OPINION

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A unifying explanation for variation in ozone sensitivity among woody plants

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Abstract

Tropospheric ozone is considered the most detrimental air pollutant for vegetation at the global scale, with negative consequences for both provisioning and climate regulating ecosystem services. In spite of recent developments in ozone exposure metrics, from a concentration-based to a more physiologically relevant stomatal flux-based index, large-scale ozone risk assessment is still complicated by a large and unexplained variation in ozone sensitivity among tree species. Here, we explored whether the variation in ozone sensitivity among woody species can be linked to interspecific variation in leaf morphology. We found that ozone tolerance at the leaf level was closely linked to leaf dry mass per unit leaf area (LMA) and that whole-tree biomass reductions were more strongly related to stomatal flux per unit leaf mass ($r^2 = 0.56$) than to stomatal flux per unit leaf area ($r^2 = 0.42$). Furthermore, the interspecific variation in slopes of ozone flux–response relationships was considerably lower when expressed on a leaf mass basis (coefficient of variation, CV = 36%) than when expressed on a leaf area basis (CV = 66%), and relationships for broadleaf and needle-leaf species converged when using the mass-based index. These results show that much of the variation in ozone sensitivity among woody plants can be explained by interspecific variation in LMA and that large-scale ozone impact assessment could be greatly improved by considering this well-known and easily measured leaf trait.

KEYWORDS
leaf mass per area, ozone flux–response relationships, ozone risk assessment, stomatal conductance, stomatal ozone uptake, woody species

1 | INTRODUCTION

Tropospheric ozone (hereafter referred to as 'ozone') causes global losses in productivity of crops, seminatural vegetation and forests equivalent to billions of US dollars annually (Ainsworth, Yendrek, Sitch, Collins, & Emberson, 2012; Avnery, Mauzerall, Liu, & Horowitz, 2011; The Royal Society, 2008). Furthermore, these negative effects on plant growth amplify the rate of ongoing climate change by weakening the carbon sink represented by living terrestrial vegetation, with this indirect climate effect of ozone potentially being of

similar magnitude as its direct radiative forcing effect in the troposphere (Sitch, Cox, Collins, & Huntingford, 2007). Accurately quantifying the impacts of ozone on plants is thus important for projecting both the impacts of atmospheric change on vegetation and the feedback of these impacts to the climate system (Sitch et al., 2007).

While the mechanisms of ozone effects on plants are relatively well understood at the biochemical, physiological, and anatomical levels (e.g. Ainsworth, 2017; Li, Calatayud, Gao, Uddling, & Feng, 2016), the large variation in ozone sensitivity among different tree species and tree functional types remains poorly understood. Large

efforts have been made to relate ozone-induced biomass reduction to the flux of ozone through leaf stomata rather than to the concentration of ozone in the air, with the rationale that the ozone flux into the intercellular air spaces surrounding the mesophyll cells represents the phytotoxically relevant ozone exposure (Matyssek et al., 2007). However, the shift from a concentration-based to a flux-based ozone index did not lead to substantially improved dose–response relationships in meta-analyses including a broad range of tree species (Büker et al., 2015; Karlsson et al., 2004). Interspecific variation in stomatal conductance (g_s) alone, which determines leaf ozone uptake, thus seems to be a rather poor determinant of interspecific variation in ozone sensitivity across a broad range of tree species, in spite of earlier indications to the contrary (Reich, 1987). As a result, large-scale ozone impact assessments for forests currently use dose–response relationships for groups of tree species categorized as 'sensitive' or 'tolerant', but without an understanding of the underlying determinants of this variation in ozone sensitivity (Karlsson et al., 2004, 2007; Sitch et al., 2007).

There are indications that plant traits other than g_s may be important in controlling plant ozone sensitivity. Firstly, leaf antioxidant defense capacity may play an important role, as found in studies with crop species (Betzelberger et al., 2010; Feng, Wang, Pleijel, Zhu, & Kobayashi, 2016). However, multispecies studies with woody species found no relationship between interspecific variation in ozone sensitivity and leaf tissue concentrations of antioxidants (Li et al., 2016; Zhang, Feng, Wang, & Niu, 2012). Furthermore, poor knowledge on how the antioxidative defense capacity varies among plant species and with variation in environmental conditions complicates its use in large-scale ozone impact assessment. Secondly, ozone sensitivity may be influenced by leaf emissions of biogenic volatile organic compounds (BVOC), because BVOC emitted from plants react with ozone in the surrounding air and can thereby decrease the amount of ozone entering the leaf through stomata (Calfapietra et al., 2013; Lerdau, 2007). However, this BVOC-mediated external line of defense is also difficult to account for in large-scale applications since the magnitude of this effect remains poorly understood (Calfapietra et al., 2013; Loreto & Schnitzler, 2010).

Thirdly, there are indications that plant sensitivity to ozone is linked to leaf morphological traits. Studies with single tree species have found that variation in ozone sensitivity among *Betula pendula* clones was related to variation in leaf thickness (Karlsson et al., 2007) and that ozone tolerance in *Neolitsea sericea* was associated with leaf hairiness (Zhang et al., 2012). Furthermore, there are indications that differences in ozone sensitivity among species may be negatively related to leaf thickness (Pihl Karlsson, 2003) or leaf mass per unit area (LMA; Bussotti, 2008; Zhang et al., 2012; Li et al., 2016). Such a link seems plausible since the oxidative stress caused by a given amount of stomatal ozone flux per unit leaf area would be distributed over a larger leaf mass, and hence diluted, in a leaf with high LMA. Since LMA is a readily available and easily measured leaf trait, the derivation of significant quantitative relationships between LMA and plant ozone sensitivity could potentially allow for improvements in large-scale ozone risk and impact assessments. Despite its wide use in environmental physiology for converting between area- and mass-based expression of physiological parameters (e.g. Duursma & Falster, 2016; Poorter, Niinemets, Poorter, Wright, & Villar, 2009), no meta-analysis has yet been conducted to explore the role of LMA in explaining the large interspecific variation in plant ozone sensitivity.

The overall aim of this study was to explore if the large and hitherto unexplained interspecific variation in ozone sensitivity among woody species to a large extent can be explained by variation in LMA, such that species with high LMA (and thus lower ozone load per unit leaf mass) have lower ozone sensitivity. Plant responses used in our meta-analyses include the onset of ozone-induced leaf visible injury as well as whole-plant biomass reductions, both available from a large number of experiments. The following two hypotheses were tested: (i) differences in the onset of ozone-induced visible leaf injury among woody species are more strongly related to LMA than to g_s; (ii) interspecific variation in ozone impacts on tree biomass production is linked to variation in LMA, making a multispecies dose–response relationship with stomatal ozone flux expressed on a leaf mass basis superior to the leaf area-based relationship currently used.

2 | MATERIALS AND METHODS

2.1 | Visible injury

Relationships of the onset of visible ozone injury with LMA, g_s and the g_s to LMA ratio were explored using data from 57 tree species studied in ozone experiments conducted in regions with subtropical, temperate and Mediterranean climates. To be comparable across experiments, we only considered studies reporting the accumulated hourly ozone concentrations over a cut-off threshold of 40 ppb (AOT40_injury) at the onset of ozone-induced visible leaf injury. The AOT40_injury value was calculated from the start of the experiment until the date that the first ozone-induced foliar injury appeared. Ozone-induced visible injury was assessed using the naked eye; see Zhang et al. (2012) for a description of the methodology. The response variable AOT40_injury is linked to leaf functioning, as shown by the strong correlation of AOT40_injury and ozone-induced reductions in photosynthesis in a previous study with 29 woody species (Li et al., 2016). Results of AOT40_injury reported hitherto in the Web of Science (Thompson-ISI, Philadelphia, PA, USA) were collected (Table S1). When there were several ozone treatments in the same experiment and/or when AOT40_injury data for a species were reported from multiple experiments (for five species), the average species-specific AOT40_injury value was used.

If possible, species-specific values of the LMA of sun leaves were taken from the experiments providing AOT40_injury data (30 species). If experiment-specific LMA data were not available, LMA values were taken from the dataset of Royer, Peppe, Wheeler, and Niinemets (2012; 13 species). For the remaining species, LMA data

were searched for in the Web of Science (Thompson-ISI, Philadelphia, PA, USA) and were found for 13 out of 14 species.

Species-specific values of g_s were mostly (47 species) taken from the AOT40_injury experiments. For five species, g_s data were obtained from other studies, while no suitable g_s data were found for the remaining five species. Since g_s varies greatly with environmental conditions, care was taken to, as far as possible, use values recorded under conditions favorable for maximum stomatal opening. All g_s data were measured at light saturation, and in most cases predominantly before noon (all except 11 species). In 12 studies, the highest values of g_s recorded (e.g. the 95% percentile) were used. For the species where g_s data were taken from the AOT40_injury studies, we used data from the low-ozone charcoal-filtered treatment only. Excluding the 15 species for which experiment-specific or prenoon g_s data were not available from the analyses did not significantly change the relationships of AOT40_injury vs. g_s, LMA or the g_s to LMA ratio shown below (data not shown). Values of g_s reported here are expressed for ozone and were converted from water vapor basis by multiplying with 0.663 as suggested by Grünhage et al. (2012). Data and references for LMA and g_s data are provided in Table S2.

2.2 | Biomass reductions

Ozone-induced biomass reductions of juvenile trees of nine European species studied in 24 experiments were related to accumulated stomatal ozone flux. The biomass and ozone flux data used in this analysis were taken from a synthesis by Büker et al. (2015); details of the original experiments used in this synthesis are listed in Table S3. In the present study, stomatal ozone flux was expressed either on a leaf area basis or on a leaf mass basis to compare the ability of the two indices to account for interspecific variation in ozone impacts on tree growth. The leaf area-based ozone flux index represents the index currently used within the Convention on Long-Range Transboundary Air Pollution (LRTAP Convention, 2010) under the United Nations Economic Commission for Europe (UNECE), while the mass-based index has not previously been used for deriving ozone dose–response relationships or making impact assessments for vegetation. The leaf mass-based stomatal ozone flux is simply the area-based flux divided by LMA, using the same species-specific LMA data as in the leaf-level dataset described above.

The 'phytotoxic ozone dose' (POD), defined as the stomatal ozone flux accumulated over a certain cut-off threshold, was calculated for field experiments with nine European tree species as described in Büker et al. (2015), using species-specific g_s model parameterizations for all species. The definitions of the flux dose accumulation period in each experiment were also the same as in Büker et al. (2015), covering >60% of the vegetation growing season in all experiments. POD was calculated on a projected leaf area basis using the index $POD_{Y} = 1$ (stomatal flux accumulated over an area-based flux cut-off threshold of $Y = 1$ nmol m^{-2} s^{-1}), as well as on a leaf mass basis using the index POD_X (X represents the mass-based flux threshold). The area-based cut-off threshold of

$Y = 1$ nmol m^{-2} s^{-1} represents the threshold currently used for area-based ozone flux–response relationships for trees by the LRTAP Convention (2010). This cut-off threshold corresponds to a mass-based cut-off threshold of $X = 0.006$ nmol g^{-1} s^{-1} for Picea abies (LMA = 177 g/m^2) and $X = 0.019$ nmol g^{-1} s^{-1} for B. pendula (LMA = 52 g/m^2), the two species with the largest number of data points in the dataset (Table S4).

For multiyear experiments, we normalized both dose and biomass response data to a single-year basis. For dose data, the mean value across years was used. For relative biomass data, we assumed a constant proportional biomass reduction for all years, using the following equation:

$$RB_{year} = RB_{total}^{1/yr}$$

where RB_{year} is the relative biomass expressed for a single growing season (a value between 0 and 1, with 1 being the relative biomass at zero ozone dose); RB_{total} is the relative biomass at the time of harvest; yr is the number of growing seasons from the start of the ozone fumigation until the time of harvest (LRTAP Convention, 2010).

3 | RESULTS

The external ozone exposure at which visible injury was detected (i.e. AOT40_injury) was significantly and positively related to LMA (Figure 1a; $p < .001$) and negatively related to g_s (Figure 1b; $p = .004$) across 57 species. The relationship with LMA ($r^2 = 0.31$) was linear and considerably stronger than the relationship with g_s ($r^2 = 0.15$), which was nonlinear and better described with a negative logarithmic function. We further investigated the residuals of these functions to examine whether the relationships of LMA and g_s with AOT40_injury were independent. The residuals of the LMA–AOT40_injury relationship were significantly related to g_s (Figure 2a; $p = .003$, $r^2 = 0.16$) and the residuals of the g_s–AOT40_injury relationship were significantly related to LMA (Figure 2b; $p < .001$, $r^2 = 0.33$), demonstrating that the onset of visible injury was independently linked to both LMA and g_s. Stomatal conductance and LMA were not significantly correlated ($r^2 = 0.001$, $p = .79$; data not shown). This was further illustrated by AOT40_injury being more strongly related to the g_s to LMA ratio (Figure 1c; $p < .001$, $r^2 = 0.37$) than to these two variables individually (Figure 1a,b). The g_s to LMA ratio is a measure of stomatal conductance expressed on a leaf mass basis.
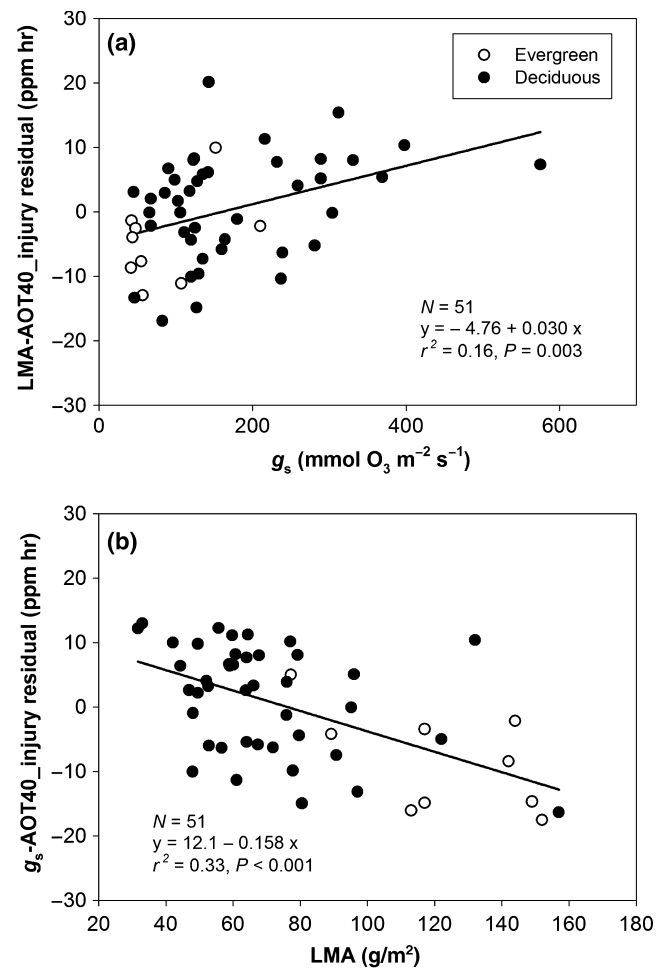
The average values of LMA and AOT40_injury were markedly lower in broadleaf deciduous species (68 g/m^2 and 16 ppm hr, respectively) than in needle-leaf evergreen species (122 g/m^2 and 31 ppm hr, respectively; Figure 1a). The leaf-level results (Figures 1 and 2) demonstrate that interspecific variation in leaf ozone sensitivity in woody plants is linked to LMA, and that LMA seems to be a more important predictor of ozone sensitivity than g_s.

Whole-tree biomass reductions in nine European tree species were related to the stomatal ozone flux expressed on both leaf area
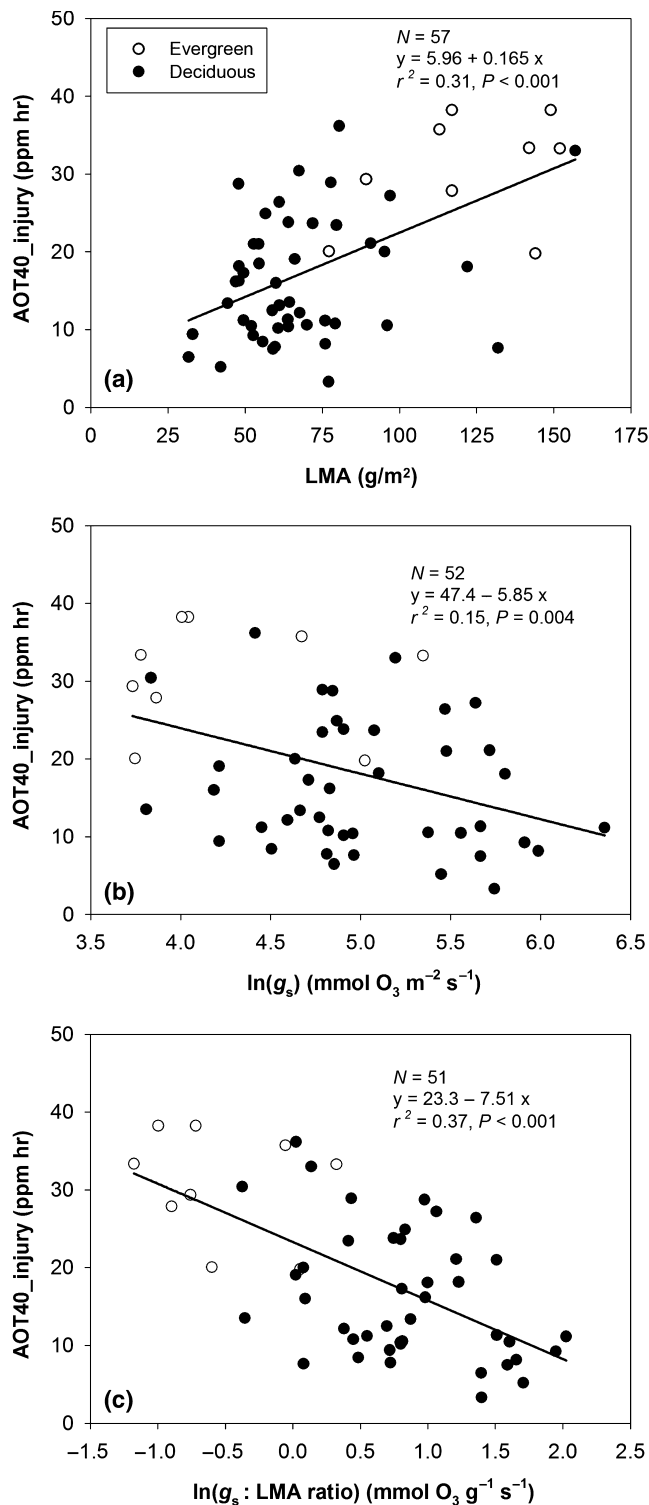
FIGURE 1 The AOT40 (accumulated ozone exposure over a concentration threshold of 40 nmol/mol) at the onset of visible leaf injury (AOT40_injury) in relation to leaf mass per unit area (LMA) (a), stomatal conductance (g_s) (b) and the g_s to LMA ratio in woody species (c). For data on specific species, see Tables S1 and S2


FIGURE 2 The residuals of (a) the LMA–AOT40_injury relationship in Figure 1a plotted against g_s, and (b) the residuals of the g_s–AOT40_injury relationship in Figure 1b plotted against LMA. AOT40_injury = the accumulated ozone exposure over a concentration threshold of 40 nmol/mol at the onset of visible leaf injury; g_s = stomatal conductance; LMA = leaf mass per unit area

(POD_Y) and leaf mass (POD_X) basis. The flux–response relationship was markedly stronger for $POD_{X = 0.006}$ ($r^2 = 0.56$; Figure 3b) and $POD_{X = 0.019}$ ($r^2 = 0.57$; Fig. S1) than for $POD_{Y = 1}$ ($r^2 = 0.42$;

Figure 3a). Broadleaf and needle-leaf species exhibited similar flux–response relationships based on $POD_{X = 0.006}$ or $POD_{X = 0.019}$ while the $POD_{Y = 1}$ relationship was substantially steeper for broadleaf compared to needle-leaf species. Furthermore, the coefficient of variation (CV) for species-specific slopes of relative biomass plotted against $POD_{Y = 1}$ or $POD_{X = 0.006}$ was considerably lower for the mass-based index $POD_{X = 0.006}$ (CV = 36%) than for the area-based index $POD_{Y = 1}$ (CV = 66%; Figure 4). Finally, the species-specific slopes of relative biomass plotted vs. AOT40 (taken from Büker et al., 2015) were more closely related to the variation in the g_s to LMA ratio (representing a leaf mass-based conductance) than to the two traits individually (Fig. S2). The relationship with LMA was rather weak and statistically nonsignificant ($p = .21$), while the relationship with g_s was driven by one single data point (species). By contrast, the relationship with the g_s to LMA ratio was consistent, strong ($r^2 = 0.69$) and statistically significant ($p = .011$).

The $POD_{X = 0.006}$ relationship was better than the $POD_{X = 0.019}$ relationship as judged by the intercept and distribution of
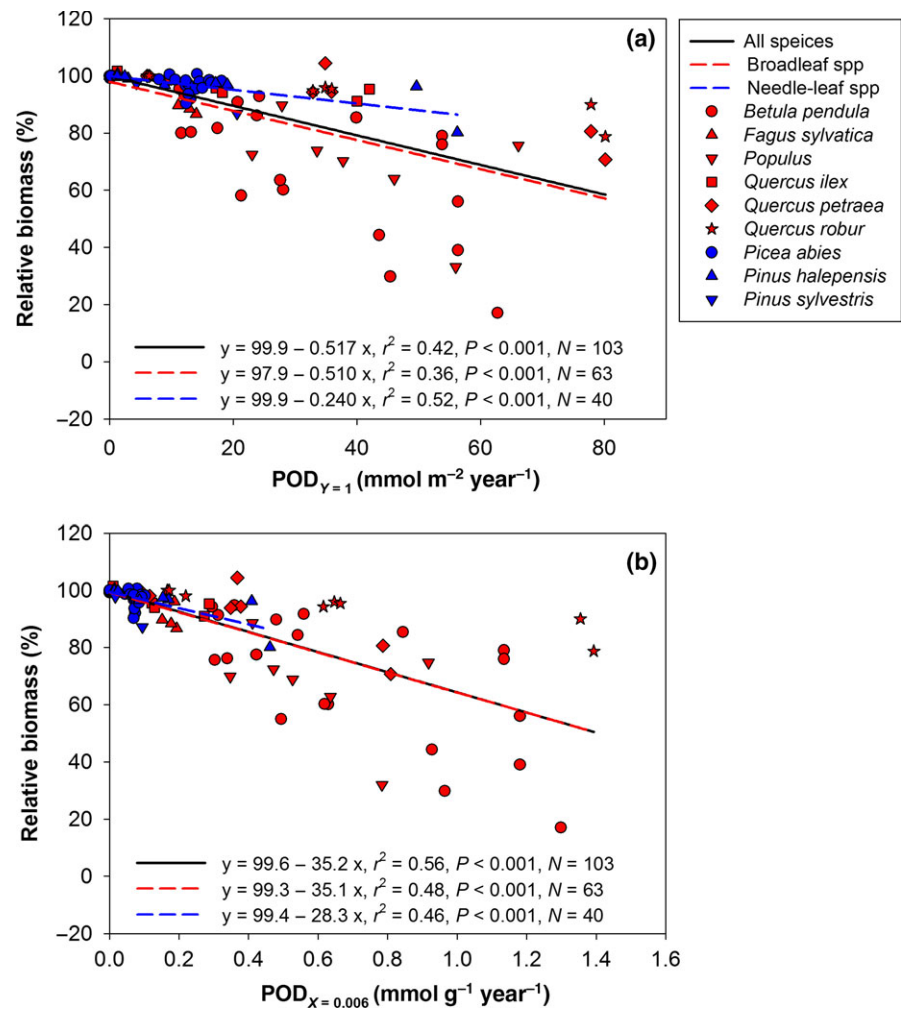
FIGURE 3 Relative biomass of nine European tree species plotted against the annual phytotoxic ozone dose (POD$_\#$; # is a cut-off threshold) expressed per unit leaf (a) area and (b) mass. Relative biomass and POD$_\#$ data from multiyear experiments are normalized to a single-year basis (see Section 2). The dashed red and blue lines represent the regressions of broadleaf and needle-leaf species, respectively, while the solid black line represents the general relationship across all species
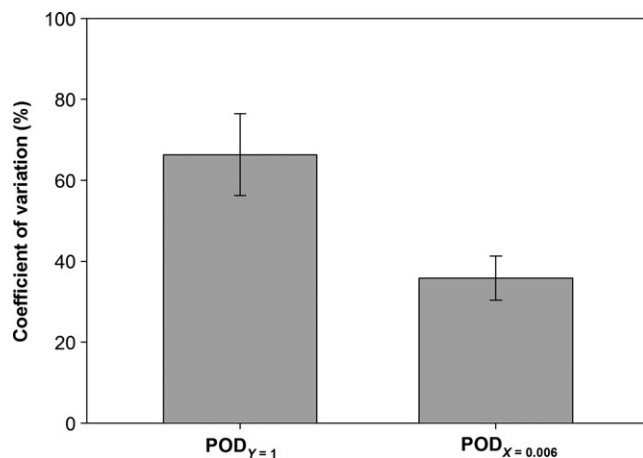
FIGURE 4 The coefficient of variation ($\pm$95% confidence interval) for species-specific slopes of relative biomass plotted against the phytotoxic ozone dose expressed per unit leaf area (POD$_{Y = 1}$; see Figure 3a) or leaf mass (POD$_{X = 0.006}$; see Figure 3b) of eight European tree species. All eight species with more than two data points in the dataset were included in the analysis, excluding *Pinus sylvestris* with two data points only

residuals for needle-leaf species, which had many data points with substantial biomass reductions at low values of POD$_{X = 0.019}$ (Fig. S1).

4 | DISCUSSION

The analyses of this study demonstrate that variation in the simple leaf trait LMA accounts for a large part of the great interspecific variation in ozone sensitivity among woody plant species (Figures 1–3). A significant part of the variation in AOT40_injury was explained by the ratio of g_s to LMA (Figure 1c), i.e. the g_s for leaf ozone uptake expressed per unit leaf mass. For ozone-induced whole-plant biomass reductions, a stomatal ozone flux index expressed on a leaf mass basis ($r^2 = 0.56$) outperformed the leaf area-based ozone flux index ($r^2 = 0.42$, Figure 3) currently used by the LRTAP Convention (2010). Furthermore, about half of the interspecific variation in ozone impacts on biomass production was accounted for by using LMA to convert from an area-based to a mass-based ozone index (Figure 4), and relationships for evergreen and deciduous species converged (Figure 3).

Several mechanisms could potentially explain why species with high LMA are less sensitive to O_3 (at a given external ozone exposure). The simplest explanation is perhaps that they have a lower ozone load per unit leaf mass (i.e. a dilution effect). Leaves with high LMA often have a thick and/or dense palisade mesophyll layer (Li et al., 2016), meaning that the internal ozone exposure per unit mesophyll cell mass will be lower in species with such leaves. Another possible explanation of ozone tolerance in species with high LMA could be a so called cross-protection. Species with high LMA are generally considered to be more tolerant to abiotic and biotic stress than species with low LMA (Bussotti, 2008; Gutschick, 1999). The evolutionary adaptations of such stress-tolerant species with high LMA are likely to have conferred protection against today's elevated ozone concentrations (Bussotti, 2008), since most environmental stress factors indirectly induce oxidative stress in plants (Sharma, Jha, Dubey, & Pessarakli, 2012). Plant traits contributing to cross-protection may be morphological (e.g. sclerophylly), physiological (stomatal conductance) or biochemical (e.g. antioxidant defense), as discussed by Bussotti (2008). A recent study with 29 woody species showed that interspecific variation in ozone sensitivity was significantly related to variation in area-based total leaf antioxidant capacity, but not to variation in mass-based antioxidant capacity or total phenols (Li et al., 2016). Lastly, it is possible that leaves with high LMA are less ozone sensitivity as a consequence of having a higher apoplastic leaf fraction compared to leaves with low LMA, as suggested by Niinemets (1999). The antioxidants of the apoplast have been proposed to play a key role in decreasing the amount of ozone (and its oxidation products) reaching the plasmalemma (Dizengremel, Jolivet, Tuzet, Ranieri, & Le Thiec, 2013; Feng et al., 2010).

Regardless of the underlying mechanisms explaining lower ozone sensitivity in species with high LMA, our results demonstrate that consideration of this easily measured and well-known leaf trait has the potential to account for much of the interspecific variation in ozone sensitivity among woody species. Large-scale application of a leaf mass-based stomatal ozone flux index is straightforward since LMA data are available for a large number of woody species as well as for different tree functional types and is readily employed in models (Duursma & Falster, 2016; Poorter et al., 2009). Meta-analyses have shown that LMA itself is not much affected by elevated O_3 and the use of LMA as an O_3 sensitivity indicator is thus not complicated by bidirectional causality of the LMA–ozone sensitivity relationship (Poorter et al., 2009).

To move from a leaf area-based to a leaf mass-based stomatal ozone flux index is a much easier step than the step from a concentration-based to an area-based stomatal flux ozone index, which has occupied much of the ozone risk and impact assessment research community over the past couple of decades (Büker et al., 2015; Emberson, Wieser, & Ashmore, 2000; Karlsson et al., 2004, 2007). We have shown here that a shift to a mass-based stomatal flux index represents a substantial improvement in accounting for variation in ozone sensitivity among tree species (Figures 3 and 4), something which was not accomplished by moving from a concentration to a leaf area-based ozone flux index (Büker et al., 2015; Karlsson

et al., 2004, 2007). A leaf mass-based stomatal ozone flux index simplifies large-scale impact assessment for trees since it potentially allows for one common dose–response relationship for all tree species (Figure 3b), removing the need for previous classifications of tree species into different groups (e.g. broadleaf vs. needle-leaf, 'sensitive' vs. 'tolerant', gymnosperms vs. angiosperms; Karlsson et al., 2004, 2007; Wittig, Ainsworth, & Long, 2007; Wittig, Ainsworth, Naiduz, Karnosky, & Long, 2009). Although we have showed here that the greater ozone sensitivity in needle vs. broadleaf species can be accounted for by considering differences in LMA, more experimental data on tropical evergreen tree species are critically needed to evaluate if the relationship presented here holds for this biome as well. In the future, consideration of variation in within-leaf anatomy, antioxidant defense capacity and BVOC emissions would likely further improve dose–response relationships for vegetation. For the time being, however, the simple consideration of LMA (dividing area-based stomatal flux by LMA) alone represents a substantial step forward in ozone risk and impact assessment.

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SUPPORTING INFORMATION

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