



## Oxidant-antioxidant balance and tolerance against oxidative stress in pioneer and non-pioneer tree species from the remaining Atlantic Forest

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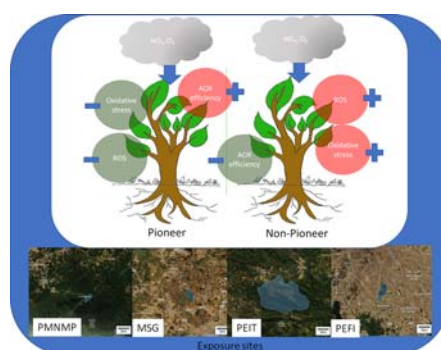
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### HIGHLIGHTS

- We assessed changes in pro-oxidant/oxidant balance in trees from Atlantic Forest.
- Pioneer trees are more tolerant against the oxidative stress than non-pioneer trees.
- Non-pioneer trees presented higher levels of ROS and a less effective antioxidant metabolism.
- Both functional groups maintained similar pro-oxidant/oxidant balance despite the ROS and antioxidant levels.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

#### Article history:

Received 24 September 2017

Received in revised form 20 December 2017

Accepted 21 December 2017

Available online xxx

Editor: Elena Paoletti

#### Keywords:

Antioxidant defenses  
Functional groups  
Reactive oxygen species  
Seasonality  
Tropical tree species

### ABSTRACT

The extensive land occupation in Southeast Brazil has resulted in climatic disturbances and environmental contamination by air pollutants, threatening the Atlantic forest remnants that still exist in that region. Based on previous results, we assumed that pioneer tree species are potentially more tolerant against environmental oxidative stress than non-pioneer tree species from that Brazilian biome. We also assumed that reactive oxygen species (ROS) are accumulated in higher proportions in leaves of non-pioneer trees, resulting in changes in the oxidant-antioxidant balance and in more severe oxidative damage at the cellular level than in the leaves of pioneer trees. We tested these hypotheses by establishing the relationship between oxidants (ROS), changes in key antioxidants (among enzymatic and non-enzymatic compounds) and in a lipid peroxidation derivative in their leaves, as well as between ROS accumulation and oscillations in environmental stressors, thus permitting to discuss comparatively for the first time the oxidant-antioxidant balance and the tolerance capacity of tree species of the Atlantic Forest in SE Brazil. We confirmed that the non-pioneer tree species accumulated higher amounts of superoxide and hydrogen peroxide in palisade parenchyma and epidermis, showing a less effective antioxidant metabolism than the pioneer species. However, the non-pioneer species showed differing capacities to compensate the oxidative stress in both years of study, which appeared to be associated with the level of ROS accumulation, which was evidently higher in 2015 than in 2016. We also applied exploratory multivariate statistics, which revealed that the oscillations in these biochemical leaf responses in both functional groups coincided with the oscillations in both climatic conditions and air pollutants, seemingly showing that they had acclimated

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to the stressful oxidative environment observed and may perpetuate in the disturbed forest remnants located in SE Brazil.

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## 1. Introduction

The extensive land occupation by metropolitan conglomerations, industrial centres and extensive agricultural lands in the southeast region of Brazil has resulted in severe forest fragmentation and also in climatic abnormalities and environmental contamination by air pollutants, which have threatened the Atlantic Forest remnants that still exist in that region (Domingos et al., 2003; Domingos et al., 2015; Brandão et al., 2017).

It is well known that the extremes in temperature generally observed in the tropics, among other natural stressors and air pollutants, may increase the production of reactive oxygen species (ROS), such as singlet oxygen ( $^1\text{O}_2$ ), superoxide anion ( $\text{O}_2^{\bullet-}$ ), hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) and hydroxyl radical ( $^{\bullet}\text{HO}$ ) in plants (Bray et al., 2000; Mittler, 2002; Del Río, 2015). In plants, ROS are also continuously produced as byproducts of various metabolic pathways located in mitochondria and chloroplasts (Foyer et al., 1994a, 1994b; Foyer and Noctor, 2003; Navrot et al., 2007), as well as in nitrogen-fixing nodules (Becana et al., 2000). These species initiate multiple oxidation events in cells and trigger injuries in proteins, pigments, lipids, and nucleic acids (Cheng et al., 2007; Feng and Kobayashi, 2009; Singh et al., 2010; Wujeska et al., 2013). Climatic stressors, in addition to affecting directly the formation, concentration and dispersion of air pollutants, can also modulate the plant responses to air pollution, as already observed in biomonitoring studies performed with *Nicotiana tabacum* “Bel-W3” (Klumpp et al., 2006; Esposito et al., 2009; Dias et al., 2011).

As ROS are an unavoidable consequences of aerobic metabolism (Garg and Manchada, 2009), plants have evolved a robust antioxidant metabolism for scavenging excessive ROS, including: enzymes (e.g., superoxide dismutase, catalase and ascorbate peroxidase) and enzyme gene expression and repairing; hydrophilic (e.g., ascorbate and glutathione) and lipophilic antioxidants (e.g., the carotenoids) and respective regeneration processes (Mittler, 2002; Foyer and Noctor, 2003; Schonhof et al., 2007; Tausz et al., 2007b; Huang et al., 2008, Gill and Tuteja, 2010; Foyer and Shigeoka, 2011; Li and Yi, 2012a, 2012b; Gill et al., 2013). All of the aforementioned processes contribute to keep the oxidant-antioxidant balance, or better the equilibrium between the formation and scavenging of ROS by increased production of antioxidant compounds and to avoid the oxidative injury in the plants. The level of oxidative injury depends on how efficiently the plants activate these antioxidants. Therefore, the tolerance against oxidative stress may be deduced by measuring key markers of the oxidant-antioxidant balance in plants growing in a stressful environment. These measurements may also reveal their ability to perpetuate in disturbed ecosystems (Tausz et al., 2001, 2003; Bussotti, 2008; Wujeska et al., 2013). The analysis of lipid peroxidation derivatives (e.g., malondialdehyde) also adds important information on the susceptibility of plants to oxidative stressors (Pignata et al., 2002; Gratão et al., 2012).

In temperate forests, the determination of leaf markers of the oxidant-antioxidant balance in a few plant species is sufficient for making inferences about the oxidative effects caused by multiple environmental stressors at the ecosystem level (Bassin et al., 2007). However, the high plant biodiversity may impose a barrier to reproducing this ecosystem approach in the Atlantic Forest remnants in SE Brazil. This limitation can be overcome by adopting the principles of functional ecology, which would consist of measuring these key biochemical markers in native species with similar ecological function in the ecosystem, such as those included in the same successional category. The functional approach seems plausible based on a few number of studies

already carried out, including Bussotti (2008) that concluded that early successional species in Mediterranean forests have a lower tolerance against oxidative stress than late secondary species and Favaretto et al. (2011) that classified native tree species of the Atlantic Forest into two major functional groups based on their tolerance against solar radiation exposure.

Brandão et al. (2017) assumed that pioneer species from disturbed remnants of the Atlantic Forest in São Paulo (Brazil) are potentially more tolerant against oxidative stress than non-pioneer species based on the levels of antioxidants. However, this hypothesis would be definitely confirmed only if the lower antioxidant capacity in non-pioneer trees occurred in parallel with increased levels of ROS in the leaves, resulting in loss of the oxidant-antioxidant equilibrium, severe oxidative damage at the cellular level and consequently decreased tolerance against oxidative stress. The present study brought a new contribution to this broader issue, permitting to discuss comparatively the oxidant-antioxidant balance and the tolerance capacity of pioneer and non-pioneer tree species of Atlantic Forest remnants affected by multiple environmental stressors in SE Brazil. We achieved this goal by establishing the relationship between oxidants (ROS), changes in key antioxidants (among enzymatic and non-enzymatic compounds) and in a lipid peroxidation derivative in their leaves, as well as between ROS accumulation and oscillations in environmental stressors.

**Table 1**

Trees species sampled in PEIT (Itacolomi), MSG (Mata de Santa Genebra), PEFI (Ipiranga) and PNMNP (Paranapuacaba). P = pioneer tree species; NP = non-pioneer tree species.

Family/species	Successional	Sampling
	Category	Site
Anacardiaceae		
1. <i>Astronium graveolens</i> Jacq.	NP	MSG
Asteraceae		
2. <i>Eremanthus erythropappus</i> (DC.) McLeisch	P	PEIT
Euphorbiaceae		
3. <i>Alchornea sidifolia</i> Müll. Arg.	P	PEFI
4. <i>Alchornea triplinervia</i> Müll. Arg.	P	MSG
5. <i>Croton floribundus</i> Spreng.	P	MSG
Fabaceae		
6. <i>Machaerium villosum</i> Vogel	NP	PEIT
7. <i>Piptadenia goanocantha</i> (Mart.) J.F. Macbr.	P	MSG
Lauraceae		
8. <i>Ocotea beulahiae</i> J.B. Baitello	NP	MSG
9. <i>Ocotea paranapiacabensis</i> Coe-Teixeira	NP	PNMNP
Melastomataceae		
10. <i>Miconia cabucu</i> Hoehene	P	PEFI, PEIT, PNMNP
11. <i>Tibouchina pulchra</i> Cogn.	P	PNMNP
Meliaceae		
12. <i>Guarea macrophylla</i> Vahl	NP	PEFI, PNMNP
13. <i>Guarea kuntiana</i> A. Juss.	NP	MSG
Myrsinaceae		
14. <i>Myrsine umbellata</i> Mart.	P	PNMNP
Myrtaceae		
15. <i>Amaioua intermedia</i> Mart. ex Schult. & Schult.	NP	PEFI
16. <i>Eugenia excelsa</i> O. Berg	NP	PEFI, PEIT
17. <i>Eugenia cerasiflora</i> Miq.	NP	PEIT
Rubiaceae		
18. <i>Psychotria suterella</i> Müll. Arg.	NP	PNMNP
19. <i>Psychotria vellosiana</i> Benth.	NP	PEIT
Solanaceae		
20. <i>Solanum granulosoleprosum</i> Dunal	P	PEFI
Winteraceae		
21. <i>Drimys brasiliensis</i> Miers	NP	PEIT

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