

Review **Hazelnut-Associated Bacteria and Their Implications in Crop Management**

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Abstract: In recent years, the cultivation of hazelnut (*Corylus avellana*) has expanded in several areas of Europe, Asia, Africa, and North and South America following the increased demand for raw materials by the food industry. Bacterial diseases caused by *Xanthomonas arboricola* pv. *corylina* and *Pseudomonas avellanae* are threats of major concern for hazelnut farmers. These pathogens have been controlled with copper-based products, which are currently being phased out in the European Union. Following the need for alternative practices to manage these diseases, some progress has been recently achieved through the exploitation of the plant's systemic acquired resistance mechanisms, nanoparticle technology, as well as preventive measures based on hot water treatment of the propagation material. However, bacteria are not only agents of the biotic adversities of hazelnut. In fact, the application of plant growth-promoting rhizobacteria at the seedling level could enhance better performance of the tree. Likewise, endophytic and epiphytic microorganisms are considered to play a notable role in plant nutrition and protection, and their effects on hazelnut fitness deserve to be further investigated. Finally, bacterial associations may also be relevant in the post-harvest phase, particularly with reference to the processes of lipid oxidation and fat degradation suffered by the kernels after grinding.

Keywords: nut crops; bacterial diseases; endophytic microorganisms; plant growth promoting bacteria; sustainable disease management

1. Introduction

Hazelnut (*Corylus avellana* L.), belonging to the Betulaceae family, is a deciduous tree native to Europe and Asia, where it is widespread as an understorey species in mixed forests. Hazelnut is the fifth most important tree nut in the world, with a total cultivated area of about 1,027,000 ha and a global production of 1.1 million metric tons [\[1\]](#page-9-0). It is mostly cultivated in Mediterranean countries, with Turkey (665,000 tons) and Italy (140,560 tons) providing about 80% of the world production; however, following a steady increase in demand from the food industry, in recent years, hazelnut cultivation has spread to new growth areas, including the southern hemisphere, characterized by a humid temperate climate [\[2\]](#page-9-1). In the Mediterranean area, these conditions basically occur in the highlands at altitudes between 500 and 1500 m, where the plant is mostly cropped in semi-extensive production systems.

The crop product is represented by the nutrient-rich kernels, protected by a dark brown fibrous perisperm and a woody shell, which are widely used in confectionery, bakery, dairy, chocolate and candy products. Their intrinsic nutritional quality has gained attention for their beneficial effects on human health. In fact, hazelnut kernels are an energy-rich food that can play an important dietary role based on their high-value lipids, proteins, carbohydrates, dietary fiber, vitamins, minerals and antioxidant phenolics [\[2,](#page-9-1)[3\]](#page-9-2). Several

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studies addressed the phenolic composition in the seed tegument of different hazelnut cultivars, highlighting differences in quantitative content $[4–7]$ $[4–7]$. Lipids are considered the main chemical components that contribute to the quality and storability of nuts and derived products [\[8,](#page-9-5)[9\]](#page-9-6). They present a high content of monounsaturated fatty acids, particularly oleic acid and omega-3 polyunsaturated fatty acids. Along with phytosterols (especially $β$ -sitosterol), these fatty acids are known to improve the cholesterol balance and triglyceride levels, reducing the risk of atherosclerosis and coronary heart disease $[10,11]$ $[10,11]$.

In addition to food use, the hazelnut has recently disclosed medicinal properties. In fact, leaves and shells have been reported to contain taxol, a blockbuster antitumor product

as a secondary metabolite in the secondary metabolite in yew trees (*Taxus* spanned *in yew* originally found as a secondary metabolite in yew trees (*Taxus* spp.) [\[12\]](#page-9-9). The availability of massive quantities of these byproducts has introduced perspectives for exploiting an alternative economic source of this drug, which could represent an integrative of the economic alternative economic source of this drug, which could represent an integration of incomes
for hazelnut farms [13,14]. for hazelnut farms [\[13,](#page-9-10)[14\]](#page-9-11).

In this brief review, the various types of ecological interactions between hazelnut and In this brief review, the various types of ecological interactions between hazelnut and bacteria (Figure [1\)](#page-1-0) are examined with reference to both the pathological point of view and bacteria (Figure 1) are examined with reference to both the pathological point of view and the beneficial perspectives that could derive in terms of fitness and productive performance the beneficial perspectives that could derive in terms of fitness and productive of the trees.

Figure 1. The multifaceted interaction between hazelnut and bacteria. **Figure 1.** The multifaceted interaction between hazelnut and bacteria.

2. Bacterial Diseases of Hazelnut

2. Bacterial Diseases of Hazelnut *2.1. Bacterial Blight*

2.1. Bacterial Blight Bacterial blight symptoms were first described in Oregon (USA) on *Corylus maxima* [\[15\]](#page-9-12), and the related pathogen was named *Xanthomonas corylina* [\[16\]](#page-9-13). Afterward, this disease was recorded in Yugoslavia [\[17\]](#page-9-14), Italy [\[18\]](#page-9-15), Turkey [\[19\]](#page-9-16), France [\[20\]](#page-9-17), Russia [\[21\]](#page-9-18), United Kingdom [\[22\]](#page-9-19), Australia [\[23\]](#page-9-20), Chile [\[24\]](#page-9-21), Iran [\[25\]](#page-9-22) and Poland [\[26\]](#page-9-23). Nowadays, *Xanthomonas* arboricola pv. *corylina* (syn. *X. campestris* pv. *corylina*) presents a worldwide distribution, with some genetic variation demonstrated by the existence of several clades and strain clusters $[27–29]$ $[27–29]$; therefore, it maintains an A2 quarantine microorganism status for the European Plant Protection Organization (EPPO), and its possible presence in plant propagation material is monitored in the territory of the European Union [\[30\]](#page-10-0).

The pathogen enters trees via pruning cuts, wounds, fresh leaf scars and frost-injured tissues. Generally, its spread is higher in wet periods with temperatures above 20 °C. Symptoms include brown shriveled buds, brown leaf spots and reddish-brown slightly sunken cankers on the [b](#page-2-0)ark (Figure 2). The main mode of spread is on infected planting material; in fact, the potential for natural spread is relatively low, although seeds from fruits picked on infected trees can produce infected seedlings [\[27](#page-9-24)[,31\]](#page-10-1). Recently, bacterial blight has been reported as a re-emerging disease in young hazelnut orchards in Oregon,

Figure 2. Typical symptoms induced by *Xanthomonas arboricola pv. corylina* on husks (A) and leaves (B).

following a rapid increase in acreage derived from a renewed development of the hazelnut

variation that is not necessarily related to the geographic origin of the strains [\[26,](#page-9-23)[32,](#page-10-2)[33\]](#page-10-3). Some differences also exist concerning the effector repertoire of the type III secretion system.
The type attain, isolated from *C*, *usuing*, and spather atmin abtained from an amamental. *Corylus* species, indeed, do not possess the *xopH* effector [\[34\]](#page-10-4). Moreover, the complete zerging openes, macea, as not possess are *nopp* energing. *Moreover*, are complete genome of three strains, respectively isolated in France, Poland and the United States, genome or ance strains, respectively isolated in France, Folding and the Strited states, has been recently sequenced, and a single 24-k plasmid was found in two strains. In all bacco leaves [36]. It was proposed to represent a new pathovar of *P. syringae,* namely pv. strains, the copper resistance gene (i.e., *copL*) and operon (i.e., *copAB*), as well as other genes $a_1a_2a_3a_4b_5$ [37]. This pathogener was subsequently in central Italy $a_1a_2b_3$ [38]. The central Italy $a_2a_3b_3$ [38]. $a_3a_4b_3$ [38]. $a_3a_4b_3$ [38]. $a_3a_4b_3$ [38]. $a_3a_4b_3$ [38]. $a_3a_4b_3$ [38]. $a_$ involved in resistance to the high concentration of copper (i.e., *cutC* and *pCuAC*), were
also found [35] monads associated with hazelnut. The first one concerned a bacterium named *Pseudomo-*At the molecular level, the population structure of *X. a.* pv. *corylina* shows some The type-strain, isolated from *C. maxima*, and another strain obtained from an ornamental also found [\[35\]](#page-10-5).

nas coryli, which was isolated from cankers and tumors from an old hazelnut tree in Po-*2.2. Bacterial Canker*

The first circumstantial description of the bacterial canker of hazelnut was carried out in Greece. The causal agent, a Gram-negative rod with one to four polar flagella, was identified as *Pseudomonas* sp., producing a blue-green diffusible fluorescent pigment, exhibiting oxidative metabolism of glucose, and inducing hypersensitive reaction on to-bacco leaves [\[36\]](#page-10-6). It was proposed to represent a new pathovar of *P. syringae*, namely pv. avellanae [\[37\]](#page-10-7). This pathovar was subsequently isolated also in central Italy [\[38\]](#page-10-8).

Before these reports, there were only two previous records concerning pseudomonads associated with hazelnut. The first one concerned a bacterium named Pseudomonas *coryli*, which was isolated from cankers and tumors from an old hazelnut tree in Poland; however, no adequate description and pathogenicity tests were reported [\[39\]](#page-10-9). Afterwards, a bacterial leaf spot of *Corylus colurna* caused by *Pseudomonas colurnae* was described in *aviumos* (USA) [40].

Characterization of strains that caused canker of hazelnut in Greece and Italy based on fatty acid and protein profiles, as well as 16S rRNA sequence analysis and percentage of DNA-DNA hybridization with other *Pseudomonas* strains, indicated that they are very distantly related to all pathovars of *P. syringae* examined, including pv. *syringae*. In addition, all other *Pseudomonas* species tested were closer to *P. syringae* than the bacterium-causing canker of hazelnut. Hence, *P. s.* pv. *avellanae* was proposed to represent a new species, namely *P. avellanae* [\[41\]](#page-10-11). From a taxonomic standpoint, the *P. avellanae* genomospecies also include pathogenic strains that infect *Actinidia chinensis* and *Prunus avium* [\[42\]](#page-10-12). The strains of this genomospecies show a restricted pathogenic aptitude, being capable of infecting solely the host plants from where they are isolated.

The extent of genetic variation found even within homogeneous groups of strains made it problematic to get to a reliable taxonomic placement [\[43\]](#page-10-13). Hence, a comprehensive study including 118 fluorescent pseudomonads associated with hazelnut decline was carried out, which differentiated two groups. The first group belonging to *P. avellanae* included strains

industry in the United States [\[28\]](#page-9-26).

isolated in northern Greece and central Italy, which do not have the *syrB* gene encoding for syringomycin production and are very virulent but pathogenically restricted to *C. avellana*. The second group, which proved to be mildly virulent for hazelnut, included other strains obtained from Piedmont, Campania, Latium, Sicily, and Sardinia, representing a distinct taxon closely related to *P. s.* pv. *syringae* [\[44\]](#page-10-14). A distinct pathovar inciting twig dieback only to hazelnut was later characterized from isolates collected in Piedmont and Sardinia. Both fatty acids and repetitive sequence-based PCR clearly discriminated these strains from other *Pseudomonas* species. Besides some nutritional tests differentiating them from related *P. syringae* pathovars, DNA sequencing indicated that they did not possess the *syrB* gene, unlike *P. avellanae* and *P. s.* pv. *syringae* [\[45\]](#page-10-15). As these strains represented a homogeneous group and a discrete phenom, the creation of a new pathovar named *P. syringae* pv. *coryli* was proposed [\[46\]](#page-10-16).

The separate identity of several species and pathovars associated with hazelnuts [\[42,](#page-10-12)[47\]](#page-10-17) was also confirmed in a comprehensive revision of *P. syringae* [\[48\]](#page-10-18), and the circumstantial finding that additional Italian strains responsible for the same symptoms were related to *P. syringae* induced to update the name *P. syringae* pv. *avellanae* with an emended description [\[49\]](#page-10-19).

A comparison of the draft genomes of nine *Pseudomonas* strains isolated from symptomatic *C*. *avellana* trees was performed to identify common and distinctive genomic traits, which revealed two clearly distinct clusters corresponding to *P*. *avellanae* and *P*. *syringae*, with the latter including the pathovars *avellanae*, *coryli* and *syringae*. No indication of recombination between these two clusters was found. All nine strains presented a genomic island of approximately 20 kb, containing the *hrp/hrc* type III secretion system gene cluster. The type III secretion system effector repertoires were remarkably different in the two groups, with a higher number of effectors in *P*. *avellanae*. Homologue genes of the antimetabolite mangotoxin and ice nucleation activity clusters were only detected in all *P*. *syringae* pvs., whereas the siderophore yersiniabactin was only present in *P*. *avellanae*. Moreover, all nine strains have genes related to sucrose metabolism and pectic enzymes, while they do not have genes coding for indoleacetic acid (IAA) and anti-insect toxin [\[50\]](#page-10-20). The complete genome sequence of two *P. avellanae* isolates revealed that strains infecting hazelnut have a peculiar set of three type III secretion effectors, while *P. avellanae* strains infecting *Prunus* and *Actinidia* possess the genomic WHOP island that is relevant for the infection of woody hosts. Comparatively, the genome of *P. syringae* contains more sequences encoding for phytotoxin synthesis, the ice nucleation cluster, but fewer effectors. Coupled with previous observations, these findings support the conjecture that the convergence into the same host by the several *Pseudomonas* species and pathovars is possible due to different unrelated mechanisms of infection and virulence tools that could suppress the host defense mechanisms. The integration into their genomes of a horizontally acquired genomic island could drive their evolution, possibly enabling them to exploit new ecological niches [\[51\]](#page-10-21).

During 2018 and 2019, a putative new pathovar was isolated in Iran. Based on phylogenetic analysis and phenotypic and pathogenicity characteristics, it is supposed to belong to *Pseudomonas amygdali*, hence provisionally named *P. amygdali* pv. *corylicola*. Symptoms observed in Iranian hazelnut orchards consisted of irregular reddish-brown necrotic spots surrounded by a yellow halo on the leaves and bracts, leading to wilting of leaves, defoliation and decay of branches [\[52\]](#page-10-22).

Besides the known ways of transmission, such as penetration of leaf scars during autumn through rain and wind [\[44\]](#page-10-14), *Pseudomonas* spp. have been found to be associated with adults of the lignicolous beetle *Anisandrus dispar* (Coleoptera, Scolytinae), both internally and as an external contaminant [\[53\]](#page-10-23), calling for further assessments concerning the possible role of insect pests of hazelnut as vectors.

As mentioned above, for *X. a.* pv. *corylina*, *P. avellanae* is prescribed to be monitored at the introduction in the EU territory of plant material from some countries [\[30\]](#page-10-0). At a first glance, there are some similarities between the symptoms of bacterial blight and bacterial

canker, with reference to shoots, twigs and stems. However, *P. avellanae* does not cause canker, with reference to shoots, twigs and stems. However, *P. avellanae* does not cause symptoms in leaves and husks [\[36\]](#page-10-6) (Figure [3\)](#page-4-0). symptoms in leaves and husks [36] (Figure 3).

at the introduction in the EU territory of plant material from some countries $[30]$

Figure 3. Disease symptoms incited by *Pseudomonas* spp.: sudden wilting in summer caused by *P. P. avellanae* (A); bark discoloration and swelling induced by *P. avellanae* on branch (B); longitudinal necrosis of wood caused by P. avellanae (C); twig dieback incited by P. syringae pv. coryli (D). **Figure 3.** Disease symptoms incited by *Pseudomonas* spp.: sudden wilting in summer caused by

2.3. Other Bacterial Pathogens

In Chile, besides bacterial blight by *X. a.* pv. *corylina* and bacterial canker (reported as In Chile, besides bacterial blight by *X. a.* pv. *corylina* and bacterial canker (reported incited by *P. s.* pv. *syringae*), *Agrobacterium tumefaciens* has been mentioned as a bacterial pathogen of hazelnut [\[54\]](#page-10-24). In Poland, *Pseudomonas fluorescens, Bacillus* spp. and *Erwinia* spp. were recovered from diseased kernels and found to be able to infect young fruits [\[55\]](#page-10-25).

This brief overview of hazel bacterial pathogens cannot overlook phytoplasmas. A few articles report on their finding and noxious impact on this crop [\[56](#page-11-0)[–61\]](#page-11-1); however, this subject requires to be more specifically treated in a dedicated review, considering that it is basically connected with the insect vectors in terms of both spread and management [\[62](#page-11-2)[,63\]](#page-11-3).

[62,63]. **3. Management of Bacterial Diseases of Hazelnut**

be controlled through spray treatments based on copper compounds [\[64\]](#page-11-4). Either Bordeaux mixture, copper hydroxide, copper oxychloride or new formulations that contain micronized copper particles are sprayed at certain key periods to reduce the possibility of penetration in some points of entry explored by the pathogens, such as the leaf scars in autumn (*P. avellanae*) or leaf, bud and husk surface during spring (*X. a. pv. corylina*). In addition, copper compounds are also frequently used before or after some adverse climatic events, such as hail, frost and heavy rain, to protect the wounds caused by such events along the twigs or branches. Likewise, their use is suggested for disinfecting and protecting pruning wounds. The success of controlling these diseases through copper compounds mainly depends on the precise timing of distribution to prevent the colonization of the tree by the bacteria. In case of delay in the treatments and in the presence of the pathogen inoculum in the orchard, indeed, it becomes impossible to reach the internal tissues of the plant organ already colonized by the bacterial cells. A new approach to control *P*. Traditionally, bacterial and other cryptogamic diseases of hazelnut are supposed to *avellanae* was developed a couple of decades ago through the spray on the tree canopy of an activator of the plant defense mechanisms based on pathogenesis-related proteins, namely acibenzolar-S-methyl [\[65\]](#page-11-5). Through this approach, the disease is reduced by means of the systemic acquired resistance (SAR) mechanisms; in fact, the compound has no direct bactericidal activity but enhances the synthesis of proteins related to the defense against microbial pathogens. The compound is to be sprayed onto the tree canopy three times, once a month, starting from the leaf sprouting. Concerning bacterial blight, an innovative technology based on the utilization of cellulose nanocrystals obtained from pruning and shelling wastes has been shown to reduce severity without inciting any phytotoxic effect [\[66\]](#page-11-6). In nurseries, the occurrence of *X. a.* pv. *corylina* onto the buds of suckers can be limited through the application of hot water treatments [\[67\]](#page-11-7), consisting in soaking the suckers in water for 30 min at a temperature ranging between 42 and 45 °C. This treatment can be applied prior to the sucker shipment.

The intensive use of copper products for more than one century has produced a negative impact on both human health and biodiversity. Throughout this long period, copper has massively contaminated the cultivated soils; in fact, Cu residues typically accumulate in the upper 15 cm of soil, leading to plant stress, reducing fertility, and decreasing microbiota diversity. By affecting organisms in the soil food web, copper negatively interferes with crop residue decomposition, nutrient storage and release, soil structure and stability, plant resistance against pathogens, and degradation or immobilization of pesticides and other pollutants. Besides the environmental risk, there is some concern for the repeated utilization of copper as the sole way to control hazelnut bacterial diseases, which could induce the development of tolerance or resistance, as already observed for *X. a.* pv. *corylina* [\[68\]](#page-11-8).

For all these deleterious side effects, the maximum copper quantity allowed in plant protection has been successively restricted in Europe over the last decades; currently, it is limited by the European plant protection legislation to a maximum of 28 kg ha⁻¹ over a period of 7 years (regulation EU 2018/1981). The final objective would be to phase copper fungicides out, as included in the list of candidates for substitution in the territory of the European Union (Part E of the Annex to Regulation 540/2011) [\[69\]](#page-11-9). In the meantime, it is essential to step up efforts to improve plant health, reverse soil degradation and protect its fertility by increasing soil organic matter and diversity of microorganisms. This should be done by discovering and adopting sustainable, innovative plant protection practices. As a system approach to sustainable agriculture, one of the main principles should be the appropriate design and management of biological processes and natural resources which are internal to the agroecosystems with the aim of promoting their resilience.

4. Other Bacteria Associated with Hazelnut

4.1. Plant Growth Promoters

Likewise assessed on many crops, great impact on the management of hazelnut may derive from the interaction with plant growth-promoting bacteria, which affect plant development either directly through the production of phytohormones and increased nutrient uptake due to phosphate solubilization and iron-chelating siderophores, or indirectly by enhancing protection against biotic and abiotic stresses [\[70\]](#page-11-10). These beneficial properties have been reported by a wide range of genera, such as *Agrobacterium*, *Alcaligenes, Allorhizobium, Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Bradyrhizobium, Enterobacter*, *Flavobacterium, Klebsiella*, *Microbacterium, Pantoea, Pseudomonas, Rhizobium* and *Serratia* [\[71\]](#page-11-11), some of which are mentioned as hazelnut associates in this review.

However, so far, little is known about the occurrence and effects of growth-promoting bacteria in hazelnut. In an experimental study carried out in Iran, selected strains of *Pseudomonas putida*, *Bacillus subtilis* and *Enterobacter cloacae*, alone and mixed, were found to improve the growth and physiological characteristics of seedlings of *C. avellana* in a forest nursery. Particularly, the greatest height, collar diameter, leaf area, net photosynthesis, transpiration rate, stomatal conductance, water use efficiency and chlorophyll content were measured after inoculation with a combination of all bacteria, while the greatest root dry weight, root volume and total plant dry weight were detected in seedlings inoculated with *P. putida* [\[72\]](#page-11-12). Moreover, *P. putida* and *B. subtilis*, respectively, improved the absorption of zinc and iron [\[73\]](#page-11-13).

Culture filtrate of a strain of *Pantoea agglomerans* (= *Erwinia herbicola*) containing IAA and other IAA-related metabolites improved the percentage of rooted-explant, adventitious root formation, plant survival and vigor, with 17.5–42.7% increase in the leaf area as compared to plants treated with potassium salt of indole-3-butyric acid [\[74\]](#page-11-14).

4.2. Endophytes

Endophytic microorganisms represent another category of the plant microbiome which is considered to play a notable role in plant nutrition and protection [\[75–](#page-11-15)[78\]](#page-11-16). They are basically defined with reference to their aptitude to dwell inside plant tissues without inciting disease symptoms, from which it follows that some pathogens may also happen to be reported as endophytic associates when they are recovered from asymptomatic tissues. In fact, the endophytic occurrence of bacteria of the *P. syringae* species complex in symptomless twigs and of both *P. avellanae* and *P. s.* pv. *syringae* in symptomless suckers was reported during investigations carried out at several locations in Latium [\[79,](#page-11-17)[80\]](#page-11-18). Moreover, the recovery of endophytic *Xanthomonas* strains in hazelnut shoots used for micropropagation [\[81\]](#page-11-19) raises concern for its possible presence in asymptomatic plants and spread through nurseries. Indeed, these findings are very relevant for hazelnut management with reference to several aspects requiring further assessments. Particularly, it should be ascertained if they are to be referred to interception during the latency period of the disease cycle, or rather if the endophytic settlement may result from an ordinary ecological habit, reflecting a facultative pathogenic aptitude which could eventually affirm in consequence of any factors promoting virulence or inducing plant susceptibility. Indeed, the evidence is increasing that the onset of many plant diseases is secondary to environmental stresses or perturbations in microbiome homeostasis [\[82](#page-12-0)[,83\]](#page-12-1).

In this scenario, the importance of interactions among species that are part of the microbiota in crop species is also evident, calling for the necessity to accumulate information on the taxonomic assortment and functions of this holobiont component. Data currently available for hazelnut are scanty and do not allow to advance valid conjectures. However, the endophytic association is confirmed by the finding of bacterial contaminants in hazelnut shoot cultures after surface sterilization of the explants in a commercial micropropagation laboratory; *Pseudomonas fluorescens, Agrobacterium radiobacter* B, *Enterobacter asburiae, Flavobacterium*, *Xanthomonas* and *Alcaligenes* spp. were identified based on colony description and observations concerning Gram stain, oxidase, starch hydrolysis, oxidation/fermentation, motility and gelatinase tests [\[81\]](#page-11-19). Likewise, bacteria of the genera *Pseudomonas* and *Brevundimonas* (the latter previously classified in *Pseudomonas*), identified through 16S rRNA sequencing and API® tests, were found to be endophytically associated in hazelnut explants used for micropropagation [\[84\]](#page-12-2).

4.3. Epiphytes and Root Associates

More bacterial associates have been recovered from the phyllosphere and other hazelnut organs without previous sterilization. Out of a sample of 138 epiphytic bacteria belonging to the genera *Pseudomonas, Bacillus, Erwinia, Enterobacter, Citrobacter* and *Klebsiella* recovered from hazelnut leaves in Poland, several isolates of *P. fluorescens* and *Bacillus* spp. and *Pantoea* (= *Erwinia*) *cypripedii* were found to be able to limit in vitro growth of *Ciboria* (= *Monilia*) *coryli* and other fungal pathogens of hazelnut [\[85](#page-12-3)[,86\]](#page-12-4). A previously cited study carried out in central Italy [\[80\]](#page-11-18) also reported the finding of a complex bacterial assortment from symptomatic twigs/branches and leaves and pollen collected on the same plants, including *Pseudomonas trivialis* (or *P. poae*)*, Pseudomonas libaniensis, Brenneria* (= *Lonsdalea*) *quercina, Roseomonas terpenica,* and other unidentified species of the genera *Microbacterium, Arthrobacter, Aeromicrobium, Sanguibacter, Roseomonas, Bacillus, Staphylococcus, Pseudomonas* and *Frigobacterium.* Moreover, a rod-shaped bacterium representing the new species *Spirosoma pollinicola* was isolated from the pollen of *C. avellana* in Giessen (Germany) and identified based on 16S rRNA sequencing. It is Gram-negative, aerobic, catalase-positive and oxidase-negative, and displays optimum growth at 25 °C and pH 7 [\[87\]](#page-12-5).

However, the diversity of bacteria associated with hazelnuts is expected to be much higher than resulting in the above studies. Evidence in this respect derives from a few studies based on high-throughput DNA sequencing of root-associated bacteria as related to the experimentally induced formation of ectomycorrhizae by truffles. In the first study carried out in France, considering mycorrhization of hazelnut with *Tuber melanosporum*, about

900 operational taxonomic units (OTUs) corresponding to nine phyla were detected in the ectomycorrhizal root tips at each of four sampling periods. The most represented genera were *Bradyrhizobium*, *Thermoleophilum*, *Terrimonas*, *Mycobacterium*, *Pedosphaera*, *Microscilla*, *Flavobacterium*, *Cytophaga*, *Gordonibacter*, *Rubrobacter*, *Streptomyces*, *Bacillus*, *Pirellula* and *Acidobacterium*; among them, the first two occurred at a higher frequency than in the surrounding rhizosphere, indicating their positive association with the ectomycorrhizae and a possible positive influence on nitrogen intake by the plant [\[88\]](#page-12-6). More recently, two analogous studies have been carried out in China, respectively considering the mycorrhization of hazelnut with *Tuber borchii* and *Tuber panzhihuanense*. In the first case, a total of 2354 OTUs representing 38 phyla, 100 classes, and 718 genera were detected, with *Rhizobium, Pedomicrobium, Ilumatobacter, Woodsholea, Streptomyces, Geobacillus* and *Hydrogenophaga* being the most abundant. Moreover, mycorrhization was found to increase bacterial diversity in roots [\[89\]](#page-12-7). In the second case, a total of 1806 OTUs representing 36 phyla, 95 classes and 775 genera were determined, with *Rhizobium, Pedomicrobium, Woodsholea, Streptomyces, Geobacillus, Devosia, Actinoplanes, Rivibacter, Herbiconiux* and *Mesorhizobium* being dominant [\[90\]](#page-12-8). Apart from an obvious variation in the respective general taxonomic assortments, the prevalence of *Rhizobia* supports the conjecture that this association may be favorable to hazelnut in terms of nitrogen uptake.

5. Antibacterial Properties of Hazelnut

Bacterial associations may also be relevant in the post-harvest phase. In fact, due to their high lipid content, hazelnut kernels can suffer damage due to lipid oxidation and fat degradation after grinding [\[91\]](#page-12-9). Lipid decomposition is mainly led by bacteria, particularly *Staphylococcus xylosus*, Enterobacteriaceae and coliforms [\[92\]](#page-12-10). The need to counteract these pathogens, which may compromise seed vitality, represents a possible explanation for the antibiotic properties displayed by the kernels [\[14\]](#page-9-11). In fact, methanol and ethyl acetate extracts from kernels of *Corylus cornuta* displayed inhibitory effects against Gram-positive *Streptococcus pneumoniae*, with minimum inhibitory concentrations (MICs) of 0.15 and 0.76 mg mL−¹ , respectively, while Gram-negative *Klebsiella pneumoniae* was sensitive at a much higher concentration (100 mg mL $^{-1}$ for both extracts) [\[93\]](#page-12-11). Moreover, extracts from hazelnut fruits were found to possess a high antimicrobial activity against Gram-positive bacteria (*Bacillus cereus, Bacillus subtilis, Staphylococcus aureus*) with a MIC of 0.1 mg mL−¹ . Conversely, some Gram-negative bacteria (*Escherichia coli, K. pneumoniae, Pseudomonas aeruginosa*) were not inhibited [\[94\]](#page-12-12). *Bacillus cereus* and *S. aureus* were also very sensitive to boiling water extract of hazel leaves at the same concentration, while *B. subtilis* was inhibited at a higher concentration (1 mg mL $^{-1}$), and again Gram-negative species displayed much lower sensitivity, with *P. aeruginosa* resistant even at 100 mg mL−¹ [\[95\]](#page-12-13).

The general higher sensitivity of Gram-positive bacteria was not confirmed in assays carried out with pollen extracts. In fact, in this case, *Yersinia enterocolitica* (Gram-) was the most sensitive in assays with ethanolic and methanolic extracts, while *S. aureus* was the most sensitive to aqueous extract [\[96\]](#page-12-14). Considering the five species tested in this study, the following ranking of sensitivity was observed against ethanol extract: *Y. enterocolitica* > *Salmonella enterica > S. aureus > Bacillus thuringiensis > E. coli*; against methanol extract: *Y. enterocolitica > S. enterica > E. coli > S. aureus > B. thuringiensis*; and against aqueous extract: *S. aureus > S. enterica > E. coli > B. thuringiensis > Y. enterocolitica*. An obvious inference is that these activities depend on the secondary metabolite assortment of the different extracts. Hence, more circumstantial data would derive from assays carried out with fractions or purified compounds separated from the extracts [\[14\]](#page-9-11). In this respect, tannins from acetonic extract hazelnut kernels displayed antibiotic activities against a panel of Gram-positive and negative bacteria, with MICs ranging from 125 µg mL−¹ against *E. coli* (Gram-), *Lactobacillus plantarum* and *Listeria monocytogenes* (Gram+), to 250 µg mL−¹ against *S. aureus* (Gram+) and *Pseudomonas fragi* (Gram-), and to 500 µg mL−¹ against *Salmonella typhimurium* (Gram-) and *Brochothrix thermosphacta* (Gram+) [\[97\]](#page-12-15). Moreover, a methanol extract of leafy covers of hazelnuts displayed antibiotic effects in disk assays against *S. aureus* and *P. aeruginosa*

(MIC = 30 µg/disk), *B. cereus* (MIC = 50 µg/disk), and *E. coli* (MIC = 100 µg/disk). Among several cyclic diarylheptanoid compounds which were purified from the extract, carpinontriol B and the novel giffonin U displayed inhibitory effects against *B. cereus* (respectively at MICs of 4 and 5 µg/disk), *E. coli* and *P. aeruginosa* (MIC = 10 µg/disk), and *S. aureus* (MIC = $30 \mu g/disk$); giffonin I showed more uniform effectiveness against all the tested strains (MIC = 40 μ g/disk), while giffonin T was less active [\[98\]](#page-12-16).

Further assessments in this intriguing research field can be expected to shed light on the circumstances which regulate infection by the key bacterial pathogens of hazelnut. Particularly, direct assays on the sensitivity to purified antibiotic substances should be carried out against pathogenic strains of *X. a.* pv. *corylina* and *Pseudomonas* spp., to assess if they display higher resistance to these products than the other Gram-negative species which have been tested so far; and if a higher expression in planta of these compounds could eventually improve hazelnut protection. Moreover, further investigations could help in assessing if the outcome of the plant-pathogen interaction depends on either the extent of constitutive antibiotic production by the different cultivars in the various environmental contexts or the interaction with other species which are part of the host's microbiome, such as the endophytic fungi.

6. Future Perspectives

The agricultural importance of hazelnuts is increasing worldwide after a general appreciation of their properties as a functional food. The exploration of novel areas of cultivation in all continents proceeds along with a growing awareness by the farmers that new approaches in disease management are to be adopted following the paradigm of sustainable agriculture, with the aim of improving the efficacy of treatments and reducing the eco-toxicity of inputs.

A better knowledge of the disease cycle of bacterial pathogens of hazelnut and the interactions established with the other plant-associated microorganisms could bring to the development of forecasting models that, in turn, could allow regulating both the timing and dosage of treatments [\[99\]](#page-12-17). Moreover, the effects of the various antibiotic compounds and of factors able to promote their synthesis in hazelnut tissues could be explored as a tool to improve plant tolerance, eventually leading to the containment of the incidence of bacterial diseases below an economic threshold. Finally, besides the direct effects on yields deriving by the positive impact on protection and nutrition offered by beneficial symbionts, the roles played by non-pathogenic bacteria associated with *C. avellana* deserve further consideration for the implications with truffle mycorrhizae and taxol biosynthesis, which may bring valuable income integration for the hazelnut farms, especially in marginal areas characterized by low soil fertility. Indeed, a more comprehensive knowledge of the composition and roles of bacterial microbiomes associated with hazelnut rhizosphere, phyllosphere and fruit is desirable for better management of this emerging nut crop.

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