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Evaluation of *Juglans* species for resistance to *Phytophthora cinnamomi*: differences in isolate virulence and response to fosetyl-Al

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Summary

Phytophthora is considered as an important pathogen on walnut, and severe losses are reported in European as well as in American walnut stands. Though several *Phytophthora* spp. are known to attack walnut, *P. cinnamomi* is considered the most virulent and widespread in southern Europe. Up to now, no walnut species or hybrid is known to have a high resistance level towards *P. cinnamomi*. Efforts are addressed in finding rootstock material graft compatible with English walnut and resistant/tolerant to *P. cinnamomi*. The extension of *P. cinnamomi* lesions on five *Juglans* species was studied to find out sources of resistance/tolerance to this pathogen. Walnut species clustered into two main groups, *J. hindsii, J. nigra*, and *J. mandshurica* were the less susceptible to the colonization of *P. cinnamomi*, while *J. regia* and *J. sieboldiana* were the most susceptible. On this account, *J. mandshurica* represents the best alternative as rootstock because its employment overcomes the risk of the occurrence of black line disease, it has good level of resistance to *Agrobacterium temefaciens* and *Brenneria nigrifluens*, and it is tolerant to *Xanthomonas arboricola* pv. *juglandis*. *J. mandshurica* is also compatible in cross-pollinations with *J. regia* and *J. nigra*. Differences in virulence of *P. cinnamomi* isolates was assessed and a marked interaction between species and isolate emerged. Treatment with fosetyl-Al by dipping was mainly efficient in reducing the length *P. cinnamomi* lesions, and an interaction between species and treatment was evident with the highest efficacy on *J. regia* and *J. sieboldiana*.

1 Introduction

Among all the *Phytophthora* species associated with walnut root and collar rot followed by die-back, *Phytophthora cinnamomi* represents the most damaging species worldwide. It is responsible for severe losses on a great number of host species (Zentmyer 1980). Root and collar infection on *Juglans* spp. are not recent in Italy. Actually, this disease was first recorded in this country by Curzi (1933) on English walnut under the names of 'nerume', 'mal nero', or 'ink disease', and it was attributed to *P. cambivora*. Successively, walnut root and collar rot were detected in the United States and attributed to *P. cinnamomi* (Crandall 1936). Since then, more than 10 species of *Phytophthora* have been recovered in association to root and collar rot in walnut orchards in the United States (Mircetich and Matheron 1983; Matheron and Mircetich 1985), but *P. cinnamomi* and *P. citricola* were determined to be the most consistent (Mircetich et al. 1998). In recent years in Italy, up to six species of *Phytophthora* have been associated to walnut decline and death namely, *P. cactorum* (Cristinzio and Verneau 1954; Belisario et al. 1997), *P. cinnamomi* (Belisario et al. 2001), and more recently *P. cambivora*, *P. citricola*, *P. cryptogea* and *P. nicotianae* (Belisario et al. 2006). In the last 10 years, the authors have isolated over 50 isolates of *P. cinnamomi* from declining walnut stands in Southern Europe, and few isolates

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of the other *Phytophthora* spp. associated to walnut decline. As reported in previous works, the pathogenicity of these *Phytophthora* spp. to walnut was evaluated by the soil infestation method on English walnut seedlings (Vettraino et al. 2003; Belisario et al. 2006). While *P. cinnamomi* is well known as an aggressive primary pathogen of English walnut, the other species of *Phytophthora* may act as predisposing factors to walnut decline, affecting root system development and increasing host vulnerability to environmental stress (Vettraino et al. 2003; Belisario et al. 2006). For these reasons *P. cinnamomi* has to be considered the most serious threat.

English (Persian) walnut (*Juglans regia*) is the most widely cultivated walnut species worldwide, either for fruit or timber production. In the last 10 years, the increment of this cultivation in Italy and southern Europe has been accompanied by changes in cultural management, type of varieties and/or rootstocks, and by an extension to the type of land-use. One or two-year-old seedlings or grafted plants, mainly on English walnut as rootstock, are used for plantation or orchard establishment respectively. In recent years, a progressive increase in the occurrence of walnut decline and death has been recorded especially where stands are subjected to prolonged water soil saturation (Belisario et al. 2006). Symptoms range from a progressive decline to sudden death, particularly evident during summer time. Symptoms on the canopy are associated with root and/or collar rot occurring on adult trees in orchards and plantations as well as on seedlings in nurseries.

Declining plants often show brown to black humid patches with abundant oozing from the collar level up into the trunk and in some cases cankers reach over 1.8 m above the ground level. The disease often spreads along the row infecting progressively all trees or several foci can be present in the same orchard. The pathogen dispersal is caused principally by water but also man and farm machinery can be responsible for infected soil dissemination. Though the disease has been known since a long time, it is still a serious threat for both European and American walnut orchards and plantations.

Different levels of resistance to *Phytophthora* spp. are known to be present among walnut species. Up to now, no species or hybrids of *Juglans* are known to have a good resistance or tolerance to *P. cinnamomi*. Paradox hybrid (*J. hindsii* × *J. regia*) rootstock are significantly more resistant than Northern California black (*J. hindsii*) or English walnut rootstock to *P. citricola* (Matheron and Mircetich 1985; Browne et al. 2006). Only Chinese wingnut (*Pterocarya stenoptera*) has proven highly resistant to *P. cinnamomi* as well as to *P. citricola*. Though wingnut is not generally graft compatible with all English cultivars, for some walnut cultivars it could offer some potentiality (Browne et al. 2006).

As neither preventive nor therapeutic treatments can eradicate the pathogen from infested tissues or soil (Browne and Viveros 2005), efforts are addressed in finding rootstock material graft compatible with English walnut and resistant/tolerant to *P. cinnamomi*. Nevertheless, among the chemicals that are efficient against *Phytophthora* spp. the systemic fungicide fosetyl-Al, though it has been studied for more than 20 years, still represents a valid mean of control. Its efficacy may act indirectly against the pathogen by triggering a host defense response (Fenn and Coffey 1984; Erwin and Ribeiro 1996). The direct effect of fosetyl-Al in reducing the mycelial growth and the production of sporangia, oospores, chlamydospores and zoospores release was already reported for *P. cinnamomi* (Coffey and Joseph 1985). More recently, a practical control of *P. cinnamomi* disease, once the pathogen has been established into the host, has been reported by stem injection with phosphite, the breakdown product of fosetyl-Al, for *Banksia* species and *Eucalyptus marginata* (Shearer et al. 2006). Fosetyl-Al action might be mediated by the host species (Durand and Sallé 1981; Shearer et al. 2006). Moreover, its stimulation effect on host defense responses has also been investigated in detached host material namely, in detached tomato leaves (Durand and Sallé 1981), in walnut logs (Belisario et al. 2007), and in detached grape leaves (Raynal et al. 1980).

The present study examines the rate of colonization of *P. cinnamomi* on different species of *Juglans* to find out sources of resistance/tolerance to this virulent pathogen to be used as rootstock and in future breeding programs. In addition, some evidences are given on the variability in virulence of *P. cinnamomi* isolates, and on the different response of the *Juglans* species to fosetyl-Al application as a possible control measure on propagation material.

2 Materials and methods

2.1 Fungal and plant material

Among a collection of over 60 isolates of *P. cinnamomi* obtained from different sources, two isolates were used for pathogenicity tests to ensure the representation of the variability of virulence that is reported for this *Phytophthora* species (Robin and Desprez-Loustau 1998). The isolates ISPaVe1931 and ISPaVe1933 were obtained from rotted collars of declining English walnut trees located in Venice and Treviso orchards respectively. Both isolates were already used in other studies on the evaluation of root damage to English walnut and on the response to potassium phosphite (Vettraino et al. 2003; Belisario et al. 2007), and Koch's postulates were fulfilled in previous works (Vettraino et al. 2003; Belisario et al. 2006). Five *Juglans* species were tested: *J. hindsii*, *J. mandshurica*, *J. nigra*, *J. regia* and *J. sieboldiana* (syn. *J. ailantifolia*). One-year-old sprouts at bud break, 2 cm in diameter and 1 m in length, were excised from a 10-year-old stand of walnut species located near Roma (Tormancina, CRA-PAV farm). They were kept in test tubes with sterile water, in the dark for less then 24 h until inoculation was performed.

2.2 *P. cinnamomi* inoculations and fosetyl-Al application

Tests were conducted by direct inoculation on excised sprouts using the method described by Vettraino et al. (2001) with some modifications. Inoculations were carried out with a cork borer to remove a 5 mm bark disk from the excised shoot. The bark disk was replaced by 5 mm plug of a 6-day-old culture grown on potato-dextrose agar (PDA) and wrapped with parafilm® (Pechney Plastic Packaging Inc., Chicago, IL) Four inoculation points per sprout and five sprouts per isolate were used, for a total of 20 replicates per isolate and per walnut species. Two sprouts per species were used as controls and they were inoculated with PDA plugs. After inoculation, shoots were incubated in test tubes with sterile water for 1 week in the dark at 22 ± 2°C and 100% relative humidity. After incubation, the length and the width of bark necrosis were measured.

To investigate on the effects of fosetyl-Al on the development of *P. cinnamomi* necrosis on the five walnut species, an experiment identical to the one described above, except that soon after inoculation sprouts were dipped in a solution of 2 g/l of fosetyl-Al (active ingredient), was carried out. The dose used was in accordance with what reported for commercial practice on fruit and ornamental trees. The dipping lasted 1 week after which the length and width of the necroses were measured, as reported for the previous experiment.

2.3 Statistical analysis

The four inoculation points in each case were done on the same sprout, leading to non-independent data. Thus, the mean values of the results obtained on each sprout were used in the statistical analysis instead of the original results, leading to a total of five independent replicates for each species, each isolate, and in the untreated and treated sprouts. Length

and width of the necroses were subjected to three-ways analysis of variance (ANOVA) testing: (i) the difference between the two isolates (effect called 'isolate'); (ii) the difference between the five walnut species (effect called 'species'); and (iii) the difference in necrosis dimensions between the shoots maintained in water and those dipped in the solution of fosetyl-Al (effect called 'treated_untreated'). Tukey's studentized range test at p = 0.05 and at p = 0.01 was used to compare pairs of treatment means of necrosis length and width for the five *Juglans* species. Interactions among all different effects were also tested.

3 Results

3.1 Resistance of *Juglans* species to *P. cinnamomi*

The five *Juglans* species responded significantly different to the inoculations with *P. cinnamomi* considering both isolates. Differences between isolates were significant both for the length and the width of the necroses. A significant interaction between species × isolate was also evident. Shoots inoculated with PDA plugs did not show any necrotic lesion. Taking into account the average length of the necrosis that developed on the untreated sprouts, walnut species clustered into two main groups significantly different: *J. sieboldiana* and *J. regia* showed the longest extension of the necrosis and they can be considered as the most susceptible, while *J. hindsii*, *J. nigra*, and *J. mandshurica* showed the least length extension and they can be considered as the most resistant to *P. cinnamomi* colonization (Table 1 and Fig. 1). Considering the average width of the necrosis two groups also emerged, the largest width of *P. cinnamomi* necrosis developed on *J. sieboldiana* and *J. hindsii* with no significant difference with *J. mandshurica* and *J. regia*. The latter two species not differed significantly from *J. nigra* which showed the lowest width of the necrosis (Table 1). *J. hindsii*, showed to be more susceptible to the radial colonization than to the longitudinal colonization of this oomycete (Table 1).

3.2 Variation in virulence of *P. cinnamomi* isolates

The isolate ISPaVe 1933 was the most virulent on almost all the walnut species with an average length of 30.7 ± 13.44 mm in comparison to ISPaVe 1931 for which the average length was 26.5 ± 13.8 mm, with the only exception for *J. regia* on which ISPaVe 1931 resulted the most virulent (Fig. 1). The same results were obtained for the width of the necrosis, with an average extension of 13.49 ± 4.5 mm for ISPaVe 1933 and 11.87 ± 3.34 mm for ISPaVe 1931 (Fig. 2).

Table 1. **Average (±SD) length and width of necrosis (mm) caused by two isolates of *Phytophthora cinnamomi* on one-year-old untreated excised sprouts of five walnut species measured 1 week after artificial inoculation (n = 40 replications).**

	Necrosis	
Species	Length	Width
Juglans hindsii	27.85 ± 4.9 b	16.15 ± 3.4 a
Juglans nigra	26.17 ± 12.4 bc	11.10 ± 3.6 b
Juglans mandshurica	33.45 ± 9.0 ab	13.10 ± 2.1 ab
Juglans sieboldiana	44.1 ± 16.4 a	16.45 ± 6.6 a
Juglans regia	46.17 ± 9.5 a	14.87 ± 1.7 ab

Means with the same letter in the same column are not significantly different at p = 0.05 by Tukey's studentized range test.

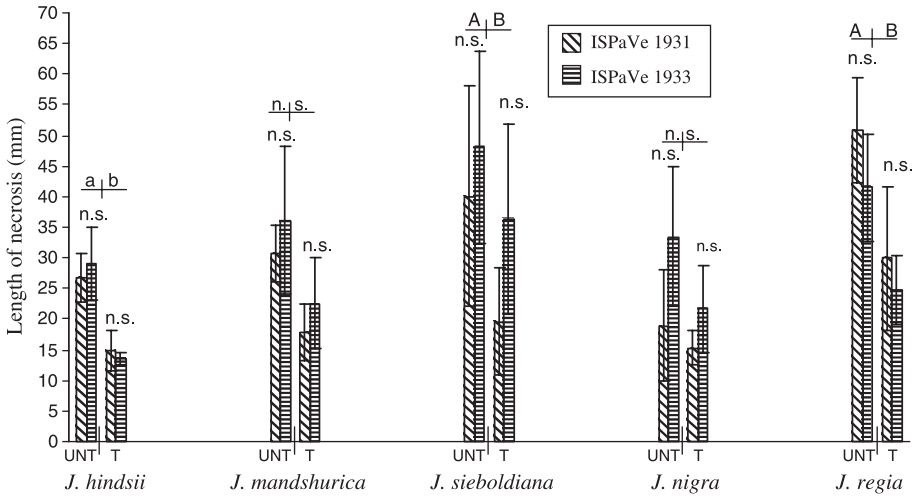

Fig. 1. Mean length (±SD) of necrosis (mm) produced by two *Phytophthora cinnamomi* isolates on excised one-year old sprouts of five walnut species 1 week after artificial inoculation. UNT: untreated; T: treated with fosetyl-Al. Horizontal bars within each pair treatments with the same letter are not significantly different according to Tukey's studentized range test. Upper case letters are used for significance level at $p < 0.01$, lower case letters at $p < 0.05$, n.s., non-significant.

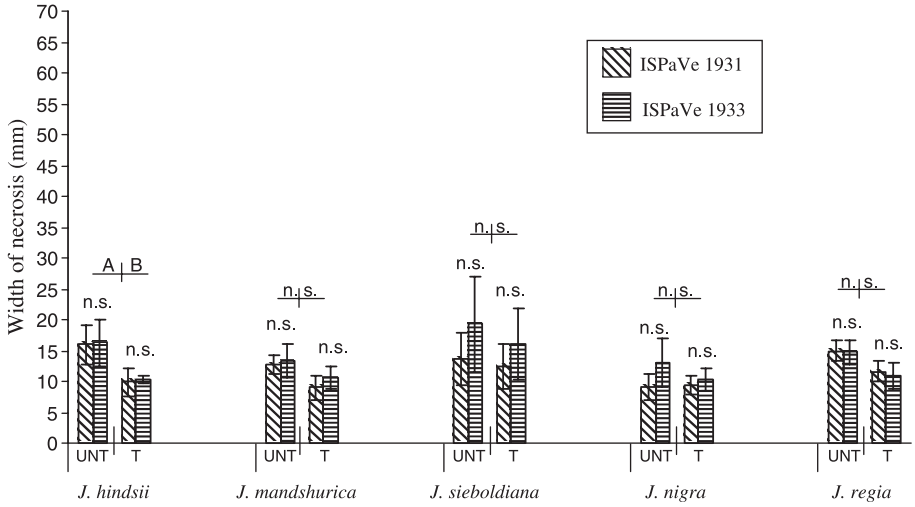

Fig. 2. Mean width (±SD) of necrosis (mm) produced by two *Phytophthora cinnamomi* isolates on excised one-year old sprouts of five walnut species 1 week after artificial inoculation. UNT: untreated; T: treated with fosetyl-Al. Horizontal bars within each pair treatments with the same letter are not significantly different according to Tukey's studentized range test. Upper case letters are used for significance level at $p < 0.01$, n.s., non-significant.

3.3 Fosetyl-Al effect

Significant variations were observed between the two groups of experiments of walnut sprouts treated with fosetyl-Al and those untreated, considering both length and width of

Table 2. **Average (±SD) length and width of necrosis (mm) caused by two isolates of *Phytophthora cinnamomi* on one-year-old excised sprouts of five walnut species dipped in fosetyl-Al and measured 1 week after artificial inoculation (n = 40 replications).**

	Necrosis	
Species	Length	Width
Juglans hindsii	14.25 ± 2.3 a	10.10 ± 1.5 a
Juglans nigra	18.50 ± 6.1 a	9.82 ± 1.7 a
Juglans mandshurica	20.15 ± 6.3 a	9.82 ± 1.9 a
Juglans sieboldiana	27.90 ± 14.7 a	14.17 ± 4.9 a
Juglans regia	27.35 ± 9.1 a	11.22 ± 1.8 a

Means with the same letter in the same column are not significantly different at p = 0.05 by Tukey's studentized range test.

the necroses of both isolates of *P. cinnamomi*. Differences in length and width of necrosis were not significant among *Juglans* species when sprouts were subjected to fosetyl-Al treatment (Table 2). Nevertheless, *J. hindsii* and *J. nigra* still showed the least extension of *P. cinnamomi* lesions. Means of the length and width of the necrosis produced on each walnut species by the two isolates taking into account the effect of treatment with fosetyl-Al are shown in Figs 1 and 2 respectively. A different efficacy of the fosetyl-Al treatment emerged in relation to the type of walnut species. *J. hindsii*, *J. sieboldiana*, and *J. regia* were the most sensitive to the treatment since the length of *P. cinnamomi* necrosis was significantly reduced in comparison to the untreated. *J. hindsii* was the only species which displayed a significantly reduction in the width of *P. cinnamomi* necrosis when treated with fosetyl-Al (Fig. 2). Reduction in the length of the necrosis was, in general, more consistent than for the width passing from 35.55 ± 13.5 mm (±SD), for the untreated, to 21.63 ± 9.9 mm for the treated shoots. In turn, the width of the necrosis passed from 14.33 ± 4.22 mm, for the untreated, to 11.03 ± 3.1 mm for the treated shoots. Standard deviation decreased when sprouts were subjected to fosetyl-Al treatment. Both the two isolates were susceptible to fosetyl-Al treatment with no significant differences. Interactions between isolates and *Juglans* species concerning the effect of fosetyl-Al were not significant.

4 Discussion

The genus *Juglans* consists of about 21 species occurring over North and South America, Europe and Asia. In the present study, five species were considered as representative of the three main continental blocks as *J. hindsii* and *J. nigra* are from North America and they are included in the black walnut group, *J. mandshurica* and *J. sieboldiana* are from Asia and they are included in the Asian butternuts, while *J. regia*, which is the most cultivated species worldwide, can be considered as an Asian-European species. The origin of Persian (English) walnut is reported to extend from Asia over eastern Europe such as the Balkan and the Carpathians (Leutaghi 1975; Aradhya et al. 2006). Over 10% of potential walnut production is lost due to pests and diseases annually. For many of the major diseases, chemical forms of control are either unavailable or ineffective. *Phytophthora* root and crown rot can be considered as an increasing source of loss in the major walnut growing areas in Europe as well as in America (Browne and Doster 2002; Belisario et al. 2006). The incidence and severity of Phytophthora root and collar rots are closely linked to soil moisture. For some *Phytophthora* spp. and some rootstocks (i.e. *J. hindsii*) the duration of soil saturation dramatically affects the disease which severity increases with the duration of

the saturation. In contrast, *P. cinnamomi* causes significant root and collar rot without soil saturation that makes this pathogen more damaging supporting its role as primary pathogen in the decline of walnut stands (Browne and Doster 2002; Belisario et al. 2006).

With the present study, we matched the objective of finding indications on the *Juglans* species that can be utilized as rootstock for fruit production or as seedlings for timber production, and in breeding programs as source of resistance/tolerance to *P. cinnamomi*. The direct method of inoculation here used allows the assessment of the ability of the isolates to develop lesion once they are inside the host plant. Although, *P. cinnamomi* infection is generally initiated by root colonization, the reliability of the direct infection with trunk or stem inoculations has been demonstrated on several hosts by assessing the variability in host susceptibility to this pathogen (Robin and Desprez-Loustau 1998). Thereby, excised sprout inoculation can be considered reliable and a good substitution to the traditional method of soil infestation as reported by Vettraino et al. (2001) and Santini et al. (2003) to give indications on the susceptibility of the host species. The two isolates of *P. cinnamomi* were chosen on the basis of their high virulence, and ISPaVe 1931 confirmed to be the most virulent on *J. regia* as reported in previous works (Vettraino et al. 2003; Belisario et al. 2006).

The two species belonging to the group of black walnuts, *J. hindsii* and *J. nigra*, were the most resistant to the colonization to *P. cinnamomi* in accordance to what reported in the literature for *P. citricola*, the most widespread *Phytophthora* species on Californian walnuts (Browne et al. 2006). Nevertheless, *J. mandshurica* did not differ significantly from *J. hindsii* and *J. nigra* in containing *P. cinnamomi* colonization both in length and width, and it was significantly more resistant than *J. regia*. On this account, this species can represent a new alternative to the employment of *J. hindsii* and *J. nigra* as rootstock, overcoming the risk of the occurrence of black line disease due to the hypersensitivity of these two species to cherry leafroll virus (Hasey et al. 2006). Moreover, as the pollen of *J. mandshurica* is compatible in cross-pollinations with *J. regia* and *J. nigra* (Krussmann 1985), its good level of resistance/tolerance to the infection by *P. cinnamomi* can be exploited in future breeding programs to reduce the incidence of root and crown rot in both nursery and production fields. Actually, breeding programs are carried out in China with *J. mandsuricha* × *J. regia* (Jusheng 2006). Studies on the employment of *J. mandshurica* as seedlings for timber production and as rootstock for fruit production should be further supported as this species has good level of resistance to *Brenneria nigrifluens* (Loreti et al. 2006), the agent of the walnut shallow bark canker, and to crown gall by *Agrobacterium tumefaciens* (Stover et al. 2007), and it is tolerant to *Xanthomonas arboricola* pv. *juglandis* (Belisario et al. 1999), the agent of walnut blight. In addition, due to its geographical origin, this species is particularly resistant to cold and its use as rootstock may be recommended in cold climates (Facciola 1990).

The significant variability in virulence between *P. cinnamomi* isolates observed in this study confirms what was already reported in investigations on the variability among isolates of the Italian population with artificial inoculation performed with different isolates on *J. regia* (Vettraino et al. 2003; Belisario et al. 2006), and of the French population on oaks (Robin and Desprez-Loustau 1998). Moreover, the presence of a marked interaction between species × isolate suggests to consider the variability in virulence in *P. cinnamomi* also in relation to a defined walnut species. In the present study, only on *J. regia* the rating of virulence between the two *P. cinnamomi* isolates was inverted.

The positive effect of fosetyl-Al in reducing *P. cinnamomi* necrosis prevents the formation of visible cankers and the progress of the colonization of *Phytophthora* in plant tissues. The effect of fosetyl-Al treatment on the width of the necrosis reduced the already small values canceling differences among walnut species and between the two

P. cinnamomi isolates, as this oomycete, colonizing the xylem, tends to develop more in length than in width (Belisario et al. 2007; Brown and Brasier 2007).

Fosetyl-Al is efficacious in controlling the disease after *Phytophthora* has become established and its level of efficacy depends upon the walnut species. Its usage is advisable by dip application on walnut roots before planting, as it is suggested for other crops (Fenn and Coffey 1984; Erwin and Ribeiro 1996).

New perspectives may open to an efficient control of *P. cinnamomi* in a short span of time by using *J. mandshurica* as rootstock and with a long term view with the introduction of this species in breeding programs with *J. regia*. At the same time, selection for resistant material should be carried out on the basis of a thorough knowledge of the variability of virulence in the *P. cinnamomi* population which might be related to a defined of walnut species.

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