betulus*, *Salix* spp., *Alnus* spp., etc. and its polyphagic behavior (Nickel 2010; Rizzoli et al. 2021), the chance of interacting with GWGVs within the forest is even higher than in cultivated vineyards.

Potential epidemiological role of GWGVs

GWGVs are present in the forests across the whole winegrowing area of Canton Ticino, especially in the compartments

Table 3 Molecular characterization of the Flavescence dorée phytoplasmas detected in symptomatic and asymptomatic leaf samples collected from gone-wild grapevines; number of analyzed and infected leaf samples, and *map* genotype (conducted on all FDp-infected samples)

Region	Plot ID	Analyzed/infected		*map* genotype
		Symptomatic	Asymptomatic	
Sopraceneri	Gerra Piano_1	0/0	5/0	–
	Gordola_2	0/0	3/0	–
	Gudo_1	0/0	3/0	–
	Losone_1	0/0	7/0	–
	Monte Carasso_1	0/0	6/0	–
	Medoscio_1	0/0	6/0	–
Sottoceneri	Bioggio_3	6/5	8/2	M54
	Collina D'Oro_1	1/1	8/0	M54
	Lamone_1	6/5	7/0	M54
	Monteggio_3	15/14	11/2	M54
	Monteggio_4	2/2	4/0	M54
	Sessa_1	2/2	7/0	M54
	Sonvico_1	4/4	9/2	M54

that formerly hosted cultivated vineyards and then experienced a forest transition due to their abandonment (Oggier et al. 2023). The widespread presence and high incidence of FDp-infected GWGVs and *S. titanus* specimens across the Sottoceneri region raises several questions regarding the actual role that the wild compartment might play in the maintenance and even spread of both FDp and its vectors. The infection rates for *S. titanus* found in this study clearly indicate the potential to have a complete and active 'grapevine - *S. titanus* - FDp' pathosystem replicated in the wild compartment (Table 2; Bressan et al. 2005). Such infection rates are in line with those documented by studies conducted in Italy by Lessio et al. (2007) and Ripamonti et al. (2020), who also highlighted the high risk posed by abandoned vineyards and GWGVs on the forest edge. Here we demonstrated that regardless of the FDp genotypes found in GWGVs and insect vectors, FDp-infected GWGVs may survive and thrive much deeper inside forest stands and not forcibly on the forest edge where the access to sunlight is usually facilitated. The clear distinction between the infection level recorded in plant and insect samples collected in Sotto- and Sopraceneri is most likely due to the different history of *S. titanus* and FDp arrival and spread in the two regions (Baggiolini et al. 1968; Linder and Jermini 2007), which are geomorphologically divided by a mountain range (Monte Ceneri). Such a physical barrier that also breaks the vineyards continuum across the study area may have significantly lowered the risk of active migration of *S. titanus* (see the vineyard area shown in Fig. 1), as already proposed by Linder and Jermini (2007) and Jermini et al. (2014) when discussing the later arrival of *S. titanus* in the Sopraceneri, i.e., ca. 30 years after its first record in 1967 in the Sottoceneri (Baggiolini et al. 1968).

The molecular analysis showed that all FDp-infected *S. titanus* specimens harbored the same FDp genotype profile (M54—*vmpA*-II—*malG*1/*G*3) identified in FDp-infected GWGVs. The *map* genotype M54 is consistently observed also in cultivated vineyards of the Swiss southern Alps and neighboring winegrowing regions (Trivellone et al. 2016; Casati et al. 2017; Malembic-Maher et al. 2020; Rizzoli et al. 2021; Rigamonti et al. 2023). This implies that *S. titanus* most likely originally transmitted M54 to GWGVs from nearby cultivated and FD-infested vineyards. This is supported by the fact that M54 has never been found in known and consistent alternative host plant species reservoirs such as *Alnus* spp. and is most probably the result of a genotype diversification that previously occurred in cultivated grapevine (Malembic-Maher et al. 2020). In terms of plant protection, this poses a high risk, since the most vicious FDp genotype (*map*-profile M54) is present in GWGVs and in *S. titanus* populations in the wild and untreated compartment. Thus, such compartment may act as a reservoir of FDp inoculum, which might easily be (re)transferred to cultivated vineyards via competent vectors.

As for the role of the best-candidate alternative FDp vector, *O. ishidae*, there are two main points worth of consideration: the first and most important one is associated with the finding of FDp-infected specimens harboring the genetic profile M54—*vmpA*-II—*malG*1/*G*3 over two consecutive years, the very same found in *S. titanus* and in GWGVs; the second one confirms previous findings reported by Casati et al. (2017) and Rizzoli et al. (2021) for the study area, i.e., the presence of *map* genotype M50 in *O. ishidae*. In particular, the finding of FDp-infected *O. ishidae* in Sessa_1 harboring the FDp profile M54—*vmpA*-II—*malG*1/*G*3 poses a great concern regarding the potential ability of *O. ishidae* to acquire FDp genotypes directly from grapevine. In fact, if the acquisition would occur on another plant species (e.g., *Corylus avellana*), the overall conceptualization of FDp epidemiology might also be challenged. So far, only

Casati et al. (2017) had indirectly reported the finding of *O. ishidae* and *C. avellana* infected by M54. The published sequences were originally described as belonging to *map*-group FD2 (Genbank accession numbers KX245021 and KX245023 for *O. ishidae* and *C. avellana*, respectively). The alignment with other published sequences, including the ones reported in this study, eventually allowed to confirm the FDp-infection associated with the *map* genotype M54 (Fig. 3). Most importantly, the insect specimens analyzed in this study were collected in the same study area at about 20 km of distance. Thus, the Swiss southern Alps are to date the only region for which the ability of *O. ishidae* to acquire the M54 *map* genotype is confirmed. This may be due to the particularity of the local vineyard agroecosystem and to the presence of GWGVs in the forest. However, it is likely that also other winegrowing regions may experience the same phenomenon, although not yet documented. In fact, despite consistent findings regarding the actual ability of *O. ishidae* to transmit FDp to grapevine in nature are still lacking, Lessio et al. (2016) and Jarausch et al. (2023) showed that it is indeed possible. In both cases however, no M54 was found and the dominant *map* genotypes were M38 (FD2) and M50 (FD1), which are commonly found in the landscape of several European countries as summarized by Malembic-Maher et al. (2020). The identification of such genotypes in insect vectors is usually associated with the presence of *Alnus* spp. stands in the proximity of leafhopper collection. In the particular case of Canton Ticino, Rizzoli et al. (2021) showed a high prevalence of M50 in both *O. ishidae* and *A. glutinosa*, while M38 was not detected in the surveyed *A. glutinosa* stands. The identification of *O. ishidae* specimens collected on GWGVs carrying the *map* genotype M50 in Losone_1 (Sopraceneri) and Sessa_1 (Sottoceneri) thus confirms previous investigations conducted in the study area (Casati et al. 2017; Rizzoli et al. 2021). In both plots, the closest *A. glutinosa* tree was at least 120 m of distance in Sessa_1 and 200 m in Losone_1, respectively.

Consequences in terms of management strategies

From a management point of view, the presence of GWGVs in forests could serve as an intermediary link and a plausible exchange point for FDp between diverse plant and leafhopper species. The coexistence of FDp-infected GWGVs in the landscape, along with recognized FDp alternative wild host plant species and uncontrolled populations of *S. titanus* and *O. ishidae* underscore the necessity for the implementation of containment strategies that include the landscape within the broader context of FDp epidemiology to effectively address the potential risks of FDp spread into and from cultivated vineyards. However, the need for an active control of GWGVs in the forest and the related vector populations has not yet been perceived as a priority by the authorities and winegrowers. Indeed, the current mandatory control measures are quite vague and only indicate abandoned vineyards and rootstock resprouts as possible FDp inoculum sources and vector habitats. As a result, GWGVs are usually ignored in the frame of the mandatory measures to control FD, allowing the vector populations to survive and develop undisturbed on GWGVs.

Although very challenging due to the practical and technical difficulties of access and treatment or legal issues (e.g., in Switzerland no insecticide applications are allowed in the forest compartment; Fedlex 1991), GWGVs thriving in forest stands should be properly taken into account when designing FD management strategies. This would better support eradication strategies in FD-infested areas, as well as ensure the prophylactic measures in winegrowing areas where FD is not yet present in cultivated vineyards.

Regarding the epidemiological role of *O. ishidae*, this study indicates that this leafhopper species could potentially spread the epidemic genotype M54. However, further research is required to ascertain whether this situation can be observed in practice within vineyard plots in historically contaminated areas where eradication seems ineffective. In FDp-free areas, this may constitute an additional risk if M54 is introduced with FDp-infected propagative material, regardless of the attested presence of the main FDp vector, *S. titanus*. Nevertheless, it is very unlikely that *O. ishidae* will match the ability and the efficiency of *S. titanus* in spreading FDp within cultivated vineyards.

Conclusion

The comprehensive exploration of GWGVs in Canton Ticino has significantly expanded our understanding of the potential role played by these habitats in the context of FDp epidemiology, including the possible localized epidemiological significance of the alternative vector, *O. ishidae*. The hypothesized migration patterns of FDp vectors from cultivated vineyards to forested areas and vice versa emphasize the need for a holistic approach in landscape management to effectively contain FD. This could be achieved by incorporating these abandoned areas into disease control strategies, as the likelihood of a flow of phytoplasmas between various compartments of the agroecosystem is not negligeable (Lessio et al. 2014; Rigamonti et al. 2023). Importantly, these reservoirs are not subject to conventional FD management practices and thus necessitate the development of tailored measures to address the unique circumstances they present. This is pivotal for effectively limiting disease spread across both wild and cultivated environments, ensure eradication, and protect FDp-free areas.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42161-024-01775-0.

Acknowledgements The authors wish to thank Nicole Togni and Beniamino Gramegna for their technical support.

Author contributions Conceptualization and methodology, A.O. and A.R.; investigation, data curation, formal analysis, visualization and writing—original draft, A.O.; investigation and validation, C.D.; writing—review & editing, A.R., M.C., C.D., and O.S.; funding acquisition, M.C. and O.S.; project administration, M.C.; supervision, M.C. and A.R. All authors have read and agreed to the published version of this manuscript.

Funding Open access funding provided by Agroscope. This research was partially funded by the Swiss Federal Office for Agriculture (grant number 627001075).

Data availability Data supporting the reported results can be found at https://doi.org/10.16904/envidat.503.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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