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ARE SVALBARD PLANTS PREPARED FOR CLIMATIC CHANGE?



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Summary:

Climatic change and global warming are imposing a new scenario for life in all Arctic region. Plant species are the basis of the terrestrials ecosystems and they can be dramatically affected by the environmental changing conditions predicted for the High Arctic. We were studying the productivity and stress tolerance of native and alien species in Longyearbyen and Barentsburg, the most populated villages in Spitsbergen (Svalbard). We select native and alien species from the same family and similar growth-form living closer each other in the same locations if possible. Gas-exchange measurements (to determine photosynthetic capacity proxy to productivity), stress tolerance tests, photosynthetic pigment profiling, leaf anatomy and leaf ion content (investment of resources) were analyzed. In terms of photosynthetic capacity and stress tolerance ability it can not be generalized a trend, different behaviors was observed depending of the families and the species, however in general alien species showed higher photoprotective status than native species. This could be an indicator of light stress under the day light-continuous growing season in the arctic in comparison to the adapted native species. As well they tend to accumulate higher phosphorus content in their leaves indicating a possible differential resource investment.

This scenario, could however change towards better performance of alien species in a either warmer, or more altered (higher nitrogen availability) scenario. Further research is needed to define the environmental responses of alien versus native plants in the High Arctic in terms of response to warmer temperatures, the midnight sun (continuous light), nutrient availability and species competition.

Keywords: global warming, alien species, invasive, photosynthesis, stress tolerance, native species

Notices:

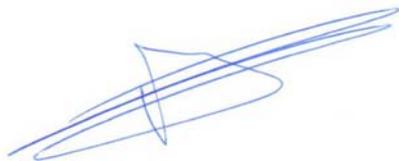
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Foreword

This report deals with the study of productivity and stress tolerance in alien and native species in Svalbard islands funded by the Svalbard Environmental Protection Fund. The work was also partially supported by the Spanish national Research Grant CTM2014-53902-C2 "TOPSTEP, Mechanistic bases for the Trade-Off between Photosynthesis and Stress Tolerance: filling gaps of knowledge for Evolutionary biology and Plant Biotechnology" funded by the Ministry of Economy and Competitiveness (Mineco) of the government of Spain and co-funded by the European Fund for Regional Development (FEDER). The project was carried out from February 2017 to March 2018. Extensive field measurements were done in the surroundings of Longeyarbyen and Barentsburg in July 2017. We are grateful to Pernille Bronken from The University Centre in Svalbard (UNIS) for her help and advice, and also to Lennart Nilsen (The Arctic University of Norway) and Virve Ravolainen (the Norwegian Polar Institute) for sharing information about alien species in Svalbard. We also want to thank to Anna Nikulina (Arctic and Antarctic Research Institute, Russia) and Galina Kashulina (Avrorin Polar-Alpine Botanical Garden-Institute, Kola Science Center, Russian Academy of Science) for their help in Barentsburg. We are grateful to AXENA (Asoc. Xuvenil para o Estudo da Natureza) youth non-gubernamental association specialized in environmental education through new technologies also helped us to divulgate our results and experiences. Thanks also to Pilar García, Inmaculada Sans and Víctor Homar from the University of Mallorca (UIB) for their support in our challenging research projects.

Palma de Mallorca, 27th March 2018

A handwritten signature in blue ink, consisting of several overlapping, fluid strokes that form a stylized, abstract shape.

Xurxo Gago
(Project Leader)

1 INTRODUCTION

It is already known that the High Arctic will suffer dramatic changes because of the climatic change and the global warming (IPCC, 2013). Benign weather conditions will affect the productivity, distribution and abundance of native plant species, but these favorable environmental conditions will not only affect the natural distribution of the species, but also the economic activities all around the Arctic region (Alsos et al., 2015). In Svalbard islands, tourism is the economic sector with the highest increases in the last few years (Ware et al., 2012), and it is known that human activities are one of the most important factors driving biological invasions, so both factors, global warming and increased human activities can led to the establishment and/or expansion of alien species. In a previous study, developed at the Longyearbyen airport, researchers investigated the number of seeds from foreign plants in the footwear of the tourists. They found an average of 3.9 foreign seeds per person, including some of the most dangerous invasive species worldwide (Ware et al., 2012; Alsos et al., 2015).

To cope with the changes driven by the climate change, plant species would balance their investments into productivity or stress tolerance traits. Previous reports described that alien/invasive species tend to maximize growth and space occupation thanks to higher assimilation carbon rates (photosynthesis) in environments not limited by nutrients or another factors (Leishman et al., 2007), however, under harsh environments, this strategy could not be successful, limiting their stress tolerance capacities.

We aim to compare the photosynthetic capacity and the desiccation stress tolerance of those species through a semi-quantitative assessment of desiccation tolerance test, called Falcon-Test (Fernández-Marín et al., 2016; López-Pozo et al., *submitted*) as well as leaf anatomical analyses, pigments, nutrient content and leaf *in vivo* complete photosynthetic characterization. Overall, this information could be really useful for the precise design and specific development of the future conservation plans of the Svalbard ecosystems, preservation of endemisms and native plants as well as the biodiversity in the framework of the Climatic Change.

2 MATERIAL AND METHODS

Sampling sites and experimental design

The study was developed in two locations in Spitsbergen: Longyearbyen (and surroundings) and Barentsburg. According to previous publications, the Species Map Service 1.6/Artsdatabanken (<http://artskart1.artsdatabanken.no>) and <http://svalbardflora.no/>, most of alien/invasive species were found in the villages and mostly close to animal farms (Figure 1).



Figure 1. "Hot-spots" sites in Barentsburg (upper picture) and Longyearbyen (lower picture) where an important number of different alien species were observed under our surveys.

Species selection criteria were based on their native origin, ecology and phylogeny: i.e. pairs of alien and native species belonging to the same family and growing close to each other within the same area were chosen (to reduce environmental effects between different locations). An example of the selected pairs of species per family can be seen in the figure 2.

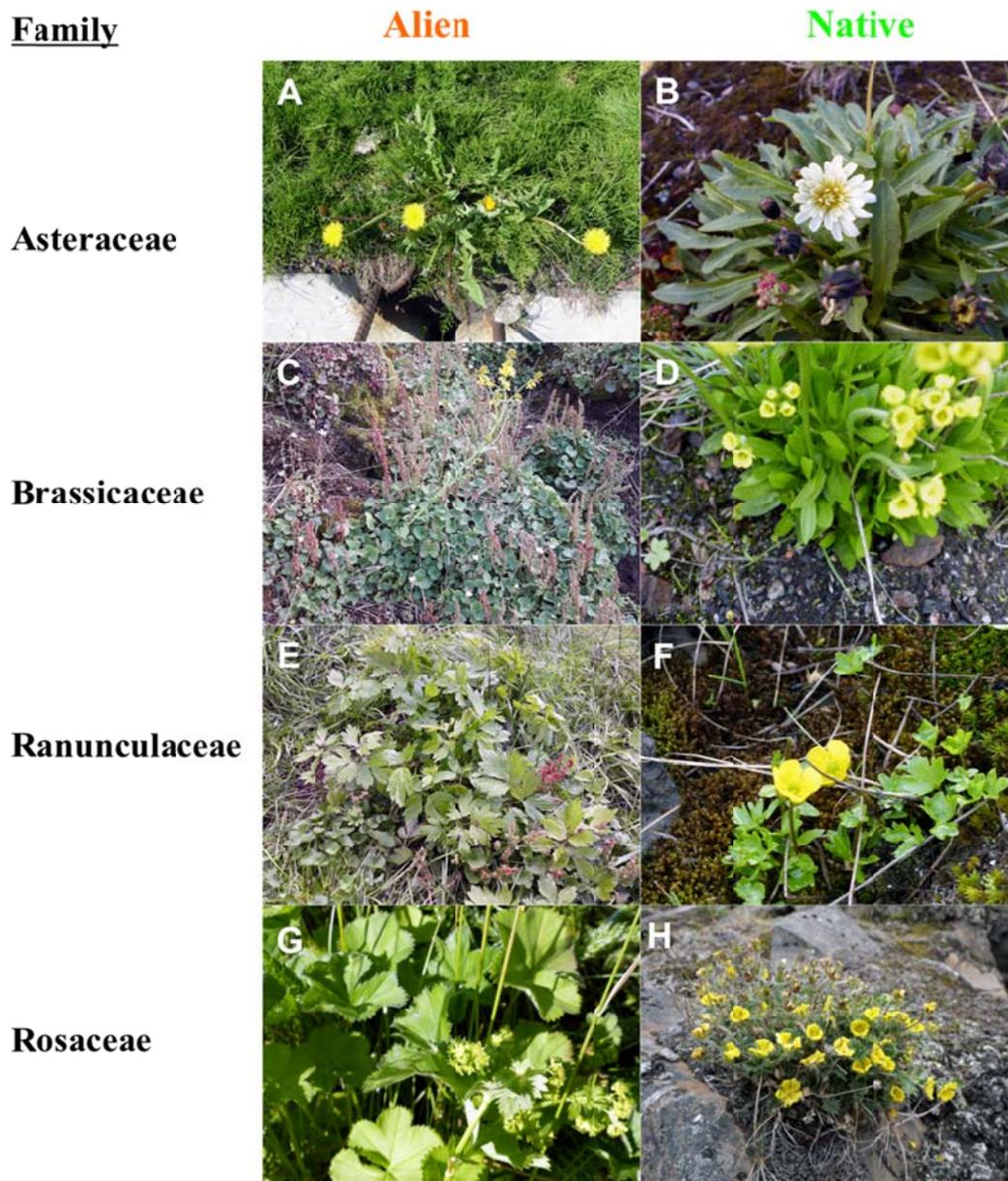


Figure 2. Example of selected species per different families in Longyearbyen and Barentsburg, a) *Taraxacum officinalis*, b) *Taraxacum arctica*, c) *Barbarea vulgaris*, d) *Draba oxycarpa*, e) *Ranunculus repens*, f) *Ranunculus nivalis*, g) *Alchemilla subcrenata* and h) *Potentilla hyparctica*.

In the Table 1, it is shown the complete list of species analyzed and the locations and coordinates of the sampling sites. To facilitate the visualization of the plots the species will be named as the acronyms proposed in Table 1. In total we measured 8 "pairs" of alien and native species from 6 different families. Leaf samples for laboratory analysis were collected in the field (Fig. 3a & c). For *in vivo* gas-exchange leaf photosynthesis and respiration characterization whole plants were collected and placed in pots for the common garden measurements (Fig. 3d). This experimental design will help us to evaluate the possible competition between the alien and native species in the same ecosystem and environment in the framework of the global warming.

Table 1. List of the measured species grouped by pairs of native and alien species per family. Location of the collected samples are organized by site (Barentsburg (BAR), Longyearbyen (LYR) and also coordinates in decimal degrees (WGS 84)).

Type	Family	Sp	Acronym	Location	Coordinates
Native	<i>Asteraceae</i>	<i>Taraxacum arctica</i>	TA	BAR	78,0658910-14,2110850
Alien	<i>Asteraceae</i>	<i>Taraxacum officinalis</i>	TR	BAR	78,0652685-14,2073447
Alien	<i>Asteraceae</i>	<i>Achillea millefolium</i>	AM	BAR	78,0650186-142105502
Native	<i>Brassicaceae</i>	<i>Draba oxycarpa</i>	DO	LYR (Huset)	78,2077680-15,5880530
Alien	<i>Brassicaceae</i>	<i>Barbarea vulgaris</i>	BV	BAR	78,0711250-14,2016750
Native	<i>Caryophyllaceae</i>	<i>Silene uralensis</i>	SU	LYR (horse farm)	78,2424861-15,5275666
Alien	<i>Caryophyllaceae</i>	<i>Stellaria media</i>	SM	LYR (horse farm)	78,2424861-15,5275666
Native	<i>Poaceae</i>	<i>Deschampsia alpina</i>	DA	LYR (horse farm)	78,2424861-15,5275666
Alien	<i>Poaceae</i>	<i>Deschampsia cespitosa</i>	DC	LYR (old dam)	78,1954260-15,5623490
Native	<i>Poaceae</i>	<i>Poa alpina</i>	PA	LYR (old dam)	78,1954220-15,5601140
Alien	<i>Poaceae</i>	<i>Poa pratensis</i>	PP	LYR (village)	78,218 -15,63375
Native	<i>Ranunculaceae</i>	<i>Ranunculus nivalis</i>	RN	LYR (Huset)	78,20785 -15,58476
Alien	<i>Ranunculaceae</i>	<i>Ranunculus acris</i>	RA	BAR (farm)	78,0711250-14,2016750
Native	<i>Ranunculaceae</i>	<i>Ranunculus sulphureus</i>	RS	LYR	78,1820060-15,7477890
Alien	<i>Ranunculaceae</i>	<i>Ranunculus repens</i>	RR	BAR (farm)	78,0711250-14,2016750
Native	<i>Rosaceae</i>	<i>Potentilla hyparctica</i>	PH	LYR (church)	78,214575-15,6070972
Alien	<i>Rosaceae</i>	<i>Alchemilla subcrenata</i>	AS	BAR (farm)	78,0711250-14,2016750

Leaf tissue desiccation tolerance analysis: the "Falcon test"

This method performs a semi-quantitative assessment of desiccation-tolerance based in the "Austin protocol", but improving its portability and sensitivity. Desiccation extent of photosynthetic tissues was monitored by measuring their relative water content (RWC) and their viability was assessed by chlorophyll *a* fluorescence techniques,

measuring the maximum photochemical efficiency (F_v/F_m) as proxy of the physiological status (Fig. 3b). Measurements were performed (i) at turgor state, (ii) after a 48-h exposition to different drying conditions. Finally, (iii) the recovery assessment after 24 h of rehydration was measured (Fernández-Marín et al., 2016; López-Pozo et al., *submitted*). This methodology allows large-scale multi-species comparisons and the establishment of correlative relationships between morpho-physiological traits and ecological attributes. Moreover, as it has minimal instrumental requirements it can be performed in remote locations (Gago et al., 2016).

In vivo leaf photosynthesis and respiration characterization and anatomical parameters

Young fully expanded leaves were clamped into the cuvette of an open gas-exchange system with an integrated fluorescence chamber head (Li-6400-40; Li-Cor Inc., NE) for simultaneous measurements of gas-exchange and chlorophyll fluorescence following the set-up criteria established previously (Fig. 3d) (Gago et al., 2013). Block temperature was kept at 15 °C during all measurements and vapor pressure deficit (VPD) at around 1.5 kPa. The temperature of 15° selected, is around 2° above the historical maximum measured in Longyearbyen, Source: <https://www.yr.no/place/Norway/Svalbard/Longyearbyen/statistics.html>).

Photosynthetic light response curves were performed at a CO₂ concentration (C_a) of 400 $\mu\text{mol mol}^{-1}$, and varying photosynthetic photon flux density (PPFD) from 0 to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. From steady-state (at C_a of 400 $\mu\text{mol mol}^{-1}$ and PPFD of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) A_N , stomatal conductance (g_s) and sub-stomatal CO₂ concentration (C_i) were recorded. Mitochondrial respiration (R_n) rates were measured after darkening the plants for 30 min.

From chlorophyll fluorescence recordings, the actual photochemical efficiency of photosystem II (ϕ_{PSII}) was obtained as $\phi_{\text{PSII}} = (F_m' - F_s) / F_m'$, being F_s the steady state fluorescence, and F_m' the maximum fluorescence during a light-saturating pulse of ca. 8000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Genty et al. 1989). Gas exchange values given by Li- 6400 were corrected using the ratio cuvette area/actual frond area as a correction factor. After the measurements of gas-exchange, leaves were placed in a drying oven at 60°C until reaching constant weight, which was taken for the estimation of structural / anatomical

parameters as leaf mass area (LMA) as dry weight/area.



Figure 3. Sample collection in Barentsburg (a), Longyearbyen (c), "Falcon test" desiccation tolerance analysis employing leaf weight and chlorophyll fluorescence of the leaf tissues under different degree of desiccation (b) and two infrared gas-analyzers coupled with chlorophyll fluorimeters to characterize photosynthesis and respiration.

Photosynthetic pigment profiling by HPLC

Chloroplast pigments were extracted from 50 mg of lyophilized material with pure acetone buffered with CaCO_3 and centrifuged twice at 12,000g. The supernatants were filtered through 0.2- μm PTFE (polytetrafluoroethylene) filters (Teknokroma, Barcelona, Spain). The pigments were separated by HPLC on a reversed-phase C18 column (Waters Spherisorb ODS1, 4.6 \times 250 mm, Milford, Massachusetts, USA) and detected with a photodiode array detector, according to the method by García-Plazaola and Becerril (1999, 2001). The pool size of the xanthophyll cycle that is related to investments to protect the photosynthetic apparatus under stress conditions, were calculated as follows:

Xanthophyll cycle size= Violaxanthin (V) + antheraxanthin (A) + Zeaxanthin (Z)

Total leaf ion content: complete ionic profiling

Leaves which had been previously oven dried at 80°C until it reached a constant weight, was ground to obtain dry powder. The measurement of different macronutrients and micronutrients levels was carried out in an ICP THERMO ICAP 6500DUO spectrometer (Ionic Services of CEBAS-CSIC; Thermo Scientific, Madrid, Spain). Total C and N contents were determined by combustion at 950°C. Total C was analyzed by infrared detection and N by thermic conductivity in the Ionic Services of CEBAS-CSIC (Murcia, Spain).

Graphs and statistics

Results are shown using box-plots, the bottom and top of the box are the 25th and 75th percentile (the lower and upper quartiles, respectively), and the band near the middle of the box represents the 50th percentile (the median). The lower and upper whiskers respectively represent the minimal and maximal value of the data. ANOVA analysis was performed to detect the relevance of the factors and their interaction ($p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *, ns), different letter means significant differences between treatments by Tukey's multiples comparisons's test ($p < 0.05$) for all the subsequent box-plots of this report. Graphs and statistical analyses were performed with the open software R (R Core Team, 2017)..

3 RESULTS AND DISCUSSION

Are arctic plants more stress tolerant than alien species?

As the Arctic is a cold desert where water can be an important limiting factor (i.e. cumulative precipitation of last 12 months in Longyearbyen was <200mm, a value lower than anywhere in continental Europe, Source: <https://www.yr.no/place/Norway/Svalbard/Longyearbyen/statistics.html>), we have applied the "Falcon test" method to evaluate the desiccation tolerance of the leaf tissues of native and alien species as a proxy to stress tolerance. We ensure during the procedure that all species analyzed reduced its relative water content (RWC) drastically to ensure a severe stress in the tissues for all species and mostly for family pair-comparisons (Fig 4a). RWC average value in the desiccation stage for all species was around 8%, so the tissues suffer water losses of more than 90% guaranteeing the water stress in the leaf samples; no differences were observed in this parameter between alien and native species within the same family (Fig. 4a). This is a relevant point to discard that F_v/F_m recovery is driving differently between species because of different desiccation degrees between them (mostly for family pair comparisons); thus differences must be led by species-specific desiccation tolerance mechanisms and traits. In the figure 4b, the values of recovery of the F_v/F_m are shown. Interestingly, 3 native species showed significant higher stress tolerance values than at least one of their alien relatives, *Taraxacum arctica*, *Ranunculus sulphureus* and *Potentilla hyparctica*. It is important to note that *Poa alpina* showed the highest recovery value of all the species analyzed here, and comparing with previously published data from our research group of species from other extreme environments on Earth like Antarctica, Atacama desert (Chile), Andean Altiplano (Salar de Surire, Chile) and Namibia desert (Namibia), we can confirm that it is one of the highest recovery values that we have ever recorded in an angiosperm species (Gago et al., 2016).

Maximum photosynthetic capacity under our experimental set-up conditions

Gas-exchange analysis was performed for all species under a common garden study. Photosynthesis, stomatal conductance, respiration and chlorophyll fluorescence data were recorded to fulfill a complete photosynthesis characterization. Light and

temperature curves were performed to determine the photosynthetic light saturation point and the physiological parameters driving leaf productivity response to temperature, respectively.

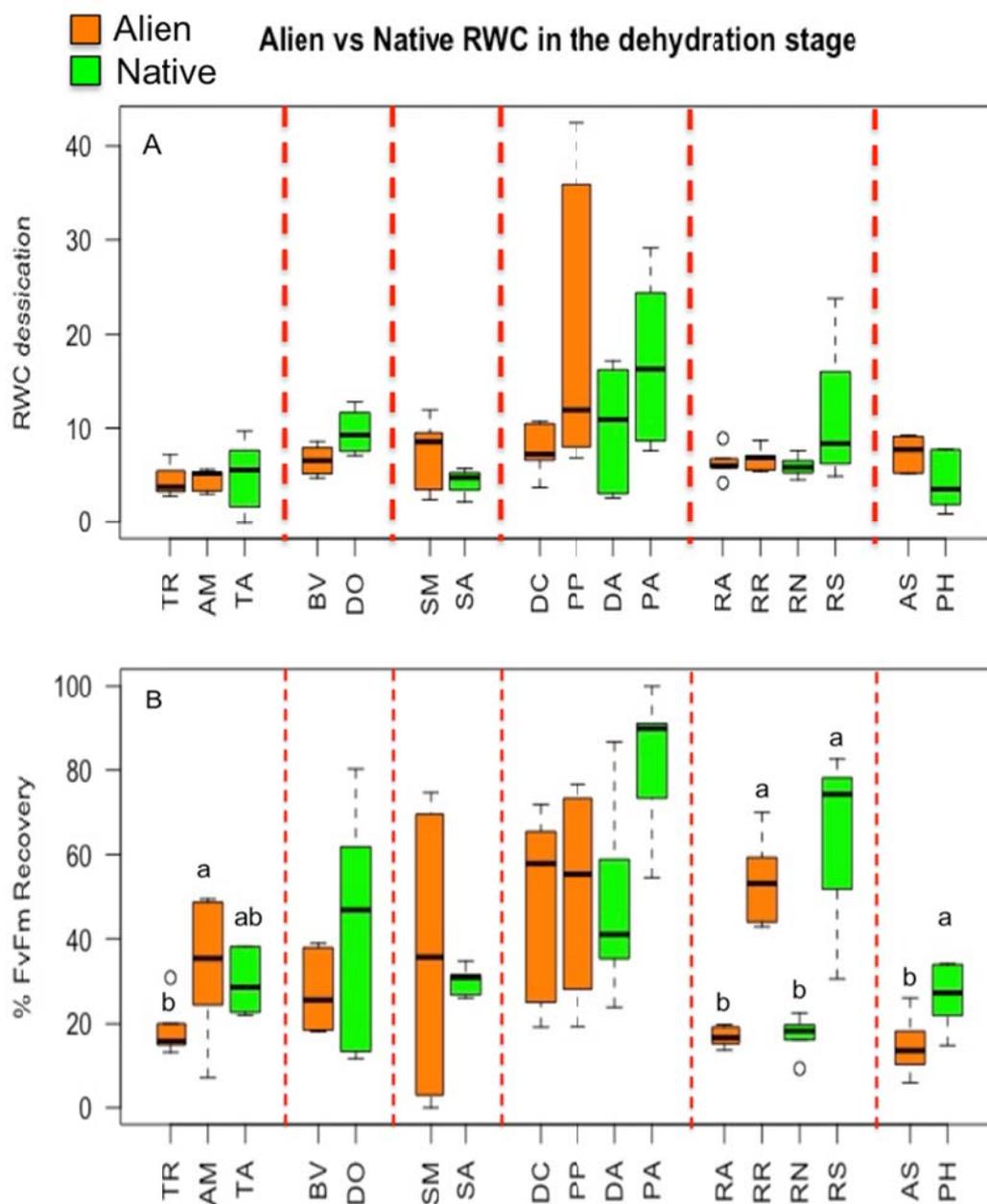


Fig. 4. a) RWC at the dehydration stage in the "Falcon Test" for all species, b) percentage of F_vF_m recovery in the rehydration stage of the tissues. Different letters means statistical differences between species within the same family by Tukey's test ($p < 0.95$). Red dashed line

split each family, from left to right: *Asteraceae*, *Brassicaceae*, *Caryophyllaceae*, *Poaceae*, *Ranunculaceae* and *Rosaceae*.

In the figure 5, it is shown the maximum photosynthesis values measured under our experimental set-up conditions. The species of the same family were measured in parallel at the same time to avoid environmental and circadian effects that could alter the comparison. Interestingly, maximum photosynthesis showed a different pattern than the observed with the F_v/F_m recovery (proxy to stress tolerance). Two alien species showed significantly higher photosynthetic capacity than their native pairs for the families *Asteraceae*, *Brassicaceae*, but for the families *Caryophyllaceae*, *Poaceae* and *Rosaceae*. The native species showed higher photosynthetic capacity than the alien species. No differences between species were found in the *Ranunculaceae* family (Fig. 5).

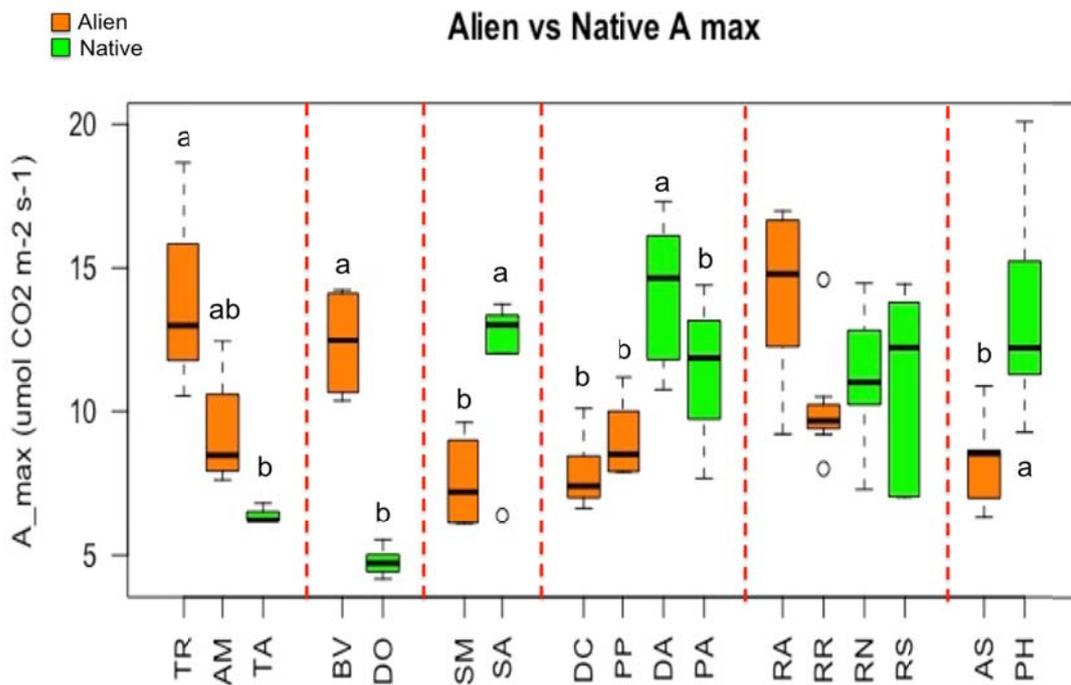


Fig. 5. Photosynthetic capacity measured under our experimental set-up. Different letters means statistical differences between species within the same family by Tukey's test ($p < 0.95$). Red dashed line split each family, from left to right: *Asteraceae*, *Brassicaceae*, *Caryophyllaceae*, *Poaceae*, *Ranunculaceae* and *Rosaceae*.

Altogether, from the F_v/F_m recovery (Fig. 4b) and the photosynthetic capacity (Fig. 5) measurements, two native species, *Poa alpina* and *Potentilla hyparctica*, developed a highly interesting performance. Both species behaved as "outliers" of the assumed trade-off between plant productivity (investments into productive-growth traits) and stress tolerance (investment into protective traits).

Photosynthetic pigment profiling

The High Arctic is considered an extreme environment for plants due to its low temperature and dry conditions ('liquid water' is scarce during most of the year) but however there is another particular environmental factor for the photosynthetic organisms: 24 hours of continuous light for 4 consecutive months. Continuous light is another significant stress factors for angiosperms (Velez-Ramirez et al. 2011) added to the harsh arctic environment provoking photo-oxidative damage in non-adapted species. In this sense, increases into carotenoid content per chlorophyll concentration are proposed as important protectors against continuous light (Demers and Gosselin, 2002). In the figure 6, it can be observed the ratio between chlorophyll *a* and *b*. Higher values for this ratio indicate smaller antenna size in the photosynthetic apparatus and, generally, an acclimation to higher irradiance (Esteban et al., 2015; Fernández-Marín et al. 2018a). Interestingly, we observed that in 4 of the 6 studied families alien species showed lower Chl *a/b* values than their comparative native species (Fig. 6a). Given that the light environment was comparable for both native and alien species, it suggests that the latter are less responsive to the environmental conditions in Svalbard. Furthermore, both VAZ/Chl and AZ/VAZ ratios (data not shown), also indicated higher demand for photoprotection in alien vs native species (Fig. 6b). These results are in agreement with data from subarctic species in which high AZ/VAZ values during summer were related to a potential incomplete acclimation to 24-h photoperiod of those species, which colonized high latitudes only recently (Fernández-Marín et al. 2018b), and suggest that recent colonizers have a lower plasticity to respond to environmental challenges than native plants.

Leaf anatomy and ionic nutrient leaf profile

Invasive species are characterized by high growth rates and quick expansion to conquer the space competing with native species (Leishman et al., 2007) that frequently means that leaves are thinner and wider than those of the native species. Leaf mass area (LMA) is a parameter indicating the relationship between the leaf area and its cell density and thickness. In the figure 7, it is shown the LMA for the species and different behaviors can be observed for the different families

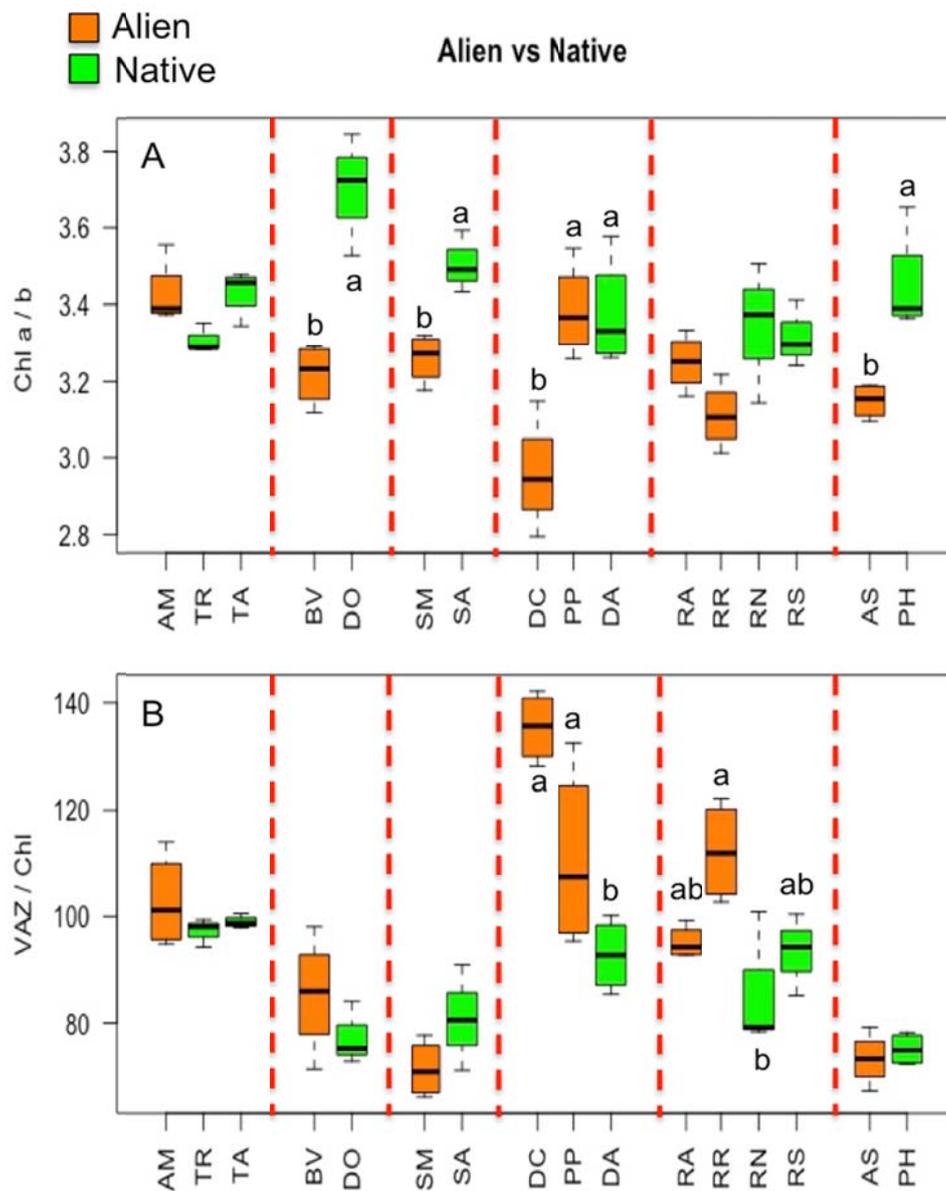


Fig. 6. A) Chlorophyll *a* / *b* ratio and B) the total VAZ pool was calculated as the sum of violaxanthin (V), antheraxantin (A) and zeaxantin (Z) and expressed on a chlorophyll (*a*+*b*) basis. Different letters means statistical differences between species within the same family by Tukey's test ($p < 0.95$). Red dashed line split each family, from left to right: *Asteraceae*, *Brassicaceae*, *Caryophyllaceae*, *Poaceae*, *Ranunculaceae* and *Rosaceae*.

In the *Asteraceae* and *Poaceae* families, alien species have higher LMA than the native ones, however in the families *Caryophyllaceae*, *Ranunculaceae* and *Rosaceae* native species showed higher LMA than alien species, which agrees with a potential higher disposition to become invasive.

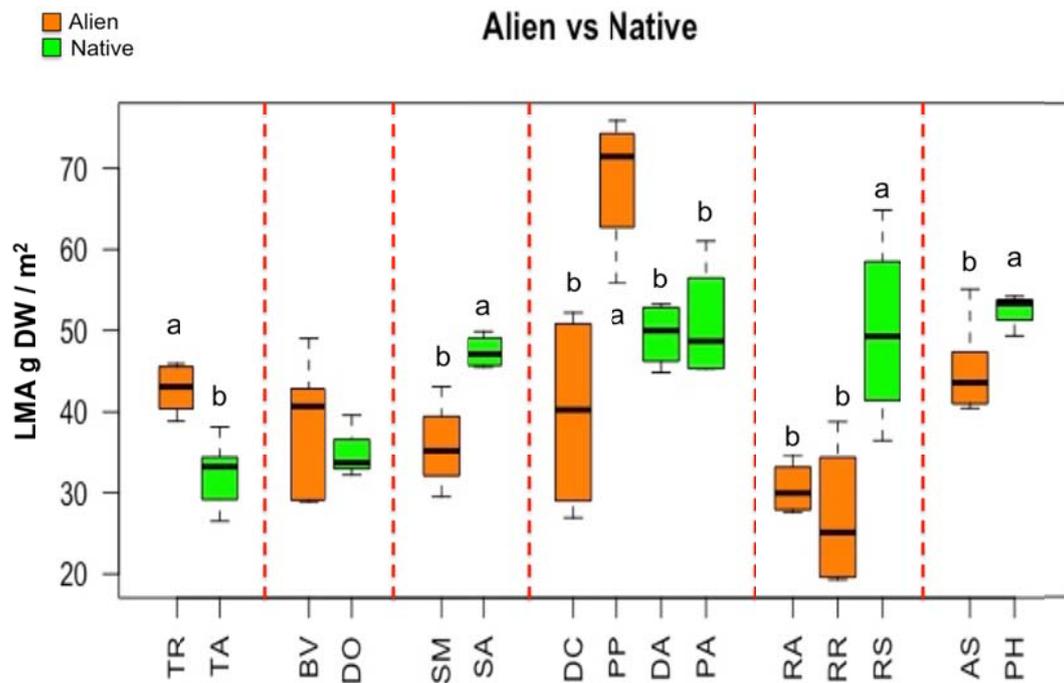


Fig. 7. Leaf mass area (LMA) per dry weight. Different letters means statistical differences between species within the same family by Tukey's test ($p < 0.95$). Red dashed line split each family, from left to right: *Asteraceae*, *Brassicaceae*, *Caryophyllaceae*, *Poaceae*, *Ranunculaceae* and *Rosaceae*.

Moreover, we performed a complete leaf ion content analysis for each species that includes the major components as C, N, P and K, as well as several relevant minor components (Fe, Cu, Mn, etc). In the figure 8, it is summarized two of the most important components for leaves; nitrogen (N) and phosphorus (P). It is described that invasive species use to show higher N and P concentrations (Gulías et al., 2003; Leishman et al., 2007). In our data higher N content in alien species was only observed in *Poaceae* and *Rosaceae* families. Both, *Taraxacum arctica* and *Potentilla hyparctica* showed higher contents of this nutrient compared to at least one of their alien pairs (Fig. 8a). P content was significant higher for alien species in 5 of the 6 families (Fig. 8b). P is an essential plant nutrient, a major component of nucleic acids, sugar phosphates, ATP, and phospholipids, all of which play important roles in photosynthesis (Reich et al., 2009). Also, it could be related to the ribulose 1-5 biphosphate (RuBP) regeneration signaled from early times as the biochemical limitation based into the light energy supply of the Calvin-Benson cycle in the famous Farquhar-von Caemmerer-Berry photosynthetic model (Farquhar et al., 1980).

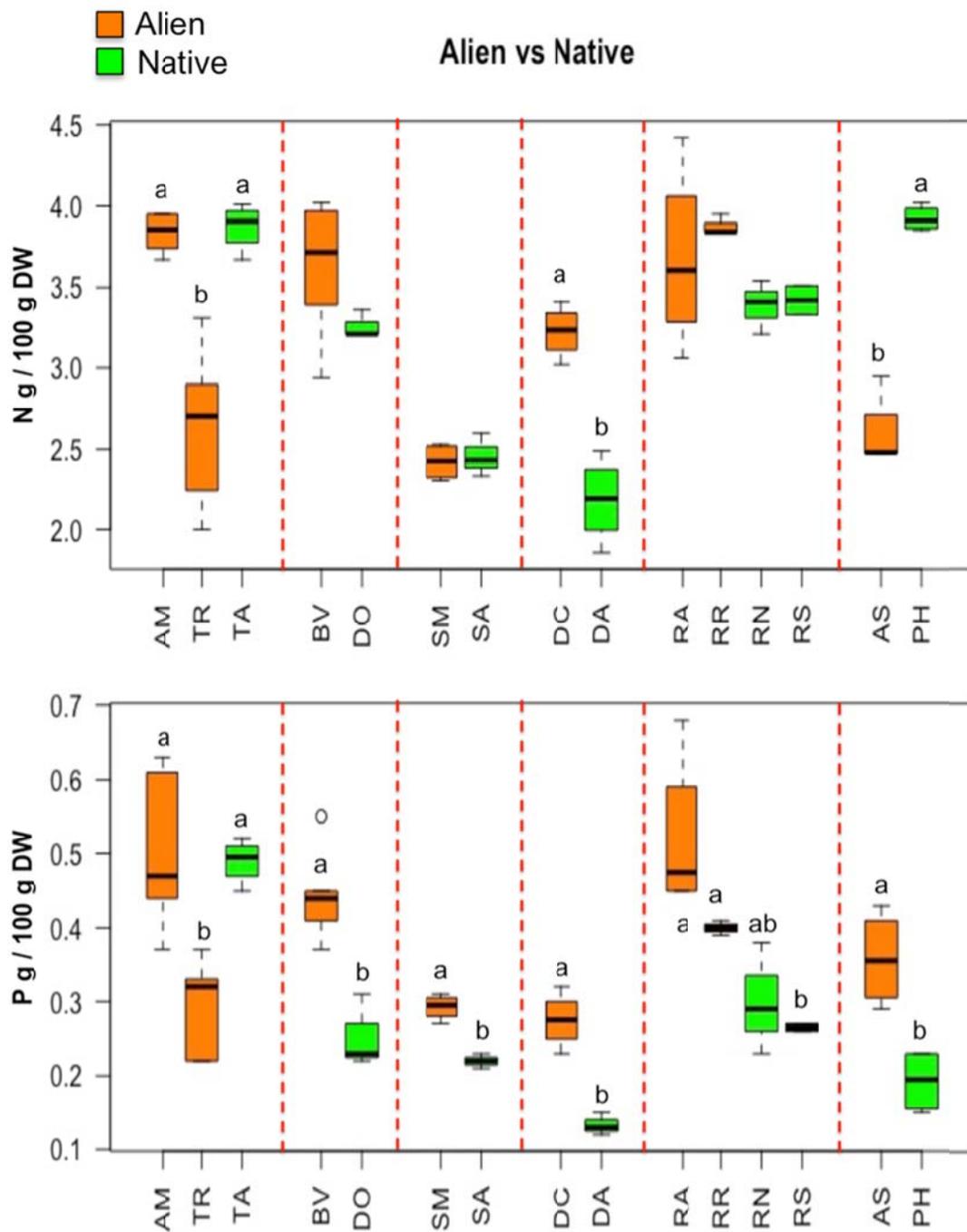


Fig. 8. Nitrogen (N) and phosphorus (P) content per leaf dry weight. Different letters means statistical differences between species within the same family by Tukey's test ($p < 0.95$). Red dashed line split each family, from left to right: *Asteraceae*, *Brassicaceae*, *Caryophyllaceae*, *Poaceae*, *Ranunculaceae* and *Rosaceae*.

4 CONCLUDING REMARKS

The High Arctic is one of the regions of the world most affected by global warming and climatic change. Also, human activities as tourism are being increased importantly in this region. Alien invasive species represent one of the major threats for native ecosystems, since they can suddenly become invasive mostly in a climate change scenario, and recently in Svalbard it was described that tourists and other human related activities, as farming, are one of the main vectors for alien/invasive species entrance (Ware et al., 2012). We evaluated a total of 17 species from 6 different families in terms of stress tolerance, photosynthetic capacity, photosynthetic pigment profile, leaf anatomy and ion content. Comparing the alien and native species within the same family, different specific behaviors were observed, several native species showed important stress tolerance values under our tests (also comparing a global dataset). Interestingly, 3 native species also showed higher photosynthetic capacity than their alien relatives and also 2 of them showed higher stress tolerance values than their alien relatives (*Poa alpina* and *Potentilla hyparctica*). In three families *Asteraceae*, *Brassicaceae* and *Ranunculaceae* alien species showed higher photosynthesis than native ones, however they showed low stress tolerance rates. At photosynthetic pigment level, data suggest that in general alien species showed higher photoprotective status than native species. This could be an indicator of light stress under the day light-continuous growing season in the arctic in comparison to the adapted native species. As a general trend, alien species showed higher P accumulation in their leaf tissues than natives, what would indicate a specific differential investment in nutrient resources.

Overall, our results reveal a current situation of equal competition capacity, in terms of photosynthetic performance (at 15°C) and leaf desiccation stress tolerance, between native and alien plant species in Svalbard. This scenario, could however change towards better performance of alien species in a either warmer, or more altered (higher nitrogen availability) scenario.

Further research is needed to define the environmental responses of alien versus native plants in the High Arctic in terms of response to warmer temperatures, the midnight sun (continuous light), nutrient availability and species competition.

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