frontiers
in Forests and Global Change

ORIGINAL RESEARCH
published: 12 May 2020
doi: 10.3389/ffgc.2020.00045

Developing Ozone Risk Assessment for Larch Species

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Ozone (O_3) risk assessment for the protection of forests requires species-specific critical levels (CLs), based on either O_3 concentrations (AOT40) or stomatal uptake (PODY) accumulation over the growing season. Larch (*Larix* sp.) is a genus with O_3-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 We analyzed published and unpublished data of Japanese larch (*Larix kaempferi*) and its hybrid F_1 (*Larix gmelinii* var.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 F_1 (2.18 and 4.36 ppm h AOT40), suggesting a higher O_3 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 O_3.

Keywords: critical level, DO_3SE model, forest, larch, parameterization, tropospheric ozone

Edited by:
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Specialty section:
This article was submitted to
Forests and the Atmosphere,
a section of the journal
Frontiers in Forests and Global
Change

Received: *19 December 2019*
Accepted: *25 March 2020*
Published: *12 May 2020*

Citation:
Hoshika Y, Paoletti E,
Agathokleous E, Sugai T and Koike T
(2020) Developing Ozone Risk
Assessment for Larch Species.
Front. For. Glob. Change 3:45.
doi: 10.3389/ffgc.2020.00045

INTRODUCTION

Tropospheric ozone (O_3) 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 O_3 concentrations, while a significant increase in O_3 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 O_3 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 O_3 flux – or phytotoxic ozone dose (POD) – is more biologically meaningful as it estimates the amount of O_3 actually entering the plants through the stomata (Paoletti and Manning, 2007). A flux threshold *Y* below which O_3 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

Convention on Long-Range Transboundary Air Pollution (CLRTAP, 2017) based on Büker et al. (2015). For easier calculation, a Y threshold of 0 nmol m^{-2} s^{-1} PLA was also recommended, if we assume that all O_3 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).

For the protection of susceptible vegetation from O_3, 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 two larch species, Yamaguchi et al., 2011; *Populus deltoides* cv. "55/56" × *P. deltoides* cv. "Imperial" and *Populus euramericana* cv. "74/76," Shang et al., 2017). Stomatal flux-based CLs are available for *F. sylvatica*, *B. pendula*, *Picea abies*, *Quercus faginea*, *Quercus pyrenaica*, *Quercus robur*, *Quercus ilex*, *Ceratonia siliqua*, and *Pinus halepensis* in the ICP Vegetation manual (CLRTAP, 2017) and for few other species in the literature (*Zelkova serrata*, Hoshika et al., 2012; *Quercus pubescens*, Hoshika et al., 2018b; *Pinus pinea*, Hoshika et al., 2017; hybrid poplars, Zhang et al., 2018; Feng et al., 2019b; *Fagus crenata*, *Quercus serrata*, *Quercus mongolica* var. *crispula*, and *Betula platyphylla* var. *japonica*, Yamaguchi et al., 2019). For estimating PODY (phytotoxic ozone dose above a threshold Y nmol m^{-2} s^{-1})-based CLs, a species-specific parameterization of the stomatal flux or DO_3SE model is required (Emberson et al., 2000; Büker et al., 2012). There is a need of more species-specific CLs for biomass loss in forest species, especially for forest species in Asia, where elevated O_3 pollution levels are a serious risk for forests at present (Li et al., 2017; Mills et al., 2018; Feng et al., 2019a).

Larch (*Larix* sp.) is a widely distributed genus (*Pinaceae* family) with global economic importance, which includes some of the few deciduous conifer species. Larch is among the dominant tree species of northern hemisphere boreal forests. Hence, its natural distribution range is very wide and spans from Siberia to Canada, passing through Europe, mountainous China, and Japan. Larches provide high-quality wood and are commercially valuable (Bardak et al., 2019). As any pioneer species, larches have a relatively high growth rate and stomatal conductance (Streit et al., 2014; Agathokleous et al., 2017; Hoshika et al., 2018c). Although their susceptibility to O_3 has been investigated in several papers (Wieser and Havranek, 1996; Matsumura, 2001; Watanabe et al., 2006; Koike et al., 2012; Agathokleous et al., 2017; Sugai et al., 2018, 2019), a comprehensive risk assessment including parameterization of the stomatal conductance model and definition of CLs for biomass losses is missing. Previous studies focused on the biomass responses to O_3 of Japanese larch (*Larix kaempferi*) and its hybrid F_1 (*Larix gmelinii* var. *japonica* × *L. kaempferi*). Hybrid F_1 displays heterosis and is important for timber production and afforestation due to more desirable characteristics compared to its parents, with a significant superiority in terms of growth rates (Ryu et al., 2009; Kita et al., 2009; Agathokleous et al., 2017; Sugai et al., 2018). A question arises whether hybrid clones, selected for fast-growing capacities, are representative of natural forest responses to O_3 when used in manipulative experiments (e.g., Di Baccio et al., 2008; Hu et al., 2015; Dusart et al., 2019; Podda et al., 2019).

Our aim was to collate published and unpublished data from previous experiments for developing a parameterization of the DO_3SE model for Japanese larch and its hybrid F_1 and estimating the CLs not to be exceeded for the protection of these larch species from O_3. Based on published research documenting a higher O_3 susceptibility of the faster-growing hybrid F_1 than the slower-growing Japanese larch (Agathokleous et al., 2017; Sugai et al., 2018), we hypothesized that the CLs of hybrid F_1 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 "larch" 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 O_3 and biomass data. Finally, data on O_3 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-O_3 air. Data from combined experiments, such as O_3 with either fertilization or CO_2, 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 g_{sto} in the DO_3SE model (CLRTAP, 2017):

$$g_{sto} = g_{max} * f_{light} * \max\{f_{min}, (f_{temp} * f_{VPD})\} \quad (1)$$

where g_{max} is the maximum stomatal conductance of either Japanese larch or its hybrid F_1, 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),

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*	OTC	June–September 2010	CF, NF60	Elevated CO_2	PODY/AOT40
	Larix gmelinii var. *japonica*	OTC	June–September 2010	CF, NF60	Elevated CO_2	PODY/AOT40
	F1 (*L. gmelinii* var. *japonica* × *L. kaempferi*)	OTC	June–September 2010	CF, NF60	Elevated CO_2	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
	F_1 (*L. gmelinii* var. *japonica* × *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, NF60	Nitrogen addition	PODY/AOT40/Gs model
	F_1 (*L. gmelinii* var. *japonica* × *L. kaempferi*)	OTC	June 2015–August 2016	CF, NF60	Nitrogen addition	PODY/AOT40/Gs model
Wang et al. (2015)	F_1 (*L. gmelinii* var. *japonica* × *L. kaempferi*)	OTC	July 2011–September 2012	CF, NF60	n.a.	PODY/AOT40
Watanabe et al. (2006)	*L. kaempferi*	OTC	April 2004–September 2005	CF, AA, 1.5AA, 2.0AA	Nitrogen addition	AOT40
Agathokleous (unpublished)	*L. kaempferi*	Field	June–August 2015	n.a.	n.a.	Gs model
	F_1 (*L. gmelinii* var. *japonica* × *L. kaempferi*)	Field	August 2017	n.a.	n.a.	Gs model

OTC, open-top chamber; CF, charcoal-filtered air; NF, non-filtered air; NF40, 40 ppb O_3; NF60, 60 ppb O_3; AA, ambient O_3 concentration; 1.5AA, 1.5 times ambient O_3 concentration; 2.0AA, twice ambient O_3 concentration; n.a., not available.

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_{sto} 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 O_3 uptake (F_{st}; nmol m^{-2} s^{-1}) was calculated as follows:

$$F_{st} = [O_3] \cdot g_{sto} \cdot \frac{r_c}{r_b + r_c} \tag{2}$$

where r_c is the leaf surface resistance [= $1/(g_{sto} + g_{ext})$; 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):

$$r_b = 1.3 \cdot 150 \cdot (L_d/u)^{0.5} \tag{3}$$

where the factor 1.3 accounts for the difference in diffusivity between heat and O_3, 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 (mmol m^{-2}) was estimated from hourly data as follows:

$$\mathrm{PODY} = \sum_{i=1}^{n} (F_{st,i} - Y) \cdot \Delta t \tag{4}$$

where Y is a species-specific threshold of stomatal O_3 uptake (nmol m^{-2} s^{-1}) and Δt = 1 h is the averaging period. $F_{st,i}$ is the ith hourly stomatal O_3 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 O_3 while several studies reported a better performance of POD0 rather than POD1 for O_3 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 O_3 concentration of 10 ppb referring to a "pre-industrial" O_3 concentration, as recommended by CLRTAP (2017).

Simple linear regression analyses were used to assess the relationships between O_3 indices (AOT40, POD0, and POD1) and relative biomass. In addition, to compare the g_{max} values between the two larches, Student's t-test was performed on values within the top five percentile in g_{sto} data. Results were considered significant at $p < 0.05$. All the analyses were performed using R 3.5.1 (R Core Team, 2018).

TABLE 2 | DO3SE model parameters for Japanese larch and hybrid F_1, where g_{max} is maximum stomatal conductance; f_{min} is minimum stomatal conductance; f_{light_a} is a parameter determining the shape of the hyperbolic relationship of stomatal response to light; T_{max}, T_{opt}, and T_{min} are the maximum, optimal, and minimum temperatures, respectively, for calculating the function f_{temp} that expresses the variation of g_{sto} with temperature; VPD_{min} and VPD_{max} are the vapor pressure deficit for attaining minimum and maximum stomatal aperture, respectively (f_{VPD}).

Parameter	Japanese larch	Hybrid F_1
g_{max}, mmol O_3 m^{-2} PLA s^{-1}	120 [95% CI: 103–188]	140 [95% CI: 110–225]
f_{min}, fraction	0.16	0.09
f_{light_a}, μmol^{-1} m^{-2} s^{-1}	0.0097	0.0096
T_{min}, °C	5	5
T_{opt}, °C	25	25
T_{max}, °C	40	40
VPD_{max}, kPa	1.6	1.6
VPD_{min}, kPa	4.0	4.2

CI denotes confidence interval.

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_{max} in hybrid larch was slightly higher than that in Japanese larch although g_{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_{sto}, data not shown). On

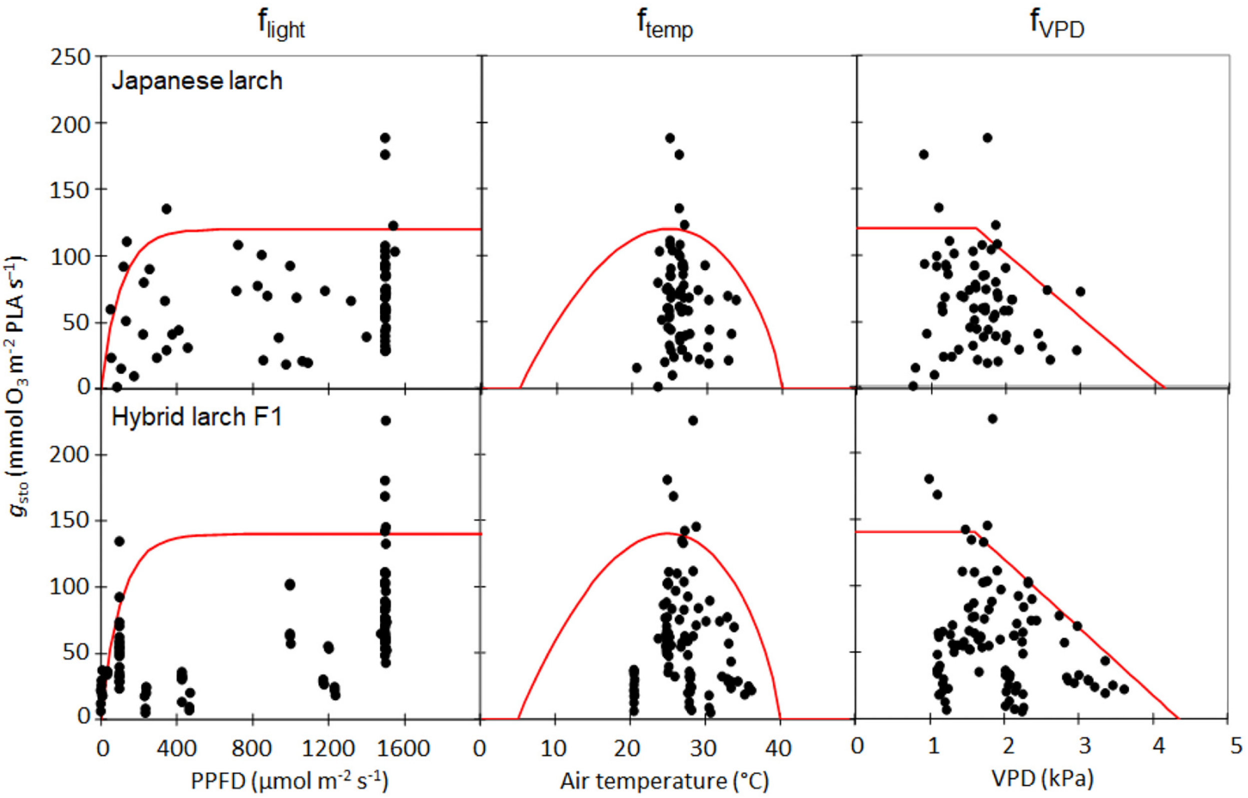

FIGURE 1 | Parameterization of the stomatal conductance (g_{sto}) model for Japanese larch (above) and its hybrid F_1 (below), where f_{light}, f_{temp}, and f_{VPD} are functions of photosynthetically photon flux density (μmol photons m^{-2} s^{-1}), air temperature (T, °C), and vapor pressure deficit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

the other hand, $f_{\min}$ 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

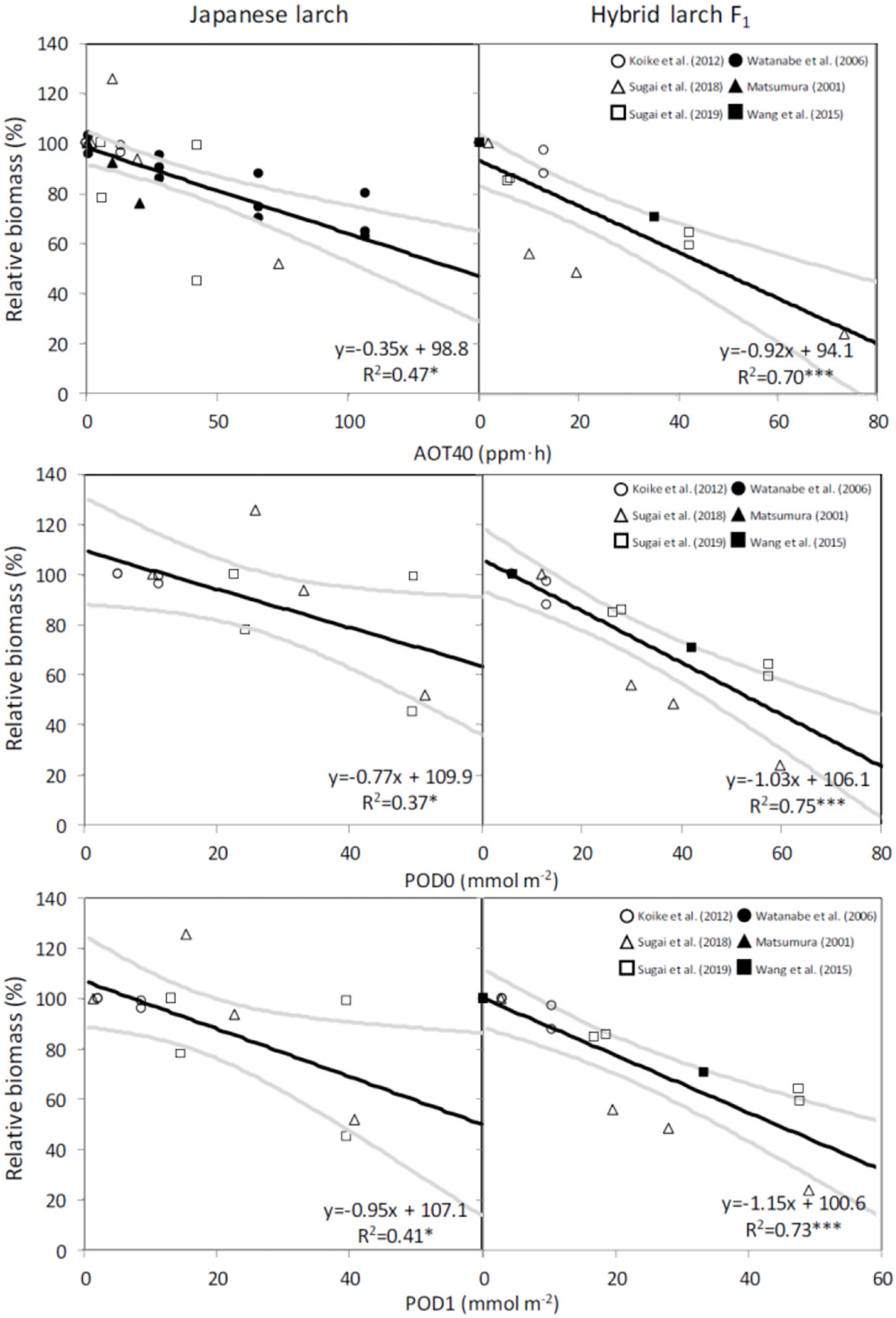

FIGURE 2 | Dose–response relationships for total biomass losses in two species of larch seedlings on the basis of AOT40, POD0, or POD1 in different experiments. Black lines denote the regressions, and gray lines denote the 95% confidence intervals. Asterisks show the level of significance: ***$p \leq 0.001$; *$p \leq 0.05$.

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**.

	Japanese larch			Hybrid larch F_1		
	2%	4%	5%	2%	4%	5%
AOT40 based, ppm h	5.79	11.59	14.48	2.18	4.36	5.45
POD0 based, mmol m^{-2}	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

potential O_3 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 O_3 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 O_3 metric used to develop dose/exposure–response relationships, susceptibility rankings can be different depending on the O_3 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 O_3 enters the leaf through the stomata (Paoletti 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 O_3-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 F_1 (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 O_3 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 O_3 of the hybrid and confirm previous studies where ecophysiological responses of the hybrid were more severely affected by O_3 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 O_3 risk assessments (Emberson et al., 2000). For larch, the information of leaf-level g_{sto} parameters was limited, although some studies tried to estimate O_3 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 O_3 uptake in European larch (*Larix decidua*). Our study is the first one to achieve a proper leaf-level parameterization (g_{max}, f_{min}, f_{light}, f_{temp}, and f_{VPD}) in larch trees to develop a flux-based approach. The maximum value of g_{sto} in European larch by Wieser and Havranek (1995) was 150 mmol O_3 m^{-2} PLA s^{-1}, which was comparable to the g_{max} values in our findings. Interestingly, hybrid larch F_1 showed a slightly higher g_{max} (140 vs. 120 mmol O_3 m^{-2} PLA s^{-1} in Japanese larch). As g_{max} is known to play the most important role in determining PODY (Tuovinen et al., 2007), the small difference in g_{max} between the two species translated into a higher stomatal uptake of O_3 by the hybrid at similar AOT40 levels; that is, the higher susceptibility of the hybrid under similar O_3 exposures was due to a higher stomatal uptake. It is well known that fast-growing species with high stomatal conductance are susceptible to O_3 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 O_3 even when evaluated on the basis of stomatal flux. Different susceptibilities to O_3 injury in the two larch species may be also due to different antioxidant capacities (Di Baccio et al., 2008). Although monoterpene 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 O_3 remains elusive.

CONCLUSION

Based on a reanalysis of literature results and new measurements, we conclude that Japanese larch and its hybrid F_1 should be classified as species with considerable O_3 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 O_3. While AOT40 suggested a higher susceptibility of hybrid F_1, PODY did not highlight marked differences between the two species. Future research should clarify the O_3 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 O_3 risks to local-to-global forests, and transferring this knowledge to environmental policy-makers.

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.

ACKNOWLEDGMENTS

This study is partly supported by the LIFE15 ENV/IT/000183 project MOTTLES and JST-2019 (Grant No. JPMJSC18HB).

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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.