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Source: Willdenowia, 45(2) : 197-207

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: <https://doi.org/10.3372/wi.45.45206>

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Vitis ×novae-angliae (Vitaceae): systematics, distribution and history of an “illegal” alien grape in Europe

Abstract

Ardenghi N. M. G., Galasso G., Banfi E. & Cauzzi P.: *Vitis ×novae-angliae* (Vitaceae): systematics, distribution and history of an “illegal” alien grape in Europe. – Willdenowia 45: 197–207. 2015. – Version of record first published online on 13 July 2015 ahead of inclusion in August 2015 issue; ISSN 1868-6397; © 2015 BGBM Berlin.

DOI: <http://dx.doi.org/10.3372/wi.45.45206>

Systematics and distribution in Europe of *Vitis ×novae-angliae* (= *V. labrusca* × *V. riparia*, Vitaceae), a naturalized North American neophyte introduced for wine production in the 19th century, are investigated. Original identification tools are provided and diagnostic characters are discussed in detail, with special reference to leaf, fruit and seed morphology and the flavour of ripe berries. The complex of events that led to its introduction and eventually to its prohibition in Europe are also taken into account. Original morphological data regarding infructescences and seeds of related taxa are also reported.

Additional key words: alien species, nothotaxa, seed morphology, *Vitis labrusca*, *Vitis riparia*

Introduction

The occurrence of *Vitis ×novae-angliae* Fernald (pro sp.) as a spontaneous alien in Europe was firstly recorded by Laguna (2005), who placed this hybrid among the “variedades más comunes cultivadas y asilvestradas” in the Iberian Peninsula and the Balearic Islands, regarding it as “rare”. Its presence in N Italy was then supposed by Ardenghi & al. (2014), who reported plants with intermediate characters between *V. labrusca* L. and *V. riparia* Michx. Some months later, Tison & de Foucault (2014) recorded, under “*V. labrusca* s.l.”, a series of hybrids of *V. labrusca* from France, among them *V. labrusca* × *V. riparia*, yet without giving any further detail regarding diagnostic characters and distribution.

This research outlines the currently known distribution of *Vitis ×novae-angliae* in Europe, confirming its presence in Italy; additionally, it provides original iden-

tification tools to allow its distinction from the parental species and other spontaneous cultigen hybrids.

The systematics of the genus *Vitis* L. in Europe have been recently treated in depth by Ardenghi & al. (2014), who assigned new names to three nothospecies largely employed as rootstocks and naturalized and/or invasive in various European countries. This paper is a subsequent step toward the investigation of this critical group, focusing on a member of the so-called “direct-producer hybrids”, natural or artificial crosses between American species or between American species and *V. vinifera* L., which represented an early solution to phylloxera, simultaneously oriented to the production of wines, which, although “surrogate”, gained great popularity in many parts of Europe (such as ‘Clinton’, a cultivar and home-made wine still well-known in N Italy). In line with the previous contribution (Ardenghi & al. 2014), a strictly taxonomic approach has been followed to evaluate the

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Table 1. Comparison of the main diagnostic features of *Vitis xnovae-angliae*, *V. labrusca*, *V. riparia* and *V. xkoberi*. Terminology is largely according to Ardenghi & al. (2014: 165) for the vegetative traits, and to Rivera & al. (2007) for the seeds; the letters “w-” and “r-” stand for “white” and “rufescent”, respectively.

	<i>V. xnovae-angliae</i>	<i>V. labrusca</i>	<i>V. riparia</i>	<i>V. xkoberi</i>
Tendrils consecutive on	2, 3+ nodes	3+ nodes	2 nodes	2 nodes
Petiole insertion (abaxial leaf surface)	w-r-floccose or w-r-arachnoid and sometimes hirtellous	tomentose	hirtellous	w-arachnoid and hirtellous
Petiole pubescence	w-r-floccose or w-r-arachnoid and sometimes hirtellous	glabrous or w-r-arachnoid	hirtellous	w-arachnoid and hirtellous
Phylloxera galls on leaf blades	present	absent	present	present
Abaxial/adaxial leaf colour	discolorous	discolorous	concolorous	concolorous
Lobes at end of central and 2 lateral nerves	absent or inconspicuous	absent or inconspicuous	acuminate to cuspidate	inconspicuous
Abaxial leaf surface	w-r-floccose to w-r- tomentose or glabrous	w-r-tomentose	hirtellous	glabrescent to hirtellous
Adaxial leaf surface	reticulate-rugose	reticulate-rugose	smooth	smooth
Tufts of hairs at vein axils	present	absent	present	absent
Vein surface (abaxial leaf surface)	w-r-floccose and hirtellous	w-r-tomentose	hirtellous	hirtellous and w-arachnoid
Leaf base	U- or V-shaped	U- or V-shaped	U-shaped	U- or lyre-shaped
Leaf margin teeth	obtuse	obtuse	acute	obtuse
Infructescence compactness	compact	compact	lax	lax or compact
Berry diameter [mm]	10–15	>12	5–9(–10)	(4–)5–9(–10)
Exocarp adherence	none or scarce	none	strong	strong
Juice colour	dark red	colourless	dark red	dark red
Flavour	“foxy” and astringent	“foxy”	astringent	astringent
Seed body shape	ellipsoid-obovoid, polygonal	ellipsoid-obovoid, polygonal	spheroidal to ellipsoid-spheroidal	spheroidal to ellipsoid-spheroidal
Seed length [mm]	6–7.2	5–8	3.5–4.5	(4–)4.2–5.1
Seed width [mm]	(3.5–)3.9–4.4	4.4–4.5(–4.7)	2.8–3.5	3.2–3.7(–3.9)
Seed apex	± rounded to slightly notched	notched	rounded	slightly notched to notched
Seed beak shape	rectangular to obtrapezoidal	broadly obtrapezoidal	broadly obtrapezoidal	subcylindric
Seed beak length [mm]	1–1.9	1.6–2.1	0.2–0.5	(0.4–)0.5–0.8
Seed beak width at base [mm]	1.9–2.2(–2.3)	2.1–2.9	0.8–1.1	0.9–1.1(–1.2)

natural variability of the nothotaxon and its relationship with the parental taxa. Viticultural and ampelographic sources played an important role in tracing the biological, historical and cultural events that led to the introduction, the success and the eventual disappearance of *V. xnovae-angliae*, indispensable requirements to understanding the ecology and geographic distribution of a taxon until now largely unknown to botanists.

Material and methods

The present paper is based on the study of material collected during field trips in N Italy between 2013 and

2015, on the revision of exsiccata held at FI, MNAV, MSNM, P, PAD, PAV and VER (herbarium codes according to Index Herbariorum: Thiers 2015+) and European floristic literature regarding the genus *Vitis* (e.g. Laguna 2004, 2005; Tison & de Foucault 2014).

The description of *Vitis xnovae-angliae* and the morphological data regarding infructescences and seeds of *V. labrusca*, *V. riparia* and *V. xkoberi* Ardenghi & al. reported in Table 1 are the result of original observations and measurements by the authors on specimens collected in the wild and currently stored at MSNM (see Specimens examined and Appendix). The *Vitis labrusca* data were completed with information acquired from literature (Moore 1991).

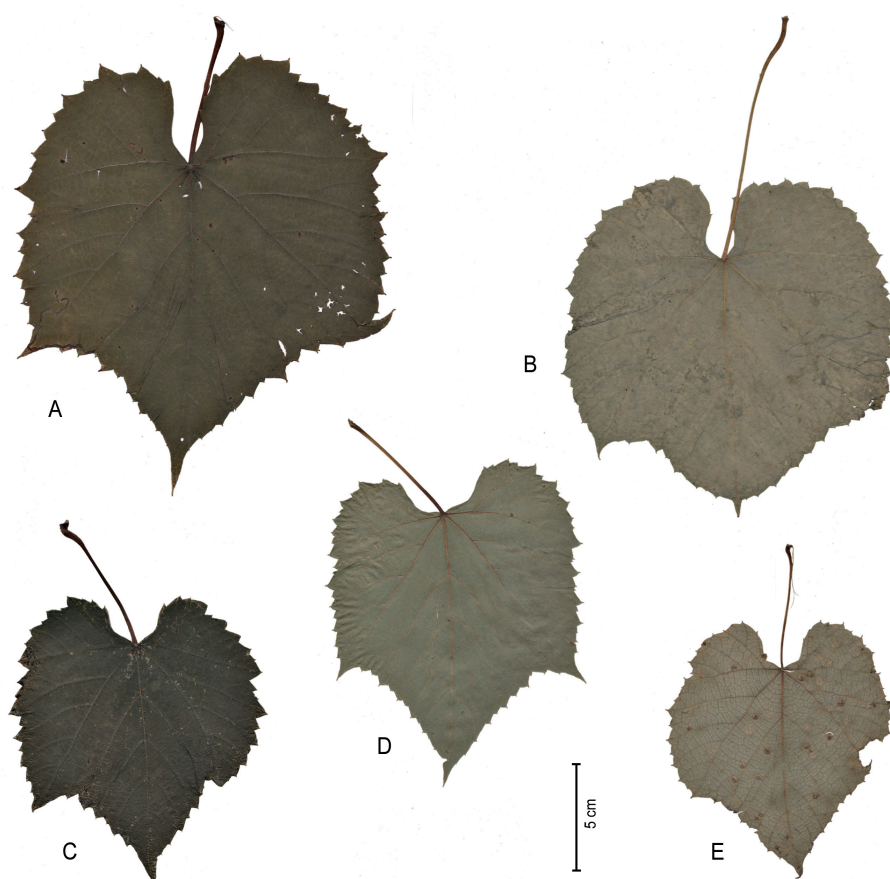


Fig. 1. *Vitis x novae-angliae* leaf blades – A & C: adaxial surface; B & D: abaxial surface; E: abaxial surface with phylloxera galls. – A & D: Santo Stefano Ticino, Italy; B & E: Bereguardo (Moriano), Italy; C: Treviglio, Italy. – Scans by N. M. G. Ardenghi.

Particular attention was paid to leaf and seed morphology, the indumentum of vegetative parts and the flavour of ripe berries. Exsiccated mature leaf blades of *Vitis x novae-angliae* were scanned at 600 dpi resolution using a Canon MP230 scanner (Fig. 1); the leaf blade and petiole indumentum were examined using a back-scattered scanning electron microscope (SEM) JEOL JSM-5610LV. Small fragments of leaf surface (about 1 cm²) were carved from dried leaves around the petiole insertion and in the centre of the leaf blade, in order to examine the trichomes on petioles, along leaf margins, at the vein axils and on the abaxial leaf surface. Leaf samples were mounted on aluminium stubs using conductive carbon adhesive tabs. Four images were taken at three different magnifications ($\times 35$, $\times 70$, $\times 100$) for the leaf details (Fig. 2). Seeds of *V. x novae-angliae*, *V. labrusca*, *V. riparia*, and *V. x koberi* were pictured by means of a Nikon D300 reflex camera (Fig. 3).

The identity of the investigated exsiccata was confirmed by their comparison with the type specimens of *Vitis x novae-angliae* stored at GH and NY, and the descriptions of both the nothospecies and the parental species provided by Fernald (1917), Moore (1991), and Ardenghi & al. (2014). Information useful to confirm the identity of our plants was additionally acquired from the

examination of cultivated individuals of 'Clinton' from Castelleone (Italy, see specimens examined) and ampelographic literature, which served also as a source for tracing the cultivation history of the *labrusca-riparia* hybrids in Europe.

Results and Discussion

Nomenclature

Vitis x novae-angliae Fernald in Rhodora 19: 146. 1917, pro sp.

= *Vitis labrusca* L. \times *V. riparia* Michx.

Lectotype (designated by Moore 1991: 364): [United States of America, Maine, Penobscot County], "Thicket by the river, Orono", 27 Jun 1906, *M. L. Fernald s.n.* (GH 00051708 [image!]; isolectotypes: GH 00061709 [image!], GH 00061747 [image!], GH 00061748 [image!], NY 00415161 [image!], PH); syntypes: *ibid.*, 17 Aug 1908, *M. L. Fernald s.n.*

(GH 00051711 [image!]); *ibid.*, late Sep 1908, *M. L. Fernald s.n.* (GH 00051710 [image!], GH 00061749 [image!]).

Description

Vines woody, deciduous, climbing or creeping-prostrate. *Branchlets* with sparse white to rufescent floccose pubescence; *bark* exfoliating in shreds on mature stems. *Tendrils* bifurcate to occasionally trifurcate, a tendril or inflorescence present at 2, 3 or more consecutive nodes. *Petiole* white to rufescent floccose, usually with hirtellous pubescence, rarely glabrous, yellowish-green; *leaf blade* usually thick and coriaceous (thinner in immature leaves), discolorous, 9–24 cm long, not conduplicately folded, broadly cordate, from subentire to slightly 3-lobed, usually with phylloxera galls; *abaxial surface* pale green, dull, glabrous, with white to rufescent floccose pubescence or with a continuous whitish to rufescent thin layer of tomentum (more evident in immature leaves), with dense to sparse floccose or arachnoid pubescence on veins at petiole insertion, sometimes accompanied by rigid hairs; *veins* with sparse to dense white to rufescent floccose and hirtellous pubescence, with lax to dense tufts of rigid hairs at axils; *adaxial surface* dark green, slightly lustrous, usually reticulate-rugose in appearance for sunken veins, gla-

brous (white to rufescent tomentose in apical leaves not yet expanded); *veins* greenish- or yellowish-white, glabrous or with arachnoid or floccose white to rufescent pubescence, occasionally hirtellous; *leaf base* U- or V-shaped. *leaf margin* with hirtellous and white to rufescent floccose pubescence, dentate-crenate, teeth obtuse (usually broadly triangular, occasionally curly bracket-shaped, pointed-arch-shaped or rounded) in mature leaves, sometimes acute in immature ones, teeth at ends of central and 2 main lateral veins usually broadly triangular, acute to shortly acuminate. *Infructescences* 3.6–10.1 cm long, 3.5–5.3 cm wide, from cylindric to obconic in outline, sometimes lobed in upper part, usually compact (berries touching each other); *peduncle* 1.4–4.8 cm long; *rachis* slightly arachnoid and/or hirtellous pubescent; *pedicels* (3–)4–7 mm long. *Berries* 16–50 per infructescence (sometimes more in cultivated plants), 10–15 mm in diam., globose, black with a thin pruinose layer; *exocarp* (“skin”) scarcely to moderately adherent to mesocarp; *mesocarp* (“flesh”) mucilaginous, grey-yellowish, dark red around seeds; *juice* staining dark red; *flavour* initially “foxy”, then decidedly sharp and astringent, finally a residual piquancy is perceived on tongue tip. *Seeds* 1–3 per berry, 6–7.2 mm long, (3.5–)3.9–4.4 mm wide (including beak); *seed body* ellipsoid-obovoid, rarely spheroidal, usually polygonal, apex from ± rounded to slightly notched, grey-brownish; *beak* 1–1.9 mm long, 1.9–2.2(–2.3) mm wide (at junction of seed body), from rectangular to obtrapezoidal in outline, brownish; *chalaza* not always well developed, 1.3–2.2 mm long, 0.9–1.3 mm wide, ovate, yellowish-brown; *fossettes* yellowish to yellowish-brown.

Systematics and identity of the specimens

French botanist and ampelographer Alexis Millardet (1838–1902) was the first to identify hybrids between *Vitis labrusca* and *V. riparia*. In 1874, he suspected a hybrid origin of the cultivars (known as “vitigni” in Italy,

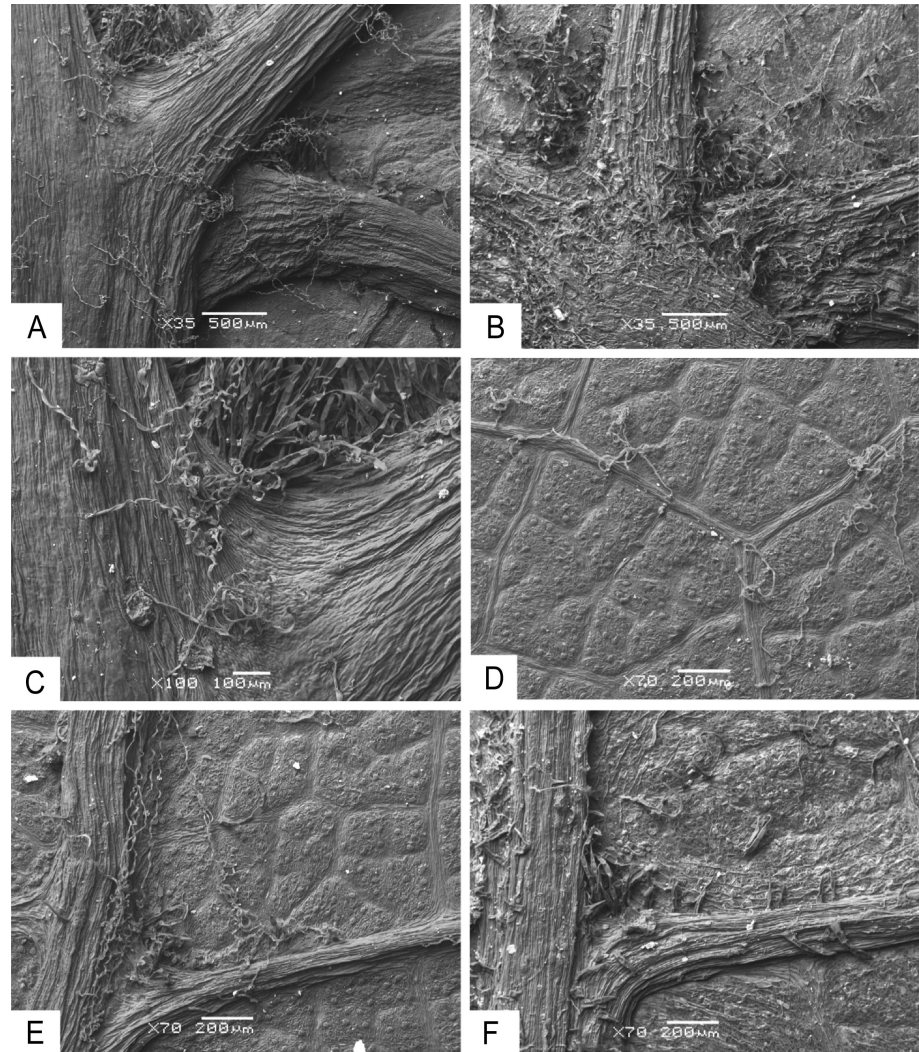


Fig. 2. *Vitis xnovae-angliae* leaf indumentum on abaxial leaf surface – A & B: petiole insertion; C: detail of petiole insertion; D: abaxial leaf surface; E & F: vein axils. – A, C–E: Santo Stefano Ticino, Italy; B & F: Missaglia, Italy. – Photographs by M. Zilioli.

and “vignes” in France) ‘Clinton’, ‘Taylor’, and ‘Vialla’ (syn. ‘La Touratte’) (Millardet 1876), until that time simply regarded as cultivars of *V. riparia* (*V. cordifolia* auct. non Michx.; *V. vulpina* auct. non L.) by different American and European authors, such as Strong (1866), Engelmann (1868) and Planchon (1875). Further studies allowed Millardet to confirm the *labrusca-riparia* parentage of these three cultivars (Millardet 1877a, b, 1880, 1882, 1885), then under the spotlight of viticulturists for their resistance to phylloxera; his results were subsequently followed by Munson (1885, 1909), Viala & Ravaz (1892), Hedrick (1908), and, with caution, by Bailey (1934). Besides ‘Clinton’ and ‘Taylor’, dozens of additional cultivars were recognized within *V. labrusca* × *V. riparia*, among them ‘Elvira’, ‘Montefiore’, ‘Noah’, ‘Oporto’, and ‘Sherman’ (Millardet 1885; Viala & Ravaz 1892; Hedrick 1908; Galet 1988). As reported in most of the aforementioned sources (e.g. Millardet 1877a, 1885; Munson 1909), later supported also by Galet (1988), ‘Clinton’ and ‘Taylor’ were spontaneous (or “accidental”,



Fig. 3. *Vitis xnovae-angliae*, *V. labrusca*, *V. riparia* and *V. xkoberi* seeds, ventral (on left) and dorsal (on right) sides, on 1 mm squared paper – A: *V. xnovae-angliae* (Albuzzano, Italy); B: *V. labrusca* (Pavia, Italy); C: *V. riparia* (Portalbera, Italy); D: *V. xkoberi* (Montù Beccaria, Italy). – Photographs by C. Ballerini.

according to their terminology) hybrids that originated in natural habitats of E North America (states of New York and Tennessee, respectively, see Hedrick 1908), then discovered and transferred into cultivation during the first half of the 19th century (to serve also as a basis for the selection of the other cultivars). However, artificial crossing between *V. labrusca* and *V. riparia* is likely to have occurred in European nurseries, as stated by Viala & Ravaz (1892), who excluded a direct employment of American “hybrides sauvages” in France, being of little viticultural interest.

In 1917, the American botanist Merritt Lyndon Fernald (1873–1950) described *Vitis novae-angliae* from New England (Fernald 1917). Although featuring characters intermediate between *V. labrusca* and *V. riparia*, Fernald did not accept his taxon as a hybrid, since, according to his own observations, the two species did not occur together, at least in some parts of the study area. More recently, Moore (1991), who examined Fernald’s specimens and typified *V. novae-angliae*, regarded it as a hybrid, as previously did Munson and Bailey, who studied the New England populations mentioned by Fernald (see Fernald 1917).

Our specimens are clearly intermediate between *Vitis labrusca* and *V. riparia* (Table 1) and correspond in every feature to the type specimens of *V. novae-angliae*, to its protologue (Fernald 1917), and to the description provided by Moore (1991). Moreover, their morphological traits (along with their ecology, see the next paragraph) coincide with those reported for the *labrusca-riparia*

black-berried cultivars, especially ‘Clinton’, by the major ampelographic sources, such as Millardet (1877c, 1880, 1885), Munson (1909) and Galet (1988). Therefore, we can safely confirm the hybrid origin of our plants and regard them as nothospecies, adopting Fernald’s binomial combination transferred to the hybrid category by Moore (1991), according to Art. 50 and Art. H.10 Note 1 of the ICN (McNeill & al. 2012).

At a first analysis, *Vitis novae-angliae* looks very similar to the parental species and another related hybrid, *V. xkoberi* (= *V. berlandieri* Planch. × *V. riparia*), from which it can be distinguished mainly on the basis of disposition of tendrils (Fig. 4), indumentum of vegetative parts (Fig. 2), leaf blade colour (Fig. 1) and consistency,

size of seeds (Fig. 3) and berries, adherence of exocarp to mesocarp (Fig. 4) and flavour of ripe berries (Table 1). Further confusion, however, may occur with hybrids of *V. aestivalis* Michx., such as those belonging to the group of cultivars named ‘Seibel’, especially *V. aestivalis* var. *lincecumii* (Buckley) Munson × *V. rupestris* Scheele × *V. vinifera*. This direct-producer hybrid was employed in various parts of Europe (including Italy); currently it is known as spontaneous in Spain (Laguna 2004) and a specimen recently collected in N Italy [Monticelli Pavese (Pavia), Umellina, lato N della strada, 47°05'10.2"N, 09°30'48.9"E (WGS84), 48 m, ciglio e scarpata stradale con *Elytrigia repens* e *Rubus* sect. *Corylifolii*, 3 Jun 2014, N. Ardenghi, P. Cauzzi & S. Bodino s.n. (MSNM)], at first identified as *V. xnovae-angliae*, is most likely to be referred to this taxon. It can be distinguished for its 3-lobed leaf blades with lyre-shaped basal sinus (acquired from *V. vinifera*), reniform to roundish in shape (as in *V. rupestris*), with abaxial leaf surface slightly glaucous, paler than the adaxial, and vegetative parts covered exclusively by reddish floccose pubescence [traits inherited from *V. aestivalis* var. *lincecumii*; according to Moore (1991) and Art. 60.1 of the ICN (McNeill & al. 2012), the correct spelling of the varietal epithet is “*lincecumii*” and not “*linsecomii*”, the latter being a typographical error].

Ecology

Similar to the parental species (see Ardenghi & al. 2014), *Vitis xnovae-angliae* is a calcifuge and heliophilous

taxon, usually occurring on moist, deep and highly fertile soils. Although superficial and well-drained soils are commonly regarded by viticulturists to promote the establishment of phylloxera on the root systems of cultivars of *V. x novae-angliae* (whose susceptibility derives from *V. labrusca*, see next paragraph), the individuals recorded from shallow anthropogenic substrates (e.g. railway ballasts) did not seem to be affected by the insect.

In its native range, *Vitis x novae-angliae* occurs in alluvial thickets, along ponds, streams, roads and fences (Moore 1991). Similarly, most of the Italian populations were discovered in woodland and shrub communities with *Robinia pseudoacacia* L., and ruderal and semi-ruderal habitats within or surrounding human settlements, often colonized by biennial and perennial vegetation of the phytosociological class *Artemisietea vulgaris* Lohmeyer, Preising & Tüxen ex Von Rochow 1951. Like other *V. riparia* hybrids (e.g. *V. x koberi* and *V. x instabilis* Ardenghi & al.), a preference for the linear transportation structures (especially railways) was noticed (Fig. 5). The largest population (located in Moriano, Bereguardo, Italy) has been recorded from an alluvial mesic woodland dominated by *R. pseudoacacia* (degrading stage of the *Populetalia albae* Braun-Blanquet ex Tchou 1948 forests), growing on a gravelly-sandy siliceous fluvial terrace. *V. x novae-angliae* is indicated for similar habitats also in France (Tison & de Foucault 2014).

Distribution

According to Moore (1991), the native range of *Vitis x novae-angliae* comprises the states of New England (NE United States), where it was described by Fernald (1917). However, its occurrence in further sites where the ranges of *V. labrusca* and *V. riparia* overlap is possible, as



Fig. 4. *Vitis x novae-angliae* additional morphological traits – A: continuous tendrils; B: stem and exfoliating bark; C: infructescence and pedicels with characteristic residuals of red mesocarp after detachment of berries; D: berry with mucilaginous mesocarp clearly separating from exocarp. – A, C, D: Albuzzano, Italy; B: Bereguardo (Moriano), Italy. – Photographs by N. M. G. Ardenghi.

suggested by the discovery, in the states of New York and Tennessee, of the spontaneous hybrids from which the cultivars ‘Clinton’ and ‘Taylor’ were obtained (Hedrick 1908).

Outside the United States, the plant is currently known from Spain (Laguna 2005), France (Tison & de Foucault 2014), and Italy (this paper); especially in the latter two countries, many of its cultivars were grown until the middle 20th century (see “History and pathways of introduction”). The distribution in Spain and France is not well defined and needs further investigation; particularly, Tison & de Foucault (2014) did not treat *Vitis labrusca* and its hybrids separately, but grouped them under the name “*V. labrusca* s.l.” (among them, hybrids



Fig. 5. *Vitis xnovae-angliae* naturalized population in Albuzzano, Italy, covering railway ballast. – Photograph by N. M. G. Ardenghi.

with *V. aestivalis* and with both *V. aestivalis* and *V. riparia* were also mentioned, whose occurrence in the wild is quite doubtful, due to their difficult reproduction from cuttings and their susceptibility to phylloxera and downy mildew, deficiencies which soon caused their rejection from French viticulture, see Galet 1988). In Italy, *V. xnovae-angliae* is currently known from the N part of the Po Plain from Lombardia to Veneto, which corresponds, along with the NE part of Emilia-Romagna, to the traditional and most important cultivation area of ‘Clinton’ in the country (Rossi 1920; Istituto centrale di statistica del Regno d’Italia 1937; Istituto centrale di statistica & Ministero dell’agricoltura e delle foreste 1973, 1974). The presence of *V. xnovae-angliae* is expected in further European countries (e.g. Austria, Hungary, Romania, Switzerland, former Yugoslavia), where the cultivation of *labrusca-riparia* hybrids is reported (Galet 1988; Ufficio federale dell’agricoltura UFAG 2014+).

Invasion status

The river Ticinum floodplain in Moriano (Beregardo) hosts the largest population of *Vitis xnovae-angliae* recorded in Italy. The plant, growing in a *Robinia pseudoacacia* woodland (*Chelidonio-Robinetalia* Jurko ex Hadač & Sofron 1980), occupies an area of 175 m², with a 50 % cover on both the shrub and tree layers, reaching the canopy at 7 m from the ground. The plant has been present in this site at least since August 2011, when one of the present authors (Ardenghi) first detected the population, but misidentified it as *V. labrusca*. The size of the stand and the high number and the diameter of the stems (Fig. 4), however, suggest that its introduction probably occurred earlier. Similarly, the presence of *V. xnovae-angliae* in Treviglio dates back at least to September 2010, when it was unintentionally pictured in a panoramic view for the web mapping service “Google Street View”.

It is likely that the Moriano population originated from discarded pruned stems (*Vitis xnovae-angliae* eas-

ily propagates from cuttings) or seeds disseminated by birds (whose feeding activities on ‘Clinton’ were already noticed by Hedrick 1908); the latter mode of dispersal is highly probable also for the other populations, especially those recorded from the railway areas, where vegetative parts are unlikely to be brought by trains or farmers. Although the seed germination capability of *V. xnovae-angliae* and related taxa is still under study by the authors, evidence of this feature is available in ampelographic literature (e.g. cultivars ‘Viola’ and ‘Noah’ are commonly reported to be seedlings of ‘Clinton’ and ‘Taylor’, respectively; see Munson 1885 and Galet 1988). Additionally, fruit production seems common in this taxon and it has been recorded from five of the known Italian populations (Albuzzano, Milano, Moriano, Santo Stefano Ticino, Treviglio).

On the basis of these observations, we consider *Vitis xnovae-angliae* naturalized in Italy, according to the definitions provided by Celesti-Grappo & al. (2009); the same invasion status has been adopted in France (Tison & de Foucault 2014).

History and pathways of introduction

The first (Euro-)American grapes to be imported in Europe were probably hybrids between *Vitis labrusca* and *V. vinifera* [*V. xalexanderi* Prince ex Jacques (pro sp.) = *V. xisabellae* Jacques (pro sp.) var. *alexanderi* (Jacques) Jacques, nom. illeg. = *V. xisabella* Otto & A. Dietr. (pro sp.) = *V. xprolifera* Raf. (pro sp.) = *V. xlabruscana* L. H. Bailey (pro sp.)], spontaneously arisen in the E United States between the late 17th and the early 18th century, and sold, under the well-known cultivar name ‘Isabella’ or ‘Isabelle’ [this name is sometimes applied to cultivars of *V. labrusca*; it seems that one of the often accepted synonyms of ‘Isabella’ is the Italian-named ‘Fragola’, which some authors, such as Hillier & Coombes (2002), incorrectly assign to *V. vinifera*], at least as early as 1830 in France (Mabberley 1999) also as an ornamental vine. As a consequence of their introduction, less than two decades later the first cases of powdery mildew [*Uncinula necator* (Schwein.) Burrill] were recorded in the United Kingdom (in 1845) and France (in 1847). Thanks to its resistance to the fungal disease, the cultivation of ‘Isabella’ increased and provided a fertile ground for the spread of new pests from North America: phylloxera [*Daktulosphaira vitifoliae* (Fitch 1855)], first recorded in France in 1863, and downy mildew [*Plasmopara viticola* (Berk. & M. A. Curtis) Berl. & De Toni], detected in 1878 (Galet 1988; Calò & al. 1996; Quéré 2012).

Since the beginning of the phylloxera crisis, two different strategies were elaborated in order to recover European viticulture: grafting of *Vitis vinifera* on phylloxera-resistant American rootstocks (see Ardenghi & al. 2014), and employment of “direct-producer hybrids”. The latter solution considered two separate categories of hybrids, suitable both for wine production and resistance to the

new pests: “Euro-American” hybrids, resulting from the crossing of *V. vinifera* with one or more American species, and “American-American” hybrids, which involved only American species. The majority of the early “American-American” hybrids saw *V. labrusca* as the primary source of resistance genes; among these, the most successful since the 1870’s were the binary crosses with *V. riparia*, mainly represented by the cultivars ‘Clinton’ and ‘Vialla’ (black-berried) and ‘Elvira’, ‘Noah’ and ‘Taylor’ (white-berried). For a brief period at the beginning of the phylloxera invasion, these cultivars were used also as rootstocks. However, the susceptibility of their roots to the insect, especially in superficial, dry, and nutrient-poor soils (character inherited from *V. labrusca*), and their sensitivity to limestone (derived from both parental species), limited their role almost to wine production, with the exception of ‘Vialla’ and ‘Clinton’: while the latter was sometimes deceptively sold as a *V. berlandieri* Planch. × *V. riparia* rootstock, five certified clones of the former are still cultivated in France as grafters (Galet 2000; FranceAgriMer 2014, 2015).

Wines obtained from the *labrusca-riparia* hybrids featured a prominent and typical “foxy” flavour (acquired from *Vitis labrusca*), always regarded with disgust by most of the oenologists, along with a low alcohol content, which prevented their conservation for more than five to six months. Nonetheless, these cultivars were progressively welcomed, both by professional viticulturists and subsistence farmers: hardiness, easy reproduction from cuttings, immunity to powdery and downy mildew, and high productivity allowed the wine production even in areas notoriously unsuitable for vineyards (especially those characterized by humid and cold climates, such as the French Atlantic départements, the Po Plain and the Prealps in Italy), and made this culture accessible at lower costs, by reducing the expenses for its management (Millardet 1885; Lampertico 1899, 1900a, b, 1904; Galet 1988). The combination of these elements led to a highly successful spread of the *labrusca-riparia* hybrids and their wines over the European countries, often earning a larger popularity than the “authentic” wine obtained from *V. vinifera*. Eventually, legislators tried to stop the phenomenon: in Italy, for example, the cultivation of every direct-producer hybrid has been banned since 1931 (Law 23 March 1931, no. 376), while in France a list of six “cépages prohibés” was drawn up in 1935, which included two *labrusca-riparia* cultivars, namely ‘Clinton’ and ‘Noah’ (Galet 1988). However, difficulties related to the application of the law and the outbreak of the Second World War increased the cultivation of the illegal direct-producers, which reached its peak in the early 1950s, especially in Italy and France, where they covered about 10 % (285 491 ha, mostly ‘Isabella’ and ‘Clinton’) and 4 % (62 478 ha) of the vine-cultivated surface, respectively (Istituto nazionale di economia agraria 1951; Galet 1988). In the subsequent decades, changes in viticulture and tastes for wine, along with further legislative tools,

caused a gradual decrease of the outlawed hybrids: during 1968–1970, in France they extended for 8585 ha, while in Italy plantations of ‘Clinton’ up to three years old covered only 464 ha (Istituto centrale di statistica & Ministero dell’agricoltura e delle foreste 1972; Galet 1988). Today, their occurrence in cultivation for wine production is mainly confined to few enthusiasts for non-commercial purposes, in compliance with Council Regulation (EC) No. 479/2008, which maintains a list of six “prohibited” direct producers (not classified as “wine grape varieties”) to be cultivated only for scientific purposes and domestic consumption: ‘Clinton’, ‘Isabella’, ‘Noah’, ‘Othello’ (the latter a hybrid between *V. labrusca*, *V. riparia* and *V. vinifera*), ‘Jacquez’ and ‘Herbemont’ (both *V. aestivalis* × *V. cinerea* (Engelm.) Millardet × *V. vinifera*).

Specimens examined

Geocoordinates are according to WGS84 or UTM ED50. ITALY: LOMBARDIA: Bereguardo (Pavia), c. 450 m SW da Cascina Orsine, 45.24725°N, 09.00742°E, 96 m, no exp., margine degradato di querceto, con *Quercus robur* e *Robinia pseudoacacia*, 6 Jul 2012, N. Ardenghi & S. Mossini s.n. (MSNM); Milano (Milano), ex-scalo ferroviario di Milano-Porta Romana, 45.44536°N, 09.20714°E, 112 m, no exp., binari di carico e scarico merci abbandonati, 15 May 2013, N. Ardenghi s.n. (MSNM); Milano (Milano), ferrovia presso il ponte su via Giovanni Pezzotti, 45.44378°N, 09.18433°E, 119 m, exp. N, massicciata ferroviaria, con *Ulmus pumila*, 15 May 2013, N. Ardenghi s.n. (MSNM); Milano (Milano), ferrovia tra i ponti su via Fedro e via Carlo Bazzi, 45.44417°N, 09.18636°E, 119 m, no exp., binari ferroviari, 15 May 2013, N. Ardenghi s.n. (MSNM); Milano (Milano), ferrovia tra la stazione FFSS di Milano-San Cristoforo e quella di Milano-Romolo, all’incirca all’altezza di via Pesto, 45.44806°N, 09.15278°E, 118 m, exp. N, massicciata, con *Robinia pseudoacacia*, 15 May 2013, N. Ardenghi s.n. (MSNM); Missaglia (Lecce), Maresso, loc. Brughiera, a N di via San Francesco, 45.692473°N, 09.370785°E, 271 m, E, margine boschivo, 23 Aug 2013, M. Villa s.n. (MSNM); Santo Stefano Ticino (Milano), stazione FFSS di Corbetta-Santo Stefano, binario 1, recinzione tra terreno incolto (cantiere edile in allestimento) e la massicciata ferroviaria, 45°28'53.2"N, 08°55'08.4"E, 144 m, no exp., recinzione, con *Rubus ulmifolius* e *Phytolacca americana*, 20 Sep 2013, N. Ardenghi s.n. (MSNM); ibid., recinzione di cantiere edile e incolto retrostante, recinzione, con *Artemisia verlotiorum*, *Phytolacca americana*, *Rubus ulmifolius*, si estende anche sulla massicciata, con *Robinia pseudoacacia* e *Parthenocissus quinquefolia*, 13 Sep 2014, N. Ardenghi (MSNM); Treviglio (Bergamo), dietro alla stazione FFSS Treviglio Ovest, incrocio tra via Murena e via Istria, 45°30'52.5"N, 09°35'27.4"E, 121 m, S, muretto e recinzione in cemento alla base della massicciata ferroviaria, 21 Sep 2013, N. Ardenghi s.n.

(MSNM, Herb. N. Ardenghi); *ibid.*, muretto e recinzione in cemento alla base della massicciata ferroviaria, con *Clematis vitalba* e *Hedera helix*, 13 Sep 2014, *N. Ardenghi s.n.* (MSNM, APP, FI); Cavaria con Premezzo (Varese), stazione FFSS di Cavaria-Oggiona-Jerago, binario 2, sopra il sottopasso di via Monte Grappa, 45°41'50.0"N, 08°48'11.6"E, 278 m, no exp., massicciata ferroviaria, con *Clematis vitalba*, *Phytolacca americana*, *Hedera helix*, 12 Oct 2013, *N. Ardenghi s.n.* (MSNM, Herb. N. Ardenghi); Castelleone (Cremona), Corte Madama, Cascina Guzzona, via Montecollero, rete di recinzione della cascina, 45°15'40.5"N, 09°47'45.4"E, 58 m, no exp., pianta culta (cultivar 'Clinton'): residuo di coltivazione sulla rete di recinzione della cascina, 27 Jul 2014, *P. Cauzzi s.n.* (MSNM); Albuzzano (Pavia), stazione FFSS, 32T 0520587.5002138, 72 m, S, massicciata ferroviaria, con *Humulus japonicus*, *Elytrigia repens*, *Fallopia convolvulus*, *Parthenocissus quinquefolia*, *Artemisia verlotiorum*, 29 Aug 2014, *N. Ardenghi s.n.* (MSNM, APP, FI); Bereguardo (Pavia), Moriano, a W dell'autostrada A7 Milano-Genova, 32T 0502739.5009493, 77 m, E, robinieto su terrazzo fluviale, vegetazione: *Robinia pseudoacacia*, *Rubus ulmifolius*, *Sambucus nigra*, *Chelidonium majus*, *Hedera helix*, *Phytolacca americana* (*Robinietaea*), suolo sabbioso-ghiaioso siliceo, 17 Oct 2014, *N. Ardenghi, P. Cauzzi & S. Pedrini s.n.* (MSNM, BR); Torre d'Isola (Pavia), Cascina Santa Sofia, lato NE dell'ex poligono militare, 45.19719°N, 09.08050°E, 63 m, no exp., arbusteto a *Rubus* sect. *Corylifolii*, *Corylus avellana* e *Crataegus monogyna*, la popolazione si estende nel prato arido adiacente, 9 May 2015, *N. Ardenghi s.n.* (MSNM); Garlasco (Pavia), via Circonvallazione alle Bozzole (SP206), lato S, davanti al "Bar Bordese", 45.21739°N, 08.93442°E, 98 m, no exp., incolto con *Artemisia verlotiorum*; margine boschivo, con *Robinia pseudoacacia*, *Ailanthus altissima* e *Sambucus nigra*, 17 May 2015, *N. Ardenghi s.n.* (MSNM). — VENETO: M.te Pastello, da Monte verso la cima, 600 m, 31 May 1985, *L. Zavarise s.n.* (VER sub *V. vinifera*); Pontecchio Polesine (Rovigo), sponda del Canal Bianco a monte di Pontecchio, 32T 0720.4989, c. 5 m, no exp., sponda, con *Cornus sanguinea* s.l. e *Rubus caesius*, May 2012, *R. R. Masin s.n.* (MSNM).

Acknowledgements

The authors are grateful to Milena Villa (Rovagnate, Italy) and Rizzieri Roberto Masin (Montegrotto Terme, Italy), for providing two gatherings of *Vitis xnovae-angliae*, and to Francesco Di Carlo and Roberta Salmaso (VER), for locating a valuable exsiccatum; Antonio Dal Lago (MNAV) and Rossella Marcucci (PAD) are acknowledged for kindly checking their collections. We express our gratitude also to Rocco Giorgio Guerini and Paolo Morandi (Azienda Agricola Guzzona, Castelleone, Italy), who allowed the authors to collect and taste their 'Clinton' grape, Giulia Ardenghi (Stradella, Italy), for

the digital image preparation, Michele Zilioli (Laboratorio di Entomologia/Microscopia Elettronica, Museo di Storia Naturale di Milano), for acquiring the images on the scanning electron microscope, Claudio Ballerini (Trivolzio, Italy), for taking the pictures of the seeds, and to Giuseppe De Paolis (Biblioteca della Scienza e della Tecnica, University of Pavia), for his patience in locating many bibliographical sources. Finally, the authors are deeply thankful to Emilio Laguna (Servicio de Vida Silvestre, Valencia) and Filip Verloove (Botanic Garden of Meise, Meise) for their valuable and constructive comments during the review process of this paper.

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Appendix

Populations sampled for the infructescence and seed measurements reported in Table 1. Geocoordinates are according to WGS84 or UTM ED50.

Vitis xnovae-angliae

ITALY: LOMBARDIA: Castelleone (Cremona), Corte Madama, Cascina Guzzona, via Montecollero, rete di recinzione della cascina, 45°15'40.5"N, 09°47'45.4"E, 58 m, no exp., pianta culta (cultivar 'Clinton'); residuo di coltivazione sulla rete di recinzione della cascina, 27 Jul 2014, P. Cauzzi s.n. (MSNM); Albuzzano (Pavia), stazione FFSS, 32T 0520587.5002138, 72 m, S, mas-

sicciata ferroviaria, con *Humulus japonicus*, *Elytrigia repens*, *Fallopia convolvulus*, *Parthenocissus quinquefolia*, *Artemisia verlotiorum*, 29 Aug 2014, *N. Ardenghi s.n.* (APP, FI, MSNM); Treviglio (Bergamo), dietro alla stazione FFSS Treviglio Ovest, incrocio tra via Murena e via Istria, 45°30'52.5"N, 09°35'27.4"E, 121 m, S, muretto e recinzione in cemento alla base della massicciata ferroviaria, con *Clematis vitalba* e *Hedera helix*, 13 Sep 2014, *N. Ardenghi s.n.* (APP, FI, MSNM).

Vitis labrusca

ITALY: LOMBARDIA: Pavia (Pavia), via Trieste, 32T 0511781.5004296, 78 m, no exp., vecchia siepe di *Ligustrum sinense*, con *Sambucus ebulus*, *Hedera helix*, *Ailanthus altissima*, *Laurus nobilis*, 29 Aug 2014, *N. Ardenghi s.n.* (MSNM).

Vitis riparia

ITALY: LOMBARDIA: Montù Beccaria (Pavia), tra la SP43 e la strada per Molino Quaroni, 32T 0523833.4987071, 122 m, no exp., incolto, con *Elytrigia repens*, 5 Aug 2014, *N. Ardenghi s.n.* (MSNM); Portalbera (Pavia), Campo Fortuna, lato N della SP67, 32T 0524441.4994353, 59 m, no exp., robinieto, 6 Aug 2014, *N. Ardenghi s.n.* (MSNM); San Damiano al Colle (Pavia), sponda sinistra del Torrente Bardonezza, a S dell'incrocio tra la SP189 e strada del Merlino, 32T 0529232.4988393, 96 m, no

exp., margine di boscaglia ripariale, con *Robinia pseudoacacia*, *Rubus caesius*, *Sicyos angulatus*, *Convolvulus sepium*, *Urtica dioica*, *Equisetum telmateia*, *Galium aparine*, 9 Aug 2014, *N. Ardenghi s.n.* (MSNM).

Vitis ×koberi

ITALY: LOMBARDIA: Bosnasco (Pavia), sponda sinistra del Torrente Bardonezza, all'altezza di Balanzine, 32T 0529947.4989362, 86 m, no exp., boscaglia ripariale, con *Robinia pseudoacacia*, *Alnus glutinosa*, *Rubus* sect. *Corylifolii*, *Salix alba*, *Juglans regia*, *Populus ×canadensis*, *Sicyos angulatus*, *Amorpha fruticosa*, 9 Aug 2014, *N. Ardenghi s.n.* (MSNM); Arena Po (Pavia), SP144, lato W della stazione FFSS, 32T 0528294.4992154, 67 m, N, massicciata ferroviaria, con *Robinia pseudoacacia*, *Anisantha sterilis*, *Galium aparine*, *Rubus* sect. *Corylifolii*, *Prunus persica*, 10 Aug 2014, *N. Ardenghi s.n.* (MSNM); Stradella (Pavia), Badia, cavalcavia di via Valle Badia, lato S, 32T 0522620.4991858, 72 m, S, fossato alla base della scarpata stradale, boscaglia mesoigrofila con *Robinia pseudoacacia* e *Salix alba*, 20 Aug 2014, *N. Ardenghi s.n.* (MSNM); Montù Beccaria (Pavia), strada per Molino Quaroni, vigneto abbandonato, 32T 0523874.4988123, 105 m, no exp., pianta culta: vigneto abbandonato, ricacci di portainnesti completamente ricoprenti i filari, 26 Aug 2014, *N. Ardenghi s.n.* (MSNM).