

Is there a future for wild grapevine (*Vitis vinifera* subsp. *silvestris*) in the Rhine Valley?

CLAIRE ARNOLD^{1,*}, ANNIK SCHNITZLER², ANNE DOUARD³,
RICHARD PETER³ and FRANÇOIS GILLET⁴

¹National Centre of Competence in Research Plant Survival, University of Neuchâtel, Rue Emile Argand 11, CH-2007 Neuchâtel, Switzerland; ²Laboratoire Biodiversité et Fonctionnement des écosystèmes (LBFE), University of Metz, F-57070 Metz, France; ³Conservatoire des Sites Alsaciens, 1, rue des Ecoles, F-67850 Offendorf, France; ⁴Laboratoire d'écologie végétale, University of Neuchâtel, Rue Emile Argand 11, CH-2007 Neuchâtel, Switzerland; *Author for correspondence (e-mail: claire.arnold@unine.ch; fax: +41-32-718-25-01)

Received 3 July 2003; accepted in revised form 19 January 2004

Key words: Alsace, Endangered species, Floodplain forest, Reintroduction, Restoration, Rhine, Vine, *Vitis vinifera* subsp. *silvestris*, Wild grapevine

Abstract. The wild grapevine, *Vitis vinifera* L. subsp. *silvestris* (Gmelin) Hegi, is considered to be an endangered taxon in Europe, mainly as a consequence of the introduction of pathogens from North America and of the destruction of its habitat. In the Rhine Valley, nearly all populations disappeared due to river management, the intensification of forestry, and the introduction of phylloxera. After a growing awareness of the need to preserve endangered forest ecosystems, attempts to reintroduce wild grapevine in the Rhine Valley were performed, particularly in the French nature reserves Erstein and Offendorf since 1992. However, regular surveys of the plants indicate the rapid decline of the populations. In 2002, we proposed to summarise the knowledge accumulated after 10 years of experiments. Results indicate that from the initial 91 individuals planted in 1992, only 14 survived in 2002 (2 in Erstein, 12 in Offendorf). The failure of the experiment may be explained by several factors: unsuitable sites (too shady, absence of support for the young plants), absence of monitoring, vandalism or predation. According to these results and recent knowledge of the ecology of the plant and of vines in general, new transplantation experiments are proposed in which the plants will be monitored during their establishment in the forests. The success of this second transplant (50 plants per reserve) will be enhanced by restoration projects of the Rhine River dynamics, with partial re-flooding. Floods should help to avoid, or at least to reduce, pest and disease expansion on future adult plants.

Introduction

The genus *Vitis* (88 species) is widespread in the temperate regions of North America and Eurasia (Gallet 1988; Scossiroli 1988; Fengquin et al. 1990). While many species of *Vitis*, and other genera of Vitaceae survived the glacial periods in the eastern part of North America and the temperate regions of China, there remains only one genus of Vitaceae in Europe, the wild grapevine (*Vitis vinifera* L. subsp. *silvestris* (Gmelin, Hegi) (Rivera and Walker 1989). Its current distribution ranges from the south Atlantic coast of Europe to the western Himalaya, between the 43rd and 49th northern parallels, from sea level up to an altitude of 1000 m.

Vitis vinifera subsp. *silvestris* is closely related to the cultivated grapevine (*Vitis vinifera* subsp. *sativa*), first domesticated 10,000 years BP around the Caspian Sea

(Mc Govern 1999). The wild subspecies is gyno-dioecious but the cultivated varieties are hermaphrodites. Both are pollinated by insects and dispersed by birds.

The wild grapevine is a deciduous woody tendril vine. In Europe, it colonises a broad range of habitats and soils. However, nowadays wild grapevines are mainly found in periodically or permanently flooded areas (Arnold 2002). Wild grapevines achieve remarkable developments and constitute blankets on the edges of moist and fertile floodplain forests, contributing to the unique environment of these northern temperate, species-rich ecosystems (Carbiener 1970; Robertson et al. 1978; Schnitzler 1995, 1996).

The distribution of the wild grapevine has dramatically been reduced over the last 150 years, with the spread of pathogens from North America (phylloxera, oidium, mildew). Most of them died, except in floodplain forests as the root–host homoptera phylloxera was sensitive to flooding (Ocete and Lara 1994). Massive death also occurred in vineyards. In France, most vineyards were destroyed and replanted afterwards using American rootstock. Phylloxera did not disappear and continued to infect populations of wild grapevines surviving in the floodplain forests in zones where the water table sank. Intensive river management, starting in the middle of the 19th century, enhanced this process.

Two other human impacts also contributed to the destruction of populations of wild *Vitis*. Shortly after river management, most of the floodplain forests were fragmented and replaced by arable crops or meadows. In remnant forests, the intensification of forest management led to the removal of the vines, considered detrimental to tree growth.

Fragmentation of wild grapevine habitats had an enormous impact on gene exchanges between populations, leading to a bottleneck, especially in gyno-dioecious plants. This also reduced the adaptability of the plant to habitat changes. The wild grapevine may however respond by a high vegetative dynamics as observed in the small remnant populations found along the Seine River upstream near Paris, along the Danube river after Vienna or in the Danube Delta (Parisot 1999; personal observations from Arnold and Schnitzler).

The plant is more sensitive to human impacts than the two other woody climbers (*Hedera helix* L. and *Clematis vitalba* L.) that coexist in the canopies of floodplain forests. These two vines, together with *Humulus lupulus* L., the American Vitaceae species (*Parthenocissus quinquefolia* (L.) Planch., *P. inserta* (A. Kern.) Fritsch., *Vitis x riparia* Michx.) or cultivars which have escaped from adjacent vineyards, are now settled in the ecological niches previously occupied by the European wild grapevine. It seems that the cultivars are usually spread by water.

Recent studies of the remaining sites in Europe indicate that the species is close to extinction (Arnold et al. 1998). In the 1980s this plant was added to the IUCN List of endangered European species. Since 1995, this species has been strictly protected in France. In this country, a research programme of inventory carried out by the INRA of Montpellier have already shown that France has 135 sites including a probable total of 300 individuals (Lacombe et al. 2002). Identifications were based on morphology but will be confirmed by molecular analysis in the following year. A similar research is carried out in Spain.

The Rhine floodplain has been greatly damaged by human management in its upper part, between Kembs (France) and Karlsruhe (Germany). Between 1817 and 1977, 80% of initial flooding areas were lost. Forests of high nature conservation value represent a very small proportion of the initial areas. Most of them suffer from the elimination of floods (Gallusser and Schenken 1992).

The decline of the wild grapevine in the upper Rhine Valley was already carefully described by French and German botanists from the middle of the 19th century. Observations have continued till now, contributing to a unique collection of data for Europe. Schultz (1846), Griesselich (1847) and Bronner (1857) detailed the outstanding abundance and beauty of thousands of wild grapevines in floodplain forests. In 1890, the number decreased to 200 individuals in Rheinland-Pfalz (Germany) and Alsace (France). The number then decreased to 77 in both regions (Issler 1938). In the following decades, plants were found only as scattered individuals in some islands or forest edges of tributaries, in Germany, France and Switzerland (Kirchheimer 1946; Schumann 1968, 1977). Today, there are about twenty individuals scattered in both Germany and Alsace (respectively the Ketsch island, Otterstadt forest in the Rheinland-Pfalz region, Eisbruch forest close to Römerberg, the Fronholz forest near Sainte-Croix en Plaine in the Alsace region).

The growing trend for restoring the potential of the larger river systems in Europe (Buijse et al. 2002) and for preserving endangered forest ecosystems has led many countries to propose coherent ecological networks of semi-natural habitats. Along the Rhine, Swiss, German and French authorities face the challenge to make way for a safer but more natural river system. Some riverine ecosystems are now protected in both Germany and France. In Alsace, there are eight nature reserves along the left side of the Rhine, facing seven protected areas on the right side of the river, in Germany. A programme of partial restoration of the hydrological functioning in the upper Rhine is scheduled for the years to come, through restoration of lateral arms and a moderate increase in water levels and water amplitudes (LIFE European Programme 2002–2005). Another programme (French–German convention of 1982) proposes to partially flood French–German border forests.

Restoration projects encourage protection of the natural richness of riverine communities. To this end, attempts of reintroductions of wild grapevines were made in the Rhine floodplain or adjacent tributaries, from plants originating from the last wild populations in the valley. In Alsace, a total of 349 wild grapevines individuals, originating from the last sites in the Rhine Valley, have been transplanted during the last decades into many forest areas of the valley. Most of the reintroduced populations declined rapidly in natural conditions (Fullenwarth 1997; oral communication of foresters). Several plants kept *ex situ* in botanical gardens and research stations are growing vigorously. This suggests that the sub-species is still dynamic and that the failure of the reintroduction campaigns is mostly due to a lack of knowledge about its ecology as well as about the ecology of woody vines in Europe (Arnold et al. 2002).

Since 1992 several ecological studies have been performed on these specific themes (Coudurier 1992; Ocete 1994; Schnitzler 1995; Arnold 2002).

The present study rests on a 10-year experiment (1992–2002) on transplantation of the wild grapevine in two natural forest reserves in Alsace. The outcome of this

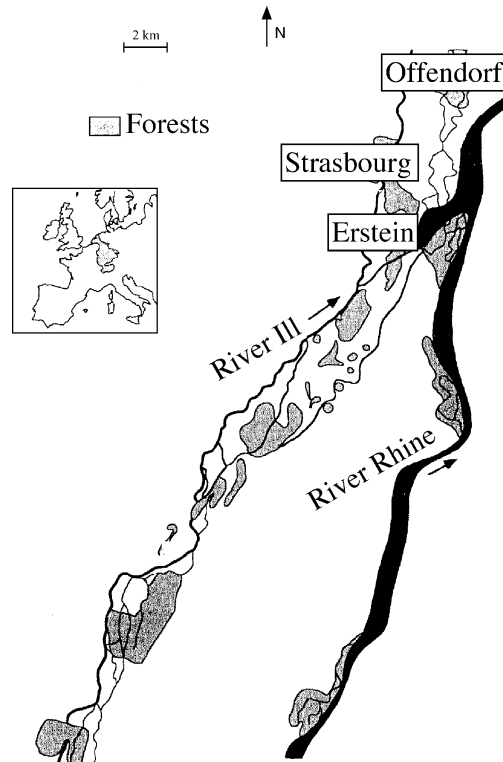


Figure 1. Map of the two studied areas along the Rhine River in France. Both nature reserves are located close to Strasbourg.

experiment, as well as knowledge about the ecology of vines in present day floodplain forests, will lead to a list of recommendations and technical guidelines to continue this first initiative. The aim of future reintroductions should be to initiate long term viable populations along the Rhine Valley and eventually to create connections between the existing natural populations.

Materials and methods

Experimental sites

The studied areas are located on the French border of the upper Rhine, in north-eastern France ($48^{\circ}05'–48^{\circ}35' N$; $7^{\circ}30'–7^{\circ}46' E$) (Figure 1). Elevation is about 140–150 m. The climate is continental with an oceanic influence, the mean annual temperature is $10^{\circ}C$ and the annual rainfall ranges from 500 to 600 mm. The Rhine deposits are calcareous, silty or silty-clayey at the surface and coarser in the deeper layers. Before management, flooding occurred between May and July, as a consequence of snowmelt in the Swiss Alps.

Riparian woodlands belong to the alliance *Alno-Ulmion* Br. Bl and Tx. 1943. Two main associations integrate the wild grapevine: softwood (*Salici albae-Populetum nigrae*) and hardwood forests (*Quercu-Ulmetum minoris*). These two associations are now scattered in Alsace and in some islands in Germany. In Alsace, the most beautiful forests can be found in the Selz, the Rhinau, the Erstein, the Strasbourg and the Offendorf natural forest reserves, although floods have been either eliminated for decades (Erstein, Offendorf) or strongly reduced in duration and intensity (Rhinau, Strasbourg).

The wild grapevine was transplanted into three of these nature reserves (Strasbourg, Erstein and Offendorf). The present paper will only consider two of them, managed by the Conservatoire des Sites Alsaciens (Erstein and Offendorf). In these two reserves, forests are left to develop freely, except for some minor management: cutting of old poplar plantations for regeneration of more natural ecosystems, hunting of wild boar populations, protection of rare, endangered species. The Erstein natural reserve, created in 1989, covers 180 ha. The Offendorf natural reserve, created in 1989, covers 60 ha. Both forest nature reserves have suffered from the elimination of floods for decades (1967 for Erstein and 1977 for Offendorf), resulting in a decrease in productivity and deep changes in species composition and forest architecture (Trémolières et al. 1998).

Experimental design

The total number of transplanted individuals was 91 (50 in Erstein and 41 in Offendorf). Plantations occurred at two different periods: in December 1992 and April 1993. The 18 vines transplanted in December 1992 were vegetative parts propagated from 20-year-old wild grapevines. They originated from German Rhine sites, and were cultivated in pots for 2 years at the La Bussière botanical garden in Strasbourg. Their height ranged from 115 to 260 cm. The sex ratio was four females to five males.

In April 1993, a second plantation of 73 vines (34 in Offendorf; 39 in Erstein) was carried out. The plants originated from vegetative parts of wild grapevines from Sainte Croix en Plaine and from Switzerland. These fragments were cultivated in soil for one year in the botanical garden of the Institut National de Recherches Agronomiques (INRA), of Colmar, until they reached heights of 45–100 cm. The sex ratio was one female to two males.

Small patches of mixed male and female individuals were randomly planted in various ecological situations of texture, moisture, canopy openness and plant community (hardwoods; softwoods; poplar plantations; edges of forest/meadow and forest (pathways or stream banks, open or closed canopy, beside different type of supports)). Plants were surrounded by a small wire fence and then left to develop freely without any human intervention.

The transplantation sites were surveyed in June and September 1993, September 1994, September 1996 and May 1997. A total of 15 vines had disappeared within a few months (David 1993). From September 1994 to May 1997, the population

decreased to 32 individuals (20 in Offendorf and 12 in Erstein) (David and Klein 1994; Fullenwarth 1997). In July 2002, the 32 vines alive in 1997 were actively searched.

Data collection

Data collected in 2002 followed the protocol from Fullenwarth (1997) as closely as possible.

Each vine was mapped, carefully inspected and measured. The presence of pathogens and evidence of herbivory or grass competition were noted. Light regime was deduced from canopy openness (CO): 1 for values inferior to 5%, 2 for values ranging from 5–20%, 3 for values superior to 20% (values deduced from hemispherical photographs taken in 1997; irradiance values are correlated to canopy openness). We distinguished three types of vegetation supports: 1 for one large and high trunk, 2 for few small-sized structured trees, 3 for an 'optimal vegetation structure' with a gradient of diameters and heights of the bushes and trees. The water content of the topsoil layer (moisture) was monitored in 1996 by a combination of three data: groundwater depth, texture, and plant indicators. Indices ranged from 1 (dry) to 5 (high moisture level). Due to the stability of the floodplain environment, we did not reanalyse it in 2002.

Statistical analysis

In order to explain the different patterns of vine development during the re-introduction experiment, a tree-based discriminant analysis was carried out on 30 vines using seven predictor variables: three semi-quantitative variables (moisture, light, vegetation support), three binary variables (pathogens, predation, competition) and one quantitative continuous variable (height in 1993). The different patterns of vine development formed the categorical response variable (four groups containing between 4 and 14 individuals), used to construct a classification tree.

Tree-based modelling is a supervised method for classification viewed as statistical decision theory (Breiman et al. 1984). A tree is produced by binary recursive partitioning of the response against the predictor variables using a divisive algorithm. Binary tree structured classifiers are constructed by repeated splits of subsets (nodes) of the measurement space into two descendant subsets (binary splits), starting with the entire measurement space itself. Each terminal subset is assigned a class label and the resulting partition of measurement space corresponds to the classifier. If the endpoint is a categorical response the model is called Classification Tree (CT), whereas endpoint is a continuous response it is called Regression Tree (RT). Compared to classical Factorial Discriminant Analysis, CT is recognised as a powerful and robust method to build empirical predictive models, if the response is a multi-level categorical variable and the predictors are both quantitative and qualitative (Breiman et al. 1984).

All calculations were done with R 1.8.1 software (The R Foundation for Statistical Computing, <http://www.r-project.org>) using the 'rpart' library.

Results

Rates of mortality

The great majority of *Vitis* transplanted in 1992/1993 failed to establish, similar to other experiments carried out in the Rhine Valley. Only 14 individuals (12 in Offendorf, see Figure 2; 2 in Erstein) remained in 2002. The rate of mortality in 10 years is higher in Erstein (96%) than in Offendorf (71%). The sex ratio of surviving vines is 9 males for 5 females, that is an average mortality of 83% for each sex.

Pattern of vine development

Development patterns of transplanted vines were varied (Table 1). Groups a, b, c, d, e concern vines that were still alive in 2002; groups f, g and h vines that died after 1996.

The five vines of group 'a' present a regular growth from 1993 to 2002. Heights range from 250 to 550 cm. There is only one plant in groups 'b' and 'c'. The individual number 18 (Offendorf) (group 'b') is characterised by a very slow growth, from 45 to 100 cm because of lack of suitable vegetation support. Individual number 29 (Erstein) (group 'c') began to grow, then sharply decreased from 201 to 25 cm, because of both grazing (the wire fencing had fallen down) and lack of small-sized support. The vine crept on the ground and reached 100 cm in length. Group 'd' (5 vines) and 'e' (2 vines) had grown vigorously during 1–3 years followed by a marked decrease. Group 'f' is a particular case of a vine that grew to be very tall in 3 years (from 43 to 420 cm) but remained relatively thin, and disappeared. No reason was found for these declines, but an attack of pathogens is suspected.

Group 'g' concerns 13 vines. All increased more or less vigorously during one to three years but were found to be dead in 2002. Group 'h' concerns 4 vines that had presented a constant decline from the beginning before dying. All had suffered from low irradiance and inadequate vegetation support.

In the following statistical analysis, groups 'b' and 'c' and 'f' were ignored and group 'e' was included into group 'd'.

Statistical analysis

A full model, fitting all data, was obtained by setting up the minimum node size to 1 (the minimum number of observations that must exist in a node in order for a split to be attempted) and the threshold complexity parameter to 0 (no prepruning). The

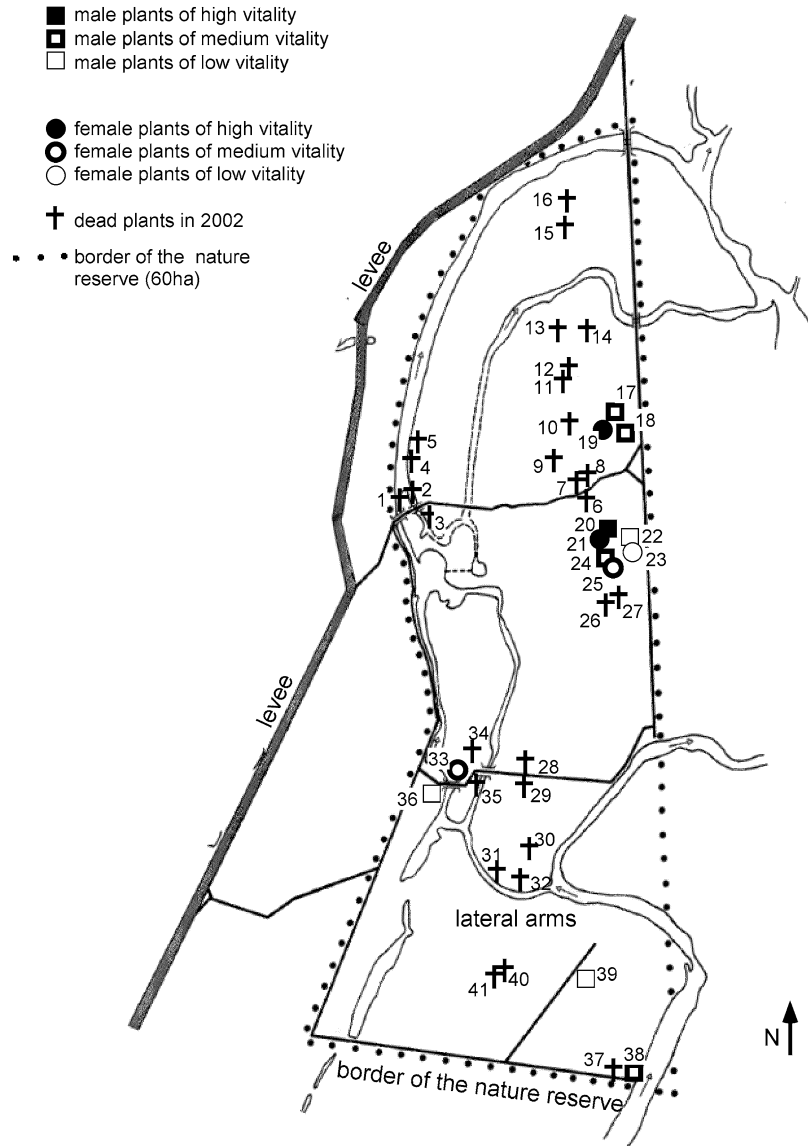


Figure 2. Evolution of the distribution of introduced wild grapevine in the Nature Reserve of Offendorf since 1992.

full classification tree contained 10 splits and all groups were classified (Figure 3). The relative error was 0, indicating that no misclassification appeared in the terminal nodes. But the relative cross-validation error, calculated after 100 cross validations, was 100%, indicating overfitting in the model.

Table 1. Development pattern and environmental descriptors used on the 32 surviving wild grapevines transplanted in 1992–1993. Sex and plant communities are nominative variables. Moisture is a semi-quantitative variable (1–5). CO (Canopy openness) and Support are semi-quantitative variables (1–3). Heights are quantitative variables given in centimetres. Pathogens, predation and competition are binary variables.

Growth pattern	Forest	Sample nbr.	Sex	Plant community	Moisture	CO	Support	Height			Pathogens			Predation			Competition						
								1993			1996			2002				1996			2002		
								1993	1994	1996	1996	2002	2002	1996	2002	1996		2002	1996	2002	1996	2002	
Regular growth 1993–2002 (group a)	Offendorf	20	Male	Forest/meadow	1	3	3	45	113	270	550	0	0	0	0	0	0						
	Offendorf	21	Female	Forest/meadow	1	3	3	45	113	270	550	0	0	0	0	0	0						
	Offendorf	19	Female	Forest/meadow	1	3	3	63	100	261	400	1	0	1	0	0	0						
	Offendorf	24	Male	Forest/meadow	2	3	3	42	108	224	250	1	0	0	0	1	0						
	Offendorf	25	Female	Forest/meadow	2	3	3	42	108	224	250	0	0	0	0	1	0						
Temporal stagnation (group b)	Offendorf	18	Male	Forest/meadow	3	2	1	42	55	55	100	0	1	0	0	0	1						
Growth, decrease, growth (group c)	Erstein	29	Male	Forest/stream	3	2	1	187	201	25	100	0	0	1	0	0	0						
Growth till 1996, decline (group d)	Offendorf	33	Female	Forest/stream	4	2	1	66	112	191	180	1	0	0	0	0	1						
	Offendorf	17	Male	Pathway	1	2	3	40	120	156	100	0	0	0	1	0	0						
	Offendorf	22	Male	Forest/meadow	1	3	3	33	136	263	100	0	0	0	1	0	1						
	Offendorf	23	Female	Forest/meadow	1	3	2	85	150	200	50	1	0	1	0	0	1						
	Offendorf	36	Male	Poplar plantation	3	3	2	77	177	400	50	1	0	0	1	0	1						
Growth till 1994, decline (group e)	Offendorf	38	Male	Forest gap	1	3	1	115	205	200	150	1	0	0	1	0	1						
	Erstein	28	Male	Forest/stream	2	2	2	182	250	190	50	0	0	0	1	0	1						
Growth till 1994, death (group f)	Offendorf	37	Male	Pathway	4	2	2	43	150	420	0	1	–	0	–	0	–						

Table 1. Continued.

Growth pattern	Forest	Sample nbr.	Sex	Plant community	Moisture	CO	Support	Height						Pathogens			Predation			Competition		
								1993		1994		1996		2002		1996	2002	1996	2002		1996	2002
Growth till 1996, death (group g)	Erstein	46	Male	Forest	4	1	1	166	174	155	0	0	0	0	0	0	0	0	0	0		
	Offendorf	15	Female	Pathway	2	1	1	125	225	150	0	1	-	0	0	-	0	-	0	-		
	Offendorf	32	Male	Forest	1	1	1	130	180	148	0	0	-	1	0	-	0	-	0	-		
	Offendorf	39	Male	Pathway	4	3	1	59	110	100	0	0	-	0	0	-	0	-	1	-		
	Erstein	14	Male	Pathway	3	2	2	59	117	63	0	0	-	0	0	-	0	-	1	-		
	Erstein	17	Male	Pathway	3	1	1	100	191	50	0	0	-	1	0	-	0	-	0	-		
	Offendorf	9	Male	Pathway	4	2	1	53	78	34	0	0	-	0	0	-	0	-	1	-		
	Erstein	48	Male	Forest/stream	4	1	1	78	85	33	0	0	-	0	0	-	0	-	0	-		
	Erstein	24	Male	Forest/stream	2	2	2	40	77	30	0	0	-	0	0	-	0	-	1	-		
	Offendorf	26	Male	Forest/meadow	3	1	2	47	135	30	0	0	-	0	0	-	0	-	1	-		
	Erstein	16	Female	Pathway	3	1	1	41	45	15	0	0	-	0	0	-	0	-	0	-		
	Erstein	45	Female	Forest/stream	4	1	1	66	75	13	0	0	-	0	0	-	0	-	0	-		
	Erstein	5	Male	Pathway	3	1	2	77	80	43	0	0	-	0	0	-	0	-	0	-		
Regular decrease, death (group h)	Erstein	7	Male	Forest/stream	4	1	1	44	37	23	0	0	-	0	0	-	0	-	1	-		
	Offendorf	12	Female	Pathway	2	1	1	260	200	136	0	0	-	0	0	-	0	-	0	-		
	Offendorf	5	Female	Forest/stream	1	2	1	48	40	37	0	0	-	0	0	-	0	-	1	-		
	Erstein	21	Female	Pathway	5	1	1	85	49	41	0	0	-	0	0	-	0	-	0	-		

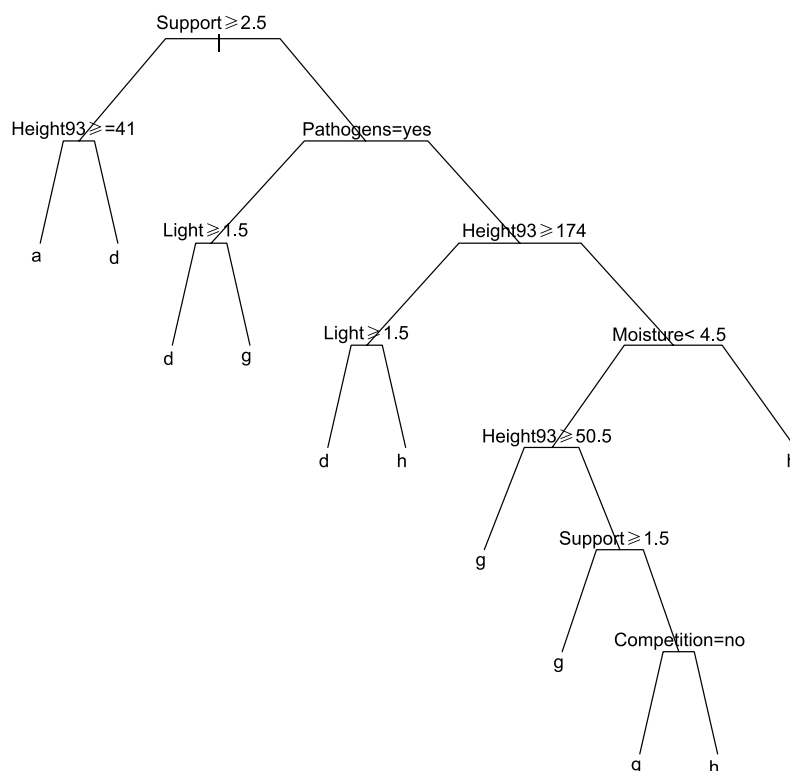


Figure 3. Full classification tree of 29 transplanted vines partitioned into four groups and constrained by seven predictor variables. Group 'a' (5 samples): regular growth, surviving; group 'd' (7 samples): decreasing growth, surviving; group 'g' (13 samples): regular growth, dying; group 'h' (4 samples): decreasing growth, dying. Support: quality of vegetation support (ordinal variable, classes 1–3); Height93: initial height of transplants (continuous variable, cm); Pathogens: evidence of pathogens (binary variable, 'yes' or 'no'); Light: canopy openness (ordinal variable, classes 1–3); Moisture: water content of the top soil (ordinal variable, classes 1–5); Predation: evidence of herbivory (binary variable, 'yes' or 'no'); Competition: evidence of competition in the herb layer (binary variable, 'yes' or 'no').

A classification tree can be interpreted as a decision tree. Starting from the top, a criterion is applied to the first discriminant predictor (here 'Support ≥ 2.5 '): if the criterion is satisfied (e.g., if Support is class 3), go down to the left and continue with a new criterion; if not, go down to the right and so on, until reaching a terminal node.

In the full classification tree, some branches could reflect anomalies due to noise or outliers in the small dataset. However, it gave a hierarchy of predictors, showing the importance of vegetation support, pathogens, initial height and light.

In order to avoid overfitting and to find the best subtree by pruning the full classification tree, an optimal complexity parameter 'cp' of 0.0625 was chosen. Any split that did not decrease the overall lack of fit by a factor of 'cp' was not

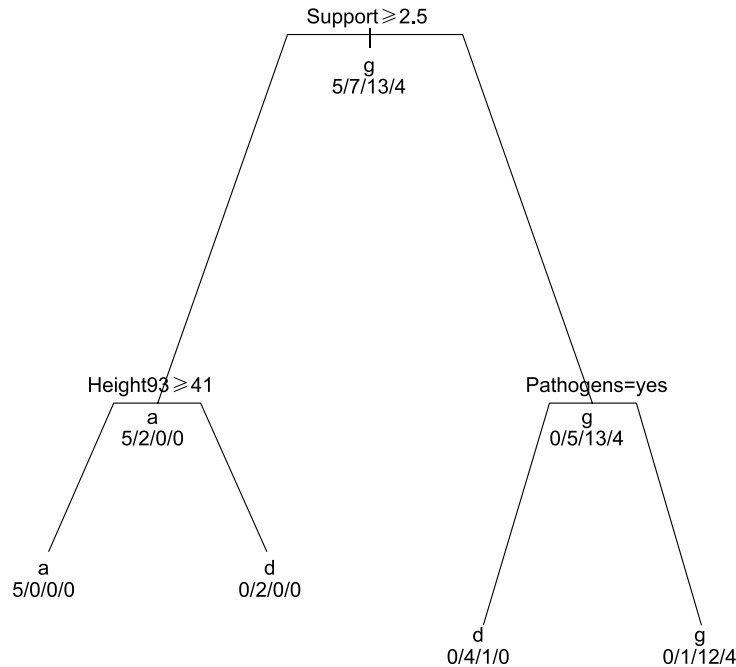


Figure 4. Pruned classification tree of 29 transplanted vines partitioned into four groups and constrained by three predictor variables. Group 'a' (5 samples): regular growth, surviving; group 'd' (7 samples): decreasing growth, surviving; group 'g' (13 samples): regular growth, dying; group 'h' (4 samples): decreasing growth, dying. Support: quality of vegetation support (ordinal variable, classes 1–3); Height93: initial height of transplants (continuous variable, cm); Pathogens: evidence of pathogens (binary variable, 'yes' or 'no'). For every node, numbers separated by back slashes indicate the number of samples selected in each group 'a', 'd', 'g' and 'h'.

attempted. For this new optimal model with three splits, the relative error was 37.5% but the x-error was minimised to 62.5%.

Among the seven predictors available in the dataset, only three were selected in the pruned classification tree to discriminate three groups in the response variable (Figure 4). The first predictor was the vegetation support: group 'a' (vines with a regular growth from 1993 to 2002) was strictly dependent on an optimal vegetation structure (support class 3). Two samples of group 'd' were found in this situation and were discriminated from group 'a' by an initial height lower than 41 cm.

If vegetation support belonged to class 1 or 2, the presence of pathogens became the discriminant predictor between groups 'd' (vines having grown vigorously during 1–3 years followed by a marked decrease) and 'g' (vine that grew to be very tall after three years but remained relatively thin, and disappeared). Surprisingly, pathogens were more frequently associated with surviving vines, suggesting that survival is probably not ensured in the future for group 'd'. The terminal node labelled 'g' included in fact all samples of group 'h', which cannot be easily discriminated by the available predictors. However, the full classification tree

showed that group 'h' could depend on various limiting factors, including light, moisture and competition.

According to this statistical analyses, the choice of an optimal vegetation support appeared as a necessary and sufficient condition for growth and survival of transplanted vines, providing a sufficient initial height of individuals.

Discussion

Requirements for the existing plantations

Results clearly indicate that high irradiance associated with suitable supports are a prerequisite for a successful adaptation. This fits with the conclusions of ecological analysis (Arnold 2002). During the first year, a quarter of the plants disappeared for two main reasons: vandalism and destruction by wild boar and ungulates. The fences were too fragile and easy to overcome. Most sites selected by managers for transplantation were also undoubtedly unsuitable for the wild grapevine, essentially because of shade, lack of supports and absence of adequate protection against plant competition and predation. Several paths, along which wild grapevines were planted, were abandoned. This led to a rapid closure of the canopy and unsuitable ecological conditions. A last factor of mortality was caused by the fall of trees during the storm of 1999.

In fact, the evolution of the plants was followed but nothing was undertaken to enhance their survival chances. This was purposely done in accordance with the management planning of the natural reserves. In other parts of the Rhine Valley, the reintroduction was also left to free development.

If one wants to ensure the survival of the 14 remaining plants a monitoring plan should be ensured, including direct intervention on the plants. To our opinion, 9 individuals (groups b, c, d, e) of the 14 remnant vines need urgent protection against predation and competition. In those places, the vegetation should regularly be cut to avoid closure of the canopy.

On the individuals of group 'a' several fungi attacks were observed. In these cases the application of an appropriate fungicide might be discussed.

In all present groups, the moisture seemed satisfactory, but growth was better in sites with moderate moisture (indices 3–4) and without effects of anoxia.

From 2004 on, the restoration projects will alter the water movement in the whole nature reserves. The water dynamics will hopefully have a positive impact on the existing sites and create new adequate sites for future reintroduction.

Proposal for the reinforcement of reintroduced populations

Given the rarity of vines in the two nature reserves, we propose a second attempt at transplantation, with a critical number of vines (that we estimate arbitrarily at about

50 plants of both sex per reserve), planted in small clumps of male and female individuals in strictly selected habitats, with careful supervision up to a certain height. The plants should, like the previous ones, be of Rhine origin. This would be done in order to preserve the Rhine genotypes already cultivated in research stations. These vines must be planted in pots rather than directly in the soil so that roots and cultivation soil could be transplanted together. This usually increases survival of young plants. If these plants establish successfully, we will envisage new reintroductions after a period of 5–10 years.

Shortly after plantation, the young plants need time for adaptation. As the erosive dynamic will never be recovered by restoration projects, this early stage requires close management. Competition with other plants should be reduced. Small bushes and herbaceous plants represent strong competitors for light and nutrients. In the natural habitat, competitiveness is naturally reduced by water dynamics. In these cases, the reduction of competitiveness should be insured by human intervention. Therefore, the selected sites should not only be suitable ecologically, but should also be accessible to machinery. The light supply should be sufficient. The canopy should be kept open till the plants reach the critical height of 2 m. The vertical structure of the vegetation is important for young wild grapevines and should grow accordingly.

In a natural situation, wild grapevines are often found in zones of high density of small trunks. This density protects young plants from grazing by ungulates. Steel wire should protect the plants from grazing and uprooting.

After reaching heights of 2–3 m, the wild grapevine should have sufficient root and leaf development to be able to face most natural environmental difficulties alone and be able to reproduce at least vegetatively.

At that stage, the two other European woody vines might interfere (*Clematis vitalba* and *Hedera helix*). The relationship between these three European climbers is under study.

The fragility of wild grapevine populations is striking if we consider the contrasting high vitality of the two other woody vines. *Hedera helix* and *Clematis vitalba* were greatly favoured by the elimination of floods (vines are sensitive to anoxia) in forests where forestry was not too destructive for ecosystems and vine communities (Schnitzler 1995). This is probably why *Hedera helix* and *Clematis vitalba* populations are particularly vigorous in the Erstein forest. Considering the ecological point of view of restoration projects, which is to re-activate natural interactive processes between species and populations, the three woody vines will adapt to each other in relation to their specific ecology. Wild grapevines seem to be more tolerant to long flooding periods in summer, as suggested by our observations after the big late spring flood of 1999 on the islands of Ketsch and Rhinau. In these two sites many *Hedera* and *Clematis* died. In Ketsch the wild grapevines living next to them were not affected by the flood.

In Alsace, the vineyards are close to the floodplain forests and represent a permanent source of phylloxera infestation. The increase of water dynamics and water level are thus of high importance for avoiding permanent attacks by this pathogen.

Evaluation of the long-term evolution of Vitis in the wild

Such a kind of surveyed reintroduction has not been carried out before and the present knowledge on this topic is rather theoretical. Thus it is difficult to make long term predictions and tell if these plants will be able to reproduce sexually or vegetatively.

In tropical regions, 90% of the vines reproduce only in a vegetative way (Hegarty and Caballe 1991). In the biggest populations of Northern Europe, in the Danube Delta, the Danube National Park in Austria, or along the Seine Valley (the most important site in France, Lacombe, oral communication), vegetative reproduction of *Vitis* is also predominant (Parisot 1999; personal observations from Arnold and Schnitzler). Genetic evidence of this process is being investigated. Concerning the sexual way of reproduction of the wild grapevine, germinations can be quite impressive, but the survival chances of one year old seedlings are limited (Arnold 2002).

In the later stage of plant establishment, the major risk seems to come from naturalised wild grapevines or cultivars.

- (i) There is a risk of genetic pollution with escaped cultivars of *Vitis*. These taxa are however rare along the Rhine but could increase with the restoration of floods. In floodplains that still benefit from more natural fluvial dynamics such as in the Loire, the Ticino or the Danube valleys, escaped cultivars are locally vigorous. However crossovers from them are not yet proven.
- (ii) The American rootstocks are resistant to mildew, oidium and the risk of spreading of fungal diseases may weaken the European wild grapevine and affect its competitiveness.
- (iii) Other escaped Vitaceae, like *Parthenocissus*, have a broad ecology. Like native woody climbers, they are strong competitors and are also resistant to most of the diseases affecting *Vitis*.

Conclusions

Even if there was a high level of mortality, this experiment showed that wild grapevines planted in suitable environments have chances of survival along the Rhine Valley. The necessity of preliminary ecological studies performed on endangered species can also be clearly seen and their use would avoid lots of costs in the case of reintroduction programmes.

The costs of reintroduction are relatively high for plantations, transplantation, monitoring, and long-term success cannot be completely guaranteed. As the plant has been protected in France since 1995, there are supplementary difficulties for the collection of plants in the wild and cultivation.

Because the wild grapevine is not the only plant to be under threat of extinction in alluvial forests, we can wonder why this particular plant must be saved rather than

others. Justifications of both risks and costs are found in some particular traits of the plant, that is

- (i) Europe has suffered much more than the other parts of the northern hemisphere from lack of available refugia during the Glacial periods, which has led to a higher decrease of Tertiary species than in America or Asia. The last representative species of the Vitaceae family must be saved in its whole range in Europe.
- (ii) Vine-rich forest ecosystems do not exist in temperate areas except in floodplain forests, in contrast to tropical forests (Hegarty and Caballé 1991). Because *Vitis* is more strictly dependent on regular flooding than the two other woody vines, its contribution to the edification of such complex forest ecosystems is highly original and must be preserved. Disappearance of *Vitis* populations can be considered as a supplementary step in the dramatic and tragic destruction of one of the most specialised forest ecosystem of the northern hemisphere (Schnitzler 2002).
- (iii) the plant is the major ancestor of the cultivated grapevines of the planet, *Vitis vinifera* subsp. *silvestris* represents a unique, invaluable resource for the civilisations of Europe. The extinction of the wild grapevine in its natural habitat would therefore be considered as an irreversible loss in cultural diversity, as well as for all wild genotypes of cultivated plants.

Acknowledgements

The authors thank the Conservatoire des Sites Alsaciens which supported the study and helped in field investigations. This project was partially supported by the National Centre of Competence in Research (NCCR) Plant Survival, research programme of the Swiss National Science Foundation as well as by the SNF project 3100-043307-95.

References

- Arnold C., Gillet F. and Gobat J.-M. 1998. Situation de la vigne sauvage (*Vitis vinifera* ssp. *silvestris*) en Europe. *Vitis* 37: 159–170.
- Arnold C. 2002. Ecologie de la vigne sauvage (*Vitis vinifera* L. ssp. *silvestris* (Gmelin) Hegi) en Europe. *Geobotanica Helvetica* 76: 1–296.
- Arnold C., Schnitzler A. and Douard A. 2002. Conservation and reintroduction of rare forest species: an example from wild grapevine (*Vitis vinifera* ssp. *silvestris* Gmelin, Hegi) in Alsace. Oral communication, International Symposium on Dynamics and Conservation of Genetic Diversity in Forest Ecosystems, Strasbourg, 2–5 December 2002.
- Breiman L., Friedman J.H., Olshen R.A. and Stone C.J. 1984. *Classification and Regression Trees*. Wadsworth.
- Bronner J.P. 1857. *Die wilden Trauben des Rheinthales*, Heidelberg.
- Buijse A.D. et al. 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater Biology* 47: 889–907.

- Carbiener R. 1970. Un exemple de type forestier exceptionnel pour l'Europe occidentale: la forêt du lit majeur du Rhin au niveau du fossé rhénan. Intérêt écologique et biogéographique. Comparaison a d'autres forêts thermohygrophiles. *Vegetatio* 20: 97–148.
- Coudurier T. 1992. Sur la place des lianes dans la forêt guyanaise. Une approche qui utilise l'architecture végétale. Ph. D. Thesis, Montpellier II University, France.
- David L. 1993. Les conditions d'éclaircissement sur les sites d'implantation de la vigne sauvage (*Vitis sylvestris* C. Gmel) dans les réserves naturelles d'Offendorf et d'Erstein. DEA, Strasbourg University, France.
- David L. and Klein J.P. 1994. Réintroduction expérimentale de la vigne sauvage (*Vitis sylvestris* C. Gmel) dans les réserves naturelles d'Erstein et d'Offendorf. *Mulhouse* 832: 73–76.
- Fengqin Z., Fangmei L. and Dabin G. 1990. Studies on germplasm resources of wild grape species (*Vitis* spp.) in China. Proceedings (Special issue of VITIS) of International 5th Symposium Grape Breeding. St Martin, Pfalz, Germany, 12–16 September, pp. 50–57.
- Fullenwarth I. 1997. Les réintroductions de vigne sauvage (*Vitis vinifera* ssp. *sylvestris* Gmelin) dans les réserves naturelles rhénanes. Mémoire, Diplôme d'Ingénieur en Techniques de l'Horticulture et du Paysage, ENSA Rennes.
- Gallusser W.A. and Schenker A. 1992. Die Auen am Oberrhein. Birkhäuser Verlag, Basel.
- Griesselich L. 1847. Deutsche Pflanzenbuch, Karlsruhe.
- Hegarty E.E. and Caballe G. 1991. Distribution and abundance of vines in forest communities In: Putz F.E. and Mooney H.A. (eds) *The Biology of Vines*. Cambridge University Press, Cambridge, pp. 313–336.
- Issler E. 1938. La vigne sauvage (*Vitis sylvestris* Gmelin) des forêts de la vallée rhénane est-elle en voie de disparition? *Bulletin de l'Association Philomatique d'Alsace et de Lorraine* 5: 413–416.
- Kirchheimer F. 1946. Das einstige und heutige Vorkommen der wilden Weinrebe im Oberrheingebiet. *Zeitschrift für Naturforschung* 1: 410–413.
- Lacombe T. et al. 2002. Contribution à la caractérisation et à la protection in situ des populations de *Vitis vinifera* L. spp. *sylvestris* (Gmelin) Hegi, en France. Oral communication, BRG National Symposium, La Châtre-Berry.
- Mc Govern. 1999. The origins and ancient history of wine. <http://www.upenn.edu/museum/Wine/wineintro.html>.
- Ocete R. and Lara M. 1994. Consideraciones sobre la ausencia de sintomas de ataque por filoxera en poblaciones autoctonas de *Vitis vinifera* L. *sylvestris* (Gmel.). *Hegi. Bol. San. Veg. Plagas* 20: 631–636.
- Pariset C. 1999. Etude sommaire de deux espèces de la forêt alluviale dans la Bassée: la vigne sauvage *Vitis vinifera* ssp. *sylvestris*, et l'orme lisse, *Ulmus laevis*. *Bulletin de l'Association des Naturalistes de la Vallée de Loing* 75: 112–119.
- Rivera D.R. and Walker M.J. 1989. A review of palaeobotanical findings of early *Vitis* in the Mediterranean and of the origins of cultivated grape-vines, with special reference to new pointers to prehistoric exploitation in the western Mediterranean. *Review of Palaeobotany and Palynology* 61: 205–237.
- Robertson P.A., Weaver G.T. and Cavanaugh J.L. 1978. Vegetation and tree species patterns near the northern terminus of the southern floodplain forest. *Ecological Monographs* 48: 249–267.
- Scossiroli R.E. 1988. Origine ed evoluzione della vite. *Atti Ist. Bot. e Lab. Critt* 7: 35–55.
- Schnitzler A. 1995. Community ecology of arboreal lianas in gallery forests of the Rhine Valley, France. *Acta Oecologica* 16: 219–236.
- Schnitzler A. 1996. Comparison of landscape diversity in forests of the upper Rhine and the middle Loire floodplains (France). *Biodiversity and Conservation* 5: 743–758.
- Schnitzler A. 2002. Les forêts naturelles d'Europe. Tec et Doc Lavoisier, Paris.
- Schultz F. 1946. Flora der Pfalz, Speyer.
- Schumann F. 1968. Die Verbreitung der Wildrebe am Oberrhein. *Die Wein-Wissenschaft* 23: 487–497.
- Schumann F. 1977. Zur Erhaltung der Wildrebe *Vitis vinifera* L. var. *sylvestris* Gmelin in den rheinischen Auwäldern. *Pfalzer Heimat*: 150–154.
- Statsoft Inc. 1995. Statistica for Windows, Release 5.0 (Computer programme/manual). Statsoft Inc., Tulsa, OK, USA.
- Trémolières M., Sanchez-Perez J., Schnitzler A. and Schmitt D. 1998. Impact of river management history on the community structure, species composition and nutrient status in the Rhine alluvial hardwood forest. *Plant Ecology* 135: 59–78.