Developing Ozone Risk Assessment for Larch Species

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Ozone (O3) risk assessment for the protection of forests requires species-specific critical levels (CLs), based on either O3 concentrations (AOT40) or stomatal uptake (PODY) accumulation over the growing season. Larch (Larix sp.) is a genus with O3-susceptible species, widely distributed in the northern hemisphere and with global economic importance. We analyzed published and unpublished data of Japanese larch (Larix kaempferi) and its hybrid F1 (Larix gmelinii var. japonica × L. kaempferi) stomatal responses for developing a parameterization of stomatal conductance model and estimating PODY-based CLs with two Y thresholds, that is, 0 and 1 nmol m−2 s−1 projected leaf area (PLA). In parallel, we estimated AOT40-based CLs. The results show that the AOT40-based CLs for a 2% and 4% biomass loss in Japanese larch were 5.79 and 11.59 ppm h, that is, higher than those in hybrid larch F1 (2.18 and 4.36 ppm h AOT40), suggesting a higher O3 susceptibility of the hybrid. However, the use of PODY reconciled the species-specific differences, because the CLs were similar, that is, 9.40 and 12.00 mmol m−2 POD0 and 2.21 and 4.31 mmol m−2 POD1 in Japanese larch versus 10.44 and 12.38 mmol m−2 POD0 and 2.45 and 4.19 mmol m−2 POD1 in the hybrid, for 2% and 4% biomass loss, respectively. Overall, the CLs were lower than those in other forest species, which suggests a relatively high susceptibility of these larches. These results will inform environmental policy-makers and modelers about larch susceptibility to O3.

Keywords: critical level, DO3SE model, forest, larch, parameterization, tropospheric ozone

INTRODUCTION

Tropospheric ozone (O3) is the most widespread phytotoxic air pollutant (Mills et al., 2018). In the period 1995–2014, control measures were effective in North America and Europe, as indicated by a decrease of O3 concentrations, while a significant increase in O3 concentrations occurred in East Asia (Chang et al., 2017; Mills et al., 2018). Ozone has a strong oxidative capacity and may cause severe injury to forests (Paoletti, 2007; Li et al., 2017). To assess O3 risk to forests, different metrics have been developed (Lefohn et al., 2018). One of the most common metrics is AOT40, that is, the accumulated exposure over an hourly threshold of 40 ppb during the growing season, although there is a general consensus that the accumulated stomatal O3 flux – or phytotoxic ozone dose (POD) – is more biologically meaningful as it estimates the amount of O3 actually entering the plants through the stomata (Paoletti and Manning, 2007). A flux threshold Y below which O3 uptake is not expected to be injurious to plants has been postulated. For all tree species, a uniform threshold of Y = 1 nmol m−2 s−1 projected leaf area (PLA) was recommended by the
For the protection of susceptible vegetation from O₃, critical levels (CLs) are recommended, defined as the “concentration, cumulative exposure or cumulative stomatal flux of atmospheric pollutants above which direct adverse effects on susceptible vegetation may occur according to present knowledge” (CLRTAP, 2017). CLs are derived for either a 2% (Norway spruce) reduction or a 4% (beech/birch, Mediterranean deciduous and evergreen species) reduction in annual new growth (based on aboveground, root, or whole-tree biomass) of young trees up to 10 years old. AOT40-based CLs for tree biomass loss (5%) are available for Fagus sylvatica and Betula pendula in a previous version of the ICP Vegetation manual (CLRTAP, 2014; AOT40-based CLs are not included in the latest version) and for some other species in the literature (e.g., 18 Japanese species including CLs are not included in the latest version). A threshold of 0 nmol m⁻² s⁻¹ PLA was also recommended, if we assume that all O₃ molecules induce a physiological reaction after uptake (De Marco et al., 2015, 2016; Anav et al., 2016), which is a plausible assumption in the light of low-dose adaptive responses (Agathokleous et al., 2019).

Our aim was to collate published and unpublished data from previous experiments for developing a parameterization of the DO₃SE model for Japanese larch and its hybrid F₁ and estimating the CLs not to be exceeded for the protection of these larch species from O₃. Based on published research documenting a higher O₃ susceptibility of the faster-growing hybrid F₁ than the slower-growing Japanese larch (Agathokleous et al., 2017; Sugai et al., 2018), we hypothesized that the CLs of hybrid F₁ have a lower susceptibility than that of the wild Japanese larch.

**MATERIALS AND METHODS**

A literature survey was conducted in Web of Science (9 December 2019), with the keywords “ozone” and “larix” or “larix” (search method: Topic). All the identified papers (n = 33 and 36 for each combination; most were duplicates) were reviewed for relevance, including whether they reported O₃ and biomass data. Finally, data on O₃ concentrations, exposure duration, and total biomass were collected from six published experiments carried out in open-top chambers (OTCs) (Table 1: Matsumura, 2001; Watanabe et al., 2006; Koike et al., 2012; Wang et al., 2015; Sugai et al., 2018, 2019) and used to calculate AOT40 and percentage losses of biomass relative to controls in low-O₃ air. Data from combined experiments, such as O₃ with either fertilization or CO₂, were not included. Data of Dahurian larch (L. gmelinii var. japonica) from the same experiments were not included because of scarcity, thus being insufficient for analysis.

Individual measurements of stomatal conductance across a range of environmental conditions were obtained from the authors Sugai et al. (2018, 2019) and Agathokleous (unpublished). Measurements by Agathokleous (unpublished) were carried out in field-grown 2-year-old larch seedlings at the Sapporo experimental forest, Hokkaido University, in Japan (Table 1). All measurements were carried out by means of Li-Cor 6400 gas analyzers (Li-Cor Inc., Lincoln, NE, United States). As soil water content measurements were missing, we used the following simplified formula for the estimation of the stomatal conductance gsto in the DO₃SE model (CLRTAP, 2017):

\[ g_{sto} = g_{max} \times f_{light} \times \max\{f_{min}, (f_{temp} \times f_{VPD})\} \] (1)

where \(g_{max}\) is the maximum stomatal conductance of either Japanese larch or its hybrid F₁, \(f_{min}\) is the species-specific minimum stomatal conductance, and \(f_{light}\), \(f_{temp}\), and \(f_{VPD}\) account for the effects of photosynthetic photon flux density (PPFD), air temperature (T), and vapor pressure deficit (VPD), respectively.
respectively, on stomata. Parameterization was carried out using a boundary line analysis (Alonso et al., 2008; Braun et al., 2010; Hoshika et al., 2012). First, the g_{st_o} data were divided into classes with the following stepwise increases for each variable: 200 µmol photons m^{-2} s^{-1} for PPFD (when the values were less than 200 µmol photons m^{-2} s^{-1}, PPFD classes at 50 µmol photons m^{-2} s^{-1} steps were adopted), 2°C for T, and 0.2 kPa for VPD. A function was fitted against each model variable based on 95th percentile values per class of environmental factors. Values of g_{max} and f_{min} were calculated as the 95th percentile and 5th percentile, respectively (Hoshika et al., 2012; Bičárová et al., 2019). For details of f_{light}, f_{temp}, and f_{VPD}, see CLRTAP (2017).

Stomatal O3 uptake (F_{st}; nmol m^{-2} s^{-1}) was calculated as follows:

\[ F_{st} = [O_3] \cdot g_{st_o} \cdot \frac{r_c}{r_b + r_c} \]  \hspace{1cm} (2)

where r_c is the leaf surface resistance [= 1/(g_{st_o} + g_{ext}); s m^{-1}] and g_{ext} is the external leaf or cuticular conductance (= 0.0004 m s^{-1}, CLRTAP, 2017). The standard DO3SE model considers the leaf boundary layer resistance (r_b):

\[ r_b = 1.3 \cdot 150 \cdot (L_d/u)^{0.5} \]  \hspace{1cm} (3)

where the factor 1.3 accounts for the difference in diffusivity between heat and O3, 150 is the empirical constant, L_d is the cross-wind leaf dimension (0.008 m for conifers, CLRTAP, 2017), and u is the wind speed. The wind speed data were not available in collected literatures. However, in OTCs, since a constant ventilation from the blowers is realized, r_b is less important compared with stomatal resistance (r_{sto}) (Unsworth et al., 1984; Uddling et al., 2004; Tuovinen et al., 2009). This is supported by the fact that the r_b/r_c ratio was small in the present study when assuming that r_{sto} was r_{sto,min} (= 1/g_{max}) and wind speed was constant inside a chamber (r_b/r_c = 0.07 and 0.06 at 1 m s^{-1} and 0.05 and 0.04 at 2 m s^{-1} of wind speed in hybrid and Japanese larch, respectively). Here, we assumed that r_b was negligible for the calculation of F_{st}.

PODY (nmol m^{-2} s^{-1}) was estimated from hourly data as follows:

\[ \text{PODY} = \sum_{i=1}^{n} (F_{st,i} - Y) \cdot \Delta t \]  \hspace{1cm} (4)

where Y is a species-specific threshold of stomatal O3 uptake (nmol m^{-2} s^{-1}) and Δt = 1 h is the averaging period. F_{st,i} is the ith hourly stomatal O3 uptake (nmol m^{-2} s^{-1}), and n is the number of hours included in the calculation period. Y is subtracted from each F_{st,i} when F_{st,i} > Y. PODY was then estimated based on hourly data of air temperature, solar photosynthetic active radiation, and VPD as registered locally and accumulated over the duration of the experiments from the six papers (Table 1). Data from Matsumura (2001) and Watanabe et al. (2006) were excluded from this analysis because of missing meteorological data.

To establish PODY-based dose-response relationships, two representative values of Y (= 0 or 1 nmol m^{-2} s^{-1}) were tested. This is because CLRTAP (2017) suggested POD1 to be suitable for biomass assessment in elevated O3 while several

**TABLE 1** Details of experiments from which data were obtained for the analysis (PODY, AOT40, and Gs model).

| References        | Species                             | Experimental setup | Duration                        | Exposure level | Other treatments | Type of assessment |
|-------------------|-------------------------------------|--------------------|---------------------------------|----------------|------------------|-------------------|
| Koike et al. (2012) | Larix kaempferi & Larix gmelinii var. japonica | OTC                | June–September 2010             | CF, NF60       | Elevated CO2     | PODY/AOT40        |
| Matsumura (2001)  | L. kaempferi                        | OTC                | June 1993–September 1995        | CF, NF         | n.a.             | AOT40             |
| Sugai et al. (2018) | L. kaempferi                        | OTC                | June 2013–September 2014        | CF, NF, NF40, NF60 | n.a.              | PODY/AOT40/Gs model |
| Sugai et al. (2019) | L. kaempferi                        | OTC                | June 2015–August 2016           | CF, NF90, NF60 | n.a.             | PODY/AOT40/Gs model |
| Koike et al. (2012) | F Iran & Larix gmelinii var. japonica | OTC                | June 2013–September 2014        | CF, NF, NF40, NF60 | n.a.              | PODY/AOT40/Gs model |
| Wang et al. (2015) | F Iran & Larix gmelinii var. japonica | OTC                | July 2011–September 2012        | CF, NF60       | n.a.             | PODY/AOT40        |
| Watanabe et al. (2006) | L. kaempferi                        | OTC                | April 2004–September 2005       | CF, AA, 1.5AAA, 2.0AA | Nitrogen addition | AOT40             |
| Agathokleous (unpublished) | L. kaempferi                        | Field              | June–August 2015                | n.a.           | n.a.             | Gs model          |
|                     | F Iran & Larix gmelinii var. japonica | Field              | August 2017                     | n.a.           | n.a.             | Gs model          |

OTC, open-top chamber; CF, charcoal-filtered air; NF, non-filtered air; NF40, 40 ppb O3; NF60, 60 ppb O3; AA, ambient O3 concentration; 1.5AA, 1.5 times ambient O3 concentration; 2.0AA, twice ambient O3 concentration; n.a., not available.
studies reported a better performance of POD0 rather than POD1 for O3 risk assessment (e.g., Sicard et al., 2016). CLs were estimated for a total biomass reduction of both 2% as suggested for deciduous species and 4% as suggested for non-Mediterranean conifer species (CLRTAP, 2017). In addition, since CLRTAP (2017) provided an AOT40-based CL corresponding to a 5% biomass reduction for forests, the CLs for the 5% biomass reduction were also shown. For PODY, CLs were calculated, referring to a "REF10" PODY calculated at a constant O3 concentration of 10 ppb referring to a “pre-industrial” O3 concentration, as recommended by CLRTAP (2017).

Simple linear regression analyses were used to assess the relationships between O3 indices (AOT40, POD0, and POD1) and relative biomass. In addition, to compare the $g_{\text{max}}$ values between the two larches, Student’s $t$-test was performed on values within the top five percentile in $g_{\text{sto}}$ data. Results were considered significant at $p < 0.05$. All the analyses were performed using R 3.5.1 (R Core Team, 2018).

## RESULTS

The parameterization of the stomatal conductance model (Figure 1) resulted in very similar values for Japanese larch and its hybrid $F_1$ (Table 2). The $g_{\text{max}}$ in hybrid larch was slightly higher than that in Japanese larch although $g_{\text{max}}$ values in the two larches were not statistically different ($p = 0.48$, Student’s $t$-test for the values within the top five percentile in $g_{\text{sto}}$, data not shown). On

### TABLE 2 | DO3 SE model parameters for Japanese larch and hybrid $F_1$, where $g_{\text{max}}$ is maximum stomatal conductance; $f_{\text{min}}$ is minimum stomatal conductance; $f_{\text{light}}$ is a parameter determining the shape of the hyperbolic relationship of stomatal response to light; $T_{\text{max}}$, $T_{\text{opt}}$, and $T_{\text{min}}$ are the maximum, optimal, and minimum temperatures, respectively, for calculating the function $f_{\text{temp}}$ that expresses the variation of $g_{\text{sto}}$ with temperature; VPD$_{\text{min}}$ and VPD$_{\text{max}}$ are the vapor pressure deficit for attaining minimum and maximum stomatal aperture, respectively ($f_{\text{VPD}}$).

| Parameter         | Japanese larch | Hybrid $F_1$ |
|-------------------|----------------|-------------|
| $g_{\text{max}}$, mmol O$_3$ m$^{-2}$ PL A s$^{-1}$ | 120 [95% CI: 103–188] | 140 [95% CI: 110–225] |
| $f_{\text{min}}$, fraction | 0.16 | 0.09 |
| $f_{\text{light}}$, µmol m$^{-2}$ s$^{-1}$ | 0.0097 | 0.0096 |
| $T_{\text{min}}$, °C | 5 | 5 |
| $T_{\text{opt}}$, °C | 25 | 25 |
| $T_{\text{max}}$, °C | 40 | 40 |
| VPD$_{\text{max}}$, kPa | 1.6 | 1.6 |
| VPD$_{\text{min}}$, kPa | 4.0 | 4.2 |

CI denotes confidence interval.

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![FIGURE 1](image-url) | Parameterization of the stomatal conductance ($g_{\text{sto}}$) model for Japanese larch (above) and its hybrid $F_1$ (below), where $f_{\text{light}}$, $f_{\text{temp}}$, and $f_{\text{VPD}}$ are functions of photosynthetically photon flux density (µmol photons m$^{-2}$ s$^{-1}$), air temperature (T, °C), and vapor pressure deficit (VPD, kPa), respectively. The results of the boundary line analysis are shown in red.
the other hand, $f_{\text{min}}$ was slightly higher in Japanese larch than in hybrid larch $F_1$.

All the dose–response relationships were significant. When AOT40 was applied, in particular, a higher slope was found for hybrid larch $F_1$ than for Japanese larch (Figure 2).

The CLs calculated on the basis of these dose–response relationships were 2.7 times higher in Japanese larch than in its hybrid $F_1$ when AOT40 was used, while PODY-based CLs were similar between the two species when using either no $Y$ threshold or a $Y$ threshold of 1 nmol m$^{-2}$ s$^{-1}$ PLA (Table 3).

**DISCUSSION**

The boreal area in the northern hemisphere where larches are widely distributed is at risk of changes due to the
potential O₃ impact on photosynthetic carbon assimilation (Sicard et al., 2017), as estimated by several global atmospheric chemistry transport models and representative concentration pathways emission scenarios. For a realistic estimate of O₃ risks to forests, CLs should be developed for the major forest species or types. Even though natural areas and plantations for larch trees are very wide and larch is a major genus of the forest category defined as boreal deciduous species, PODY-based CLs were not yet available for larch and are suggested here for the first time.

Organismic “sensitivity” may be defined as “the response of an organism (i.e., biological deviation) above or below a homeostatic state (control) of a set of biological traits, after sensing some environmental stress-inducing agents” (Agathokleous and Saitanis, 2020). However, “the organismal predisposition to be inhibited or adversely affected by or die of a xenobiotic,” as expressed by “negative (inhibitory or adverse) effects induced by diseases or environmental challenges,” is termed susceptibility (Agathokleous and Saitanis, 2020). Hence, organismic susceptibility can be assessed by studying dose/exposure–response relationships and, in particular, by comparing CLs among organisms (Agathokleous and Saitanis, 2020). Since the CLs are affected by the O₃ metric used to develop dose/exposure–response relationships, susceptibility rankings can be different depending on the O₃ metric used (Agathokleous et al., 2019).

So far, CLs have been estimated for a total biomass reduction in either deciduous broadleaf and Mediterranean conifer species (recommended biomass loss: 2%) or non-Mediterranean evergreen conifer species (recommended biomass loss: 4%) (CLRTAP, 2017). As larch is both a deciduous species and a non-Mediterranean conifer species, we decided to calculate the CLs for both the loss thresholds of 2% and 4%. We decided also to calculate the CLs for AOT40, although this metric is known for not being able to assess how much O₃ enters the leaf through the stomata (Paolletti and Manning, 2007). However, it is still the legislative standard in Europe (Directive 2008/50), is used in many other continents (e.g., Agathokleous et al., 2018; Pleijel et al., 2019) because it is simple to calculate, and helps in the comparison with other results in the literature. The AOT40-based CL suggested so far for O₃-susceptible deciduous broadleaves (F. sylvatica and B. pendula), 5 ppm h for a 5% biomass loss; CLRTAP, 2014, 2017) is similar to that of hybrid larch F₁ (5.45 ppm h for 5% biomass loss), while Japanese larch showed a markedly higher AOT40-based CL corresponding to 5% loss (i.e., 14.48 ppm h). Based on a reanalysis of only two of the papers investigated here (Matsumura, 2001; Watanabe et al., 2006), Yamaguchi et al. (2011) had already suggested high O₃ susceptibility for Japanese larch. In fact, the AOT40-based CLs that they recommended were consistent with those found in our work (i.e., 8–15 ppm h). In addition, our results would suggest a higher susceptibility to O₃ of the hybrid and confirm previous studies where ecophysiological responses of the hybrid were more severely affected by O₃ exposure than those of Japanese larch (Koike et al., 2012; Sugai et al., 2019).

An accurate parameterization of stomatal conductance model is essential for the flux-based O₃ risk assessments (Emberson et al., 2000). For larch, the information of leaf-level gsto parameters was limited, although some studies tried to estimate O₃ uptake at stand level by sap-flow measurements (Nunn et al., 2007) and at forest level by eddy covariance (Finco et al., 2017). Wieser and Havranek (1995) previously reported just stomatal VPD responses to estimate stomatal O₃ uptake in European larch (Larix decidua). Our study is the first one to achieve a proper leaf-level parameterization (gmax, fmin, flight, femp, and fVPP) in larch trees to develop a flux-based approach. The maximum value of gsto in European larch by Wieser and Havranek (1995) was 150 mmol O₃ m⁻² PLA s⁻¹, which was comparable to the gmax values in our findings. Interestingly, hybrid larch F₁ showed a slightly higher gmax (140 vs. 120 mmol O₃ m⁻² PLA s⁻¹ in Japanese larch). As gmax is known to play the most important role in determining PODY (Tuovinen et al., 2007), the small difference in gmax between the two species translated into a higher stomatal uptake of O₃ by the hybrid at similar AOT40 levels; that is, the higher susceptibility of the hybrid under similar O₃ exposures was due to a higher stomatal uptake. It is well known that fast-growing species with high stomatal conductance are susceptible to O₃ because of an elevated stomatal uptake (Feng et al., 2018; Hoshika et al., 2018a). When the CLs are calculated on a PODY basis, in fact, the two species showed surprisingly similar CLs: 9.40 and 12.00 mmol m⁻² POD0 and 2.21 and 4.31 mmol m⁻² POD1 in Japanese larch versus 10.44 and 12.38 mmol m⁻² POD0 and 2.45 and 4.19 mmol m⁻² POD1 in the hybrid, for 2% and 4% biomass loss, respectively. These POD1-based values are below the CL recommended for non-Mediterranean trees (5.7 mmol m⁻²; CLRTAP, 2017), suggesting that these larches are more susceptible to O₃ even when evaluated on the basis of stomatal flux. Different susceptibilities to O₃ injury in the two larch species may be also due to different antioxidant capacities (Di Baccio et al., 2008). Although monoterpen emissions from leaves were preliminarily studied (Mochizuki et al., 2017), the role of antioxidants, secondary metabolites, and other leaf defensive molecules in the response of these two species to O₃ remains elusive.

### TABLE 3 | Critical levels for larch protection from ozone corresponding to a total biomass loss of 2%, 4%, or 5% and based on the dose-response relationships in Figure 2.

| Species | 2% | 4% | 5% | 2% | 4% | 5% |
|---------|----|----|----|----|----|----|
| Japanese larch | 5.79 | 11.59 | 14.48 | 2.18 | 4.36 | 5.45 |
| Hybrid larch F₁ | 9.40 | 12.00 | 13.29 | 10.44 | 12.38 | 13.35 |
| POD1 based, mmol m⁻² | 2.21 | 4.31 | 5.36 | 2.45 | 4.19 | 5.06 |
CONCLUSION

Based on a reanalysis of literature results and new measurements, we conclude that Japanese larch and its hybrid F1 should be classified as species with considerable O3 susceptibility as compared to the CLs available so far for other forest species. We also found that AOT40 and PODY can give very different results when assessing a species’ susceptibility to O3. While AOT40 suggested a higher susceptibility of hybrid F1, PODY did not highlight marked differences between the two species. Future research should clarify the O3 susceptibility of hybrid clones versus their wild forest species and increase the number of forest species with a species-specific parameterization and PODY-based CLs, especially in the Asian continent. This kind of information is needed for improving our modeling capacities, assessing O3 risks to local-to-global forests, and transferring this knowledge to environmental policy-makers.

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DATA AVAILABILITY STATEMENT

Basic raw data are available with YH (Italy) or TK (Japan).

AUTHOR CONTRIBUTIONS

EP conceptualized the work and wrote the manuscript. EA, TS, and TK provided the data. YH analyzed the data. All authors reviewed the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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