



# Synergism and antagonisms between nutrients induced by copper toxicity in grapevine rootstocks: Monocropping vs. intercropping

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## HIGHLIGHTS

- 196.17 performs better than Fercal in monocropping systems in Cu toxicity.
- Phenolic compounds are involved in alleviating Cu toxicity.
- The grapevine exudation pattern was influenced by the intercropping with oat.
- Ionic analysis of intercropped plants reveals a competition between plant species.
- The effectiveness of intercropping is rootstock dependent.

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## ABSTRACT

The long-term use of Cu-containing fungicides contaminates vineyards soils, which can induce Cu toxicity and nutrient imbalances in several plant species. The aim of this work was to evaluate the effect of Cu toxicity on two grapevine rootstocks, Fercal and 196.17, and to elucidate if intercropping with oat can alleviate grapevine Cu toxicity. Plants were hydroponically-cultivated and treated with different Cu concentrations. At harvest the biomass accumulation, the SPAD index and the symplastic and apoplastic root and leaves ionome were measured to evaluate possible synergistic and/or antagonistic effects on other micro- and macronutrients. The root exudation analysis was correlated with genes expression (VvPEZ-like), whereas PCA analysis performed on the grapevine and oat ionome revealed that both mono- and intercropped 196.17 rootstock display a positive effect on Zn and Mn in the root tissues at high Cu concentrations. An increase of Zn and Mn in roots was also reported for the intercropped Fercal rootstock at high Cu concentrations while an antagonistic relation was reported for root Zn concentration in the monocropped Fercal rootstock. Our results showed that grapevine and oat compete for nutrient uptake and that this phenomenon can possibly alleviate grapevine Cu toxicity. However, Fercal rootstock is able to take advantage from oat, while 196.17 is disadvantaged by the intercropping system. Even though intercropping system seems to be a valuable tool to counteract grapevine Cu toxicity, the application of this agricultural practice has shown to be species dependent and should be evaluated for each rootstock.

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## 1. Introduction

The use of copper (Cu)-containing fungicides is one of the most widespread used approach in both the organic and integrated cultivation to counteract fungal diseases as the downy mildew (Gessler et al., 2011). However, the repeated application of such

fungicides led to the Cu accumulation in many agricultural soils (Mackie et al., 2012), reaching often toxic concentrations, up to 3215 mg kg<sup>-1</sup> (Mirlean et al., 2007 in Mackie et al., 2012), that can cause plant stress and reduce soil quality and fertility (Brunetto et al., 2016). The features of Cu toxicity in plants have been studied in many different plant species. Generally, Cu accumulates mainly in roots rather than in shoots, even though the different distribution and translocation of Cu depends on its concentration in the root-growing medium (Adrees et al., 2015). Nevertheless, both shoots and roots exhibit specific symptoms of toxicity. At shoot

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level, high Cu concentrations induce a pale green to white interveinal chlorosis on mature leaves altering photosynthesis, enzyme activities and membrane permeability (Brunetto et al., 2016), whilst at root level, Cu reduces root length and leads to root tips darkening and thickening (Feigl et al., 2013). High concentrations of Cu in the growing medium also interfere with the plant mineral nutrition. Several studies reported an alteration of both the macro- and micronutrient content in both shoots and roots, even though these modifications depend on plant tissue and species (De Freitas et al., 2015). To counteract or prevent these effects, plants have evolved different mechanisms. In this respect, low molecular-weight organic compounds released by roots and microorganisms play thereby a fundamental role. In fact, exudates (such as phenolic compounds and carboxylic acids), thanks to their complexing properties, are key actors in both internal and external Cu tolerance strategies: plants mitigate Cu toxicity by either accumulating the metal in their tissues (*internal accumulating mechanism*) or by excluding the metal from root cells, thus preventing its uptake and translocation (*external exclusion mechanism*) (Leitenmaier and Küpper, 2013). Although, the exudation pattern induced by Cu toxicity is plant species specific (Jung et al., 2012), an overview of the general exudation pattern as a consequence of Cu toxicity in cultivated plants like grapevines has never been characterized and correlated with the acquisition rate of the nutrient in the rhizosphere.

With respect in particular to grapevine plants and the consequence of high Cu availability, a reduction in the root growth, ascribable to the nutritional stress, has been reported (Juang et al., 2012). Although this parameter has been shown to depend on the grapevine variety, on the contrary the reduction of shoot development did not result species and/or cultivar-dependent (Romeu-Moreno and Mas, 1999). The preferential accumulation in the root apparatus of Cu has been ascribed to the higher reactivity of this

tissue and it might represent an exclusion mechanism preventing the Cu allocation to the shoot (Juang et al., 2012).

From the agronomic perspective, the possibility to control and to mitigate the Cu toxicity and thus the plant-available Cu fraction in soil is particularly desired, especially by using specific practices. Such methods are based on different principles ranging from phytostabilization, obtained through the addition of inorganic and organic compounds able to immobilize Cu and thus preventing the root uptake, to phytoextraction, which uses hyperaccumulating plants (Mackie et al., 2012). The treatment with CaCO<sub>3</sub> (*i.e.* liming), for instance, has shown to both reduce the Cu bioavailability and increase the availability of calcium (Ca) and magnesium (Mg), thus counteracting the Cu-induced alteration of the root structure (Ambrosini et al., 2015). In addition, Mg can compete with Cu for the root active sites reducing the effects of Cu toxicity (Juang et al., 2014). Recently, phosphorus (P) fertilization has been proposed as an agronomic practice to indirectly prevent the symptoms of Cu toxicity, improving root growth and plant biomass (Baldi et al., 2018) and hindering the competition between Cu and other essential nutrients. In fact, Cu toxicity has shown to reduce the shoot content of macronutrients (Ca, Mg, K and P) most likely due to an interference with the ions uptake and translocation (Kopittke and Menzies, 2006). In this respect, also the root release of organic compounds, featuring a pronounced metal complexing capacity, may be of particular interest. It is interesting to note that when this phenomenon occurs in the rhizosphere of two intercropped plant species (one metal tolerant and one not metal tolerant), it is evident that both can benefit of it (Brunetto et al., 2016), independently from the relative contribution on metal stabilization. For this reason, the agronomic practice of intercropping might represent a promising approach, environment-friendly and sustainable, to mitigate the Cu toxicity in soils that are slightly or moderately contaminated with heavy metals (Brunetto et al., 2016). However,

**Table 1**  
SPAD index, root and shoot biomass (DW) and shoot-to-root ratios of mono- and intercropped Fercal and 196.17 rootstock plants at harvest treated with different Cu concentrations (0, 0.2, 5, 25, 50 µM). SPAD index, root and shoot biomass (DW) and shoot-to-root ratios of oat plants grown either with Fercal or 196.17 rootstock plants are also shown. All SPAD indexes are provided as means of at least 20 leaves ± SE. Small letters indicate significant differences (one way ANOVA) within each growing condition, capital letters indicate significant difference (one way ANOVA) within each grapevine Cu concentration and stars indicate the statistical difference (T-test) within Fercal or 196–17 intercropped oat grown at the same Cu concentration.

Growing condition	0 µM Cu	0.2 µM Cu	5 µM Cu	25 µM Cu	50 µM Cu
<b>SPAD index</b>					
Fercal monocropped	20.9 ± 0.7 <sup>ns,B</sup>	22.7 ± 0.7 <sup>ns,B</sup>	22.9 ± 0.7 <sup>ns,A</sup>	23.7 ± 0.7 <sup>ns,BC</sup>	22.7 ± 0.6 <sup>ns,C</sup>
Fercal intercropped	22.1 ± 0.6 <sup>a,B</sup>	22.5 ± 0.6 <sup>a,B</sup>	22.4 ± 0.6 <sup>a,A</sup>	23.6 ± 0.4 <sup>ab,C</sup>	25.4 ± 0.5 <sup>b,C</sup>
Oat (Fercal)	16.1 ± 0.6 <sup>a,A</sup>	18.3 ± 0.6 <sup>a,A</sup>	21.0 ± 0.6 <sup>b,A</sup>	20.8 ± 0.6 <sup>b,B</sup>	17.9 ± 0.6 <sup>a,A</sup>
196.17 monocropped	19.6 ± 1.8 <sup>ns,B</sup>	20.2 ± 1.7 <sup>ns,AB</sup>	18.4 ± 2.2 <sup>ns,A</sup>	19.3 ± 1.4 <sup>ns,A</sup>	22.1 ± 1.9 <sup>ns,BC</sup>
196.17 intercropped	16.1 ± 0.6 <sup>a,A</sup>	18.5 ± 0.6 <sup>a,A</sup>	21.0 ± 0.6 <sup>b,A</sup>	20.8 ± 0.6 <sup>b,AB</sup>	18.0 ± 0.6 <sup>a,A</sup>
Oat (196.17)	26.33 ± 0.5 <sup>c,C</sup>	26.8 ± 0.6 <sup>c,C</sup>	28.2 ± 0.4 <sup>c,B</sup>	24.0 ± 0.4 <sup>b,C</sup>	20.7 ± 0.6 <sup>a,B</sup>
<b>Shoot biomass</b>					
Fercal monocropped	1130.0 ± 119.0 <sup>b,B</sup>	1078.0 ± 113.4 <sup>b,C</sup>	1120.0 ± 211.8 <sup>b,C</sup>	1254.0 ± 84.8 <sup>b,B</sup>	464.0 ± 155.5 <sup>a,AB</sup>
Fercal intercropped	908.0 ± 110.8 <sup>ns,B</sup>	950.0 ± 26.1 <sup>ns,BC</sup>	794.0 ± 122.5 <sup>ns,BC</sup>	870.0 ± 135.2 <sup>ns,AB</sup>	580.0 ± 100.3 <sup>ns,B</sup>
Oat (Fercal)	32.1 ± 0.5 <sup>bc,***</sup>	32.4 ± 2.3 <sup>bc,*</sup>	36.8 ± 1.4 <sup>c,**</sup>	29.6 ± 2.1 <sup>b,***</sup>	22.3 ± 0.8 <sup>a,**</sup>
196.17 monocropped	331.0 ± 82.2 <sup>ns,A</sup>	623.4 ± 124.8 <sup>ns,AB</sup>	527.4 ± 128.3 <sup>ns,AB</sup>	520.8 ± 138.8 <sup>ns,A</sup>	305.8 ± 44.7 <sup>ns,AB</sup>
196.17 intercropped	248.0 ± 60.1 <sup>ab,A</sup>	517.1 ± 99.5 <sup>b,A</sup>	98.0 ± 46.5 <sup>a,A</sup>	428.0 ± 124.3 <sup>ab,A</sup>	154.0 ± 41.9 <sup>a,A</sup>
Oat (196.17)	52.5 ± 1.8 <sup>c</sup>	40.5 ± 1.3 <sup>b</sup>	48.4 ± 2.8 <sup>bc</sup>	45.4 ± 1.5 <sup>bc</sup>	31.3 ± 2.1 <sup>a</sup>
<b>Root biomass</b>					
Fercal monocropped	108.8 ± 10.9 <sup>ns,B</sup>	109.4 ± 13.0 <sup>ns,C</sup>	99.3 ± 7.2 <sup>ns,C</sup>	78.4 ± 5.5 <sup>ns,NS</sup>	68.5 ± 9.4 <sup>ns,B</sup>
Fercal intercropped	102.1 ± 17.1 <sup>ns,B</sup>	99.2 ± 12.3 <sup>ns,BC</sup>	86.7 ± 14.0 <sup>ns,BC</sup>	77.4 ± 8.6 <sup>ns,NS</sup>	66.7 ± 10.3 <sup>ns,B</sup>
Oat (Fercal)	5.9 ± 0.3 <sup>bc,***</sup>	5.6 ± 0.3 <sup>bc,***</sup>	6.3 ± 0.5 <sup>c,***</sup>	4.7 ± 0.5 <sup>b,***</sup>	2.3 ± 0.1 <sup>a,***</sup>
196.17 monocropped	47.5 ± 9.5 <sup>ns,A</sup>	53.1 ± 11.8 <sup>ns,AB</sup>	52.3 ± 10.4 <sup>ns,AB</sup>	56.5 ± 11.6 <sup>ns,NS</sup>	34.5 ± 3.4 <sup>ns,A</sup>
196.17 intercropped	35.0 ± 5.7 <sup>ns,A</sup>	38.5 ± 10.6 <sup>ns,A</sup>	26.3 ± 7.7 <sup>ns,A</sup>	46.4 ± 6.0 <sup>ns,NS</sup>	41.3 ± 7.4 <sup>ns,AB</sup>
Oat (196.17)	16.4 ± 0.6 <sup>c</sup>	13.7 ± 0.5 <sup>b</sup>	15.0 ± 0.6 <sup>bc</sup>	15.3 ± 0.6 <sup>bc</sup>	10.3 ± 0.7 <sup>a</sup>
<b>Shoot-root ratio</b>					
Fercal monocropped	10.7 ± 1.3 <sup>ab,C</sup>	10.2 ± 0.9 <sup>ab,BC</sup>	11.1 ± 1.7 <sup>ab,B</sup>	16.2 ± 1.2 <sup>b,C</sup>	6.8 ± 2.5 <sup>a,AB</sup>
Fercal intercropped	9.3 ± 0.5 <sup>ns,BC</sup>	10.7 ± 2.0 <sup>ns,BC</sup>	10.0 ± 1.5 <sup>ns,B</sup>	11.3 ± 1.5 <sup>ns,BC</sup>	8.5 ± 0.5 <sup>ns,AB</sup>
Oat (Fercal)	5.8 ± 0.5 <sup>ns,AB</sup>	5.8 ± 0.3 <sup>ns,B</sup>	7.1 ± 1.5 <sup>ns,AB</sup>	7.8 ± 1.5 <sup>ns,AB</sup>	10.0 ± 0.8 <sup>ns,B</sup>
196.17 monocropped	7.0 ± 0.7 <sup>a,ABC</sup>	12.9 ± 1.5 <sup>b,C</sup>	10.3 ± 1.4 <sup>ab,B</sup>	8.5 ± 1.2 <sup>ab,AB</sup>	9.0 ± 1.3 <sup>ab,AB</sup>
196.17 intercropped	6.5 ± 1.5 <sup>a,ABC</sup>	14.8 ± 1.8 <sup>b,C</sup>	3.2 ± 0.6 <sup>a,A</sup>	8.8 ± 1.7 <sup>ab,AB</sup>	3.3 ± 0.7 <sup>a,A</sup>
Oat (196.17)	3.2 ± 0.0 <sup>ns,A</sup>	3.0 ± 0.1 <sup>ns,A</sup>	3.3 ± 0.4 <sup>ns,A</sup>	3.0 ± 0.2 <sup>ns,A</sup>	3.1 ± 0.2 <sup>ns,A</sup>

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