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Influence of altitude and enhanced ultraviolet-B radiation on tuber production, seed viability, leaf pigments and morphology in the wild potato species *Solanum kurtzianum* Bitter & Wittm collected from an elevational gradient

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ABSTRACT

Climate change could lead to an upward shift in plant distribution, exposing populations to higher levels of ultraviolet (UV)-B radiation. In the framework of an *in situ* strategy for conserving potato wild relatives, we evaluated the effect of high UV-B levels on natural population of *Solanum kurtzianum*. The hypothesis is that plants from naturally higher altitudes are more adapted to increased UV-B radiation. Two populations from low and high altitudes were field supplemented using UV-B-lamps (+UV-B) or excluded from it with plastic filters. Additionally, to assess in which extent the plant responses to these artificial experimental conditions are reproducible in natural conditions, three genotypes were cultivated in two mountain experimental gardens (EG) at different elevations. +UV-B treatment induced changes in leaf morphology and increases in phenolic compounds in both populations, indicating plant adaptation, since chlorophylls and reproductive structures were not negatively affected. These results indicate that this environmental factor may not limit the displacement of populations towards sites with higher UV-B levels. Meanwhile, in higher-altitude EG a tubers yield reduction, mainly through a decreased tuber number and a bigger accumulation of phenolic compounds than in +UV-B treatment were observed, suggesting that UV-B is not the only factor involved in plants adaptation to high altitude environments.

1. Introduction

An intrinsic component of sunlight is ultraviolet (UV) radiation that is conventionally divided into UV-A (315–400 nm), UV-B (280–315 nm) and UV-C (100–280 nm). During the evolution of Earth, the formation of a stratospheric ozone layer led to changes in the spectral composition of sunlight reaching the ground [1]. Due to the ozone layer, UV-C is completely absorbed and the biosphere is affected by UV-A and part of the UV-B radiation [2]. The dynamic of ambient UV-B levels depends, not only on stratospheric ozone layer, but also on solar angle (time of the day, season and latitude), cloud cover and altitude [3,4]. The photon energy increases as wavelength shortens, thus solar UV-B radiation is the most energetic fraction of sunlight that reaches the ground.

Although UV-B radiation is potentially harmful, it is mainly an environmental signal that has diverse and complex effects on higher plants causing large photobiological effects related to protection and repair mechanisms, as well as photomorphogenic responses that allow plant acclimation [5–7]. It has become increasingly clear that under realistic UV-B exposure conditions, the UV-damage is a rare event [4,8–10]. The harm is more evident when plants are exposed to UV-B without previous acclimatization. In particular, plants that naturally grow in high-UV radiation environments (*e.g.* higher altitudes) produce more photoprotective pigments (UV absorbing compounds; UVAC) and may be less vulnerable to damage by increased UV-B than those endemic from low-UV radiation locations [9,11].

Climate change may have important impacts on future Earth incident UV radiation [8,12,13] and is expected to have a directional impact on the distribution, abundance, species assemblage, phenology and physiology of a wide range of species. Poleward and upward shifts

Abbreviations: Car, carotenoids; Chl, chlorophylls; EG, experimental garden; FW, fresh weight; LA, leaflet area; LSD, least significant difference; PAR, photosynthetically active radiation; SVI, seedling vigour index; UV, ultraviolet; UVAC, UV absorbing compounds; VNR, Villavicencio Natural Reserve

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Table 1
Solanum kurtzianum Bitter & Wittm populations and genotypes under study.

Population (P)/Genotype (G) Label	Localization	Altitude (m a.s.l.)	Cultivation condition				Germination assay
			UV-B experiment[a]		Altitudinal experiment[b]		
			+UV-B	-UV-B	EG-1141	EG-2113	
P-1141	S 32° 34′ 39” W 68° 56′ 45”	1141	21	20	–	–	+
P-1200	S 32° 32′ 04” W 68° 57′ 02”	1200	–	–	–	–	+
P-1300	S 32° 32′ 05” W 68° 57′ 02”	1300	–	–	–	–	+
P-1713	S 32° 30′ 52” W 69° 00′ 33”	1713	–	–	–	–	+
P-1900	S 32° 30′ 06” W 69° 01′ 10”	1900	–	–	–	–	+
P-2000	S 32° 30′ 05” W 69° 01′ 19”	2000	–	–	–	–	+
P-2010	S 32° 30′ 05” W 69° 01′ 22”	2010	18	13	–	–	+
G-1141-1	S 32° 34′ 39” W 68° 56′ 45”	1141	–	–	6	6	–
G-1935-2	S 32° 30′ 05” W 69° 01′ 19”	1935	–	–	6	6	–
G-2166-3	S 32° 32′ 05” W 69° 01′ 32”	2166	–	–	6	6	–

[a] Genotype number assayed in each conditions: artificial UV-B conditions by lamps (+UV-B) and filters (−UV-B).
[b] Biological replicates (clones) assayed in each conditions: mountain experimental garden located at 1141 (EG-1141) and 2113 (EG-2113) m a.s.l. in the same hill region.

are the most frequent types of range shifts predicted in response to warming [14–17]. Thus, mountain ecosystem are relevant observational sites to study plant responses to climate change of endemic plant communities that are in constant interaction with surrounding environmental changes [14,18]. In ecology, a great challenge is predict plant responses to climate change. Some models are made mainly through experimental approaches and may led to under estimate plant responses when are compared with observational studies [19]. In this framework, it is necessary a better understanding about how species respond to experimental increased levels of UV-B and to compare to what extent the observed responses reflect what actually happens in the real-world context. This approach can be of value to evaluate species vulnerability in order to avoid potentially biodiversity loss.

The potato, *Solanum tuberosum* L., is the most important non-cereal food crop worldwide [20] and many investigations have been conducted to study its response to increased UV-B levels. Changes in biochemical compounds and morphological response in leaves have been reported [21,22]. Also, there is evidence of decreases and changes in the biomass partition of the plant [23]. As commercial and highly productive crops can be more vulnerable to biotic and abiotic factors due to genetic uniformity, then crop wild relatives are useful in breeding programs (for review see [24]). However, the role and effect of UV-B radiation in wild potato species from an altitudinal gradient has not been studied yet.

Hundreds of wild potato species have been described, which are adapted to multiple habitats along the Andean region in the Americas [25], growing from sea level up to 4500 m a.s.l. [26]. *Solanum kurtzianum* Bitter & Wittm. is considered the Argentinean wild potato best adapted to arid regions [27], distributed along a transect of approximately 900-km long with a mean altitude of 1562 m a.s.l. [26]. Potential breeding use has been described for *S. kurtzianum* germplasm, which in turn has been successfully incorporated into modern cultivar pedigrees (for detail see [28]). Although tubers are important to maintain natural populations, botanical seeds play a relevant role on *S. kurtzianum* population establishment [29]. Our group is implementing an *in situ* conservation project of this species in a mountain protected area, the Villavicencio Natural Reserve (VNR), where *S. kurtzianum* was found in the range from 1082 to 2490 m a.s.l. [28].

The aims of this work were to study the effects of elevated UV-B on the potato wild relative *S. kurtzianum* and to contribute to *in situ* conservation programs. Specifically, to know whether *S. kurtzianum* populations that grow in the upper part of the VNR altitudinal range are more adapted to support higher UV-B levels than those from the lower one and to evaluate the effect of UV-B on seed viability and seedling development, as an environmental factor that possibly affects the distribution of this species. Variations in tuber production, morphological and biochemical characters, seed germination and seedling development of *S. kurtzianum* germplasm, collected along an altitudinal gradient and subsequently subjected to contrasting UV-B conditions (artificially supplemented by lamps and filtered), were studied. To assess in which extent these artificial experimental conditions reflect the reality on natural conditions, the UV-B responses were compared with those observed in naturally contrasting conditions by cultivating genotypes at different elevations in a mountain area, *i.e.* including other environmental factors besides UV-B. That is, three experimental approaches were evaluated: i) UV-B experiment, in which two populations were cultivated in field with supplemental UV-B and filtered UV-B radiation; ii) altitudinal experiment, in which selected genotypes were cultivated in two mountain experimental gardens (EG) located at 1141 and 2113 m a.s.l, respectively in VNR; and iii) a germination assay, in which the seed viability and seedling development were assayed on seeds collected from the UV-B experiment and from natural populations along the altitudinal gradient.

2. Materials and methods

2.1. Plant material

2.1.1. Seed collection from natural populations

Botanical seeds were collected from natural populations of *S. kurtzianum* across an altitudinal gradient in the VNR (Table 1). The collection sites were geo-referenced using a global positioning system (GPS) device and each evaluated population was labelled with the corresponding altitude (*e.g.* population “P-1141” was collected at 1141 m a.s.l.). Each population was constituted from a set of seeds

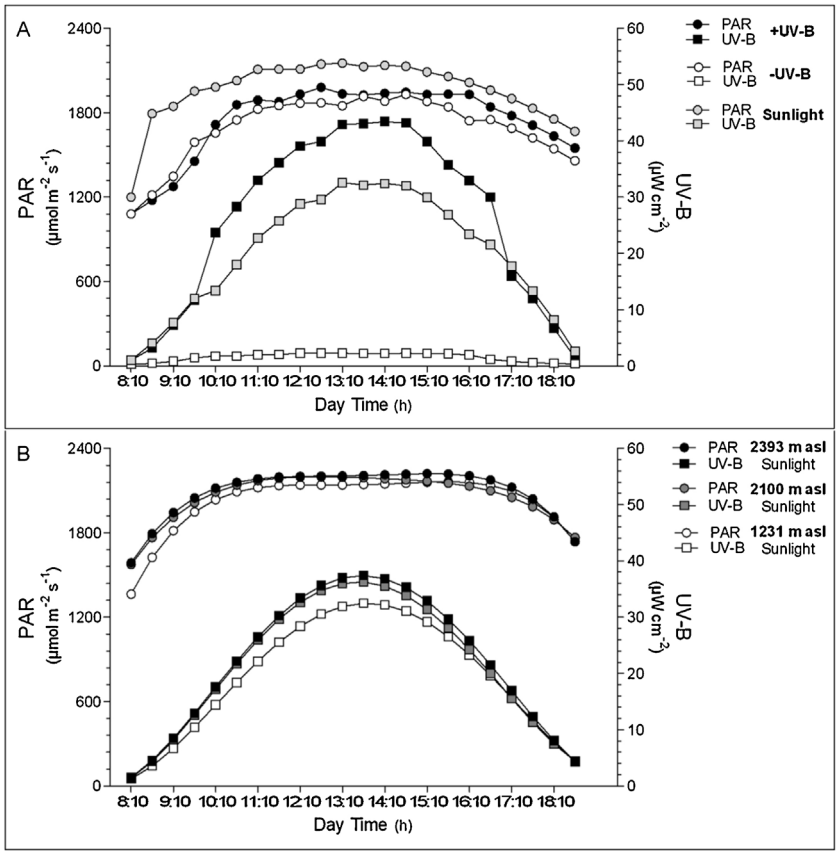

Fig. 1. Diurnal variation of erythemal UV-B irradiance (µW cm^{-2}) and PAR fluence rate (µmol m^{-2} s^{-1}) registered during a representative sunny mid-January day at: (A) Facultad de Ciencias Agrarias (FCA; S 33°0′, W 68°52′ and 940 m a.s.l.), directly from sunlight and from the −UV-B and +UV-B treatments; and at (B) an elevational gradient of 1162 m in the Villavicencio Natural Reserve.

(genotypes). Fruits collected from 20 randomly selected plants in the field in 2011, were disaggregated and seeds stored at 4° C until use.

2.1.2. Tuber obtaining as starting plant material for experiments

In February 2014, 100 of the obtained seeds per population were soaked 24 h in 1500 ppm gibberellic acid to break dormancy, then placed on Petri dishes with 0.8% (w/v) water-agar solution in a growth chamber under white fluorescent day light (photosynthetically active radiation; PAR of 133.8 µmol m^{-2} s^{-1} and UV-B of 0.13 µW cm^{-2}) with a 16-h photoperiod at 25° C constant temperature. The seedlings were transplanted into 5 L pots filled with organic compost and cultivated four months in the same conditions. Based on the tubers formed during this growing season, a set of plants were selected for using in experimental conditions (see section 2.2). Tubers were harvested, stored in paper bags at 4° C for three months and then maintained at room temperature until they broke dormancy. In January 2015, sprouted tubers were used as starting plant material and cultivated according to the experimental conditions detailed below (section 2.2). Two populations, P-1141 and P-2010, were used in UV-B experiment (see *2.2.1* and Table 1). In altitudinal experiment, from populations P-1141, P-1935 and P-2166 one genotype (one plant) per population were selected based on the number of tubers produced (G-1141-1, G-1935-2 and G-2166-3) and assayed in experimental gardens (see *2.2.2* and Table 1). In this last experiment, in order to assess the plant responses under uncontrolled environmental conditions, clones of each genotype were used to exclude genetic variability as an additional factor to be considered. In addition, seeds collected from P-1200, P-1300, P-1713, P-1900 and P-2000 and those collected from the UV-B experiment were used to assess germination capacity and seedling growth (see 2.2.3 section and Table 1).

2.2. Experimental conditions

2.2.1. UV-B experiment with artificial contrasting UV-B conditions using lamps and filters: population level analysis

Two UV-B regimes were set in field at 940 m a.s.l. at the Facultad de Ciencias Agrarias Campus (S 33°0′, W 68°52′) to treat populations during almost three months (16 January until 8 April, 2015). Genotypes from populations P-1141 and P-2010 (Table 1) were grown from sprouted tubers on 250 mL pots, daily irrigated and weekly fertilized with Fertiliser KSC II PHYT-actyl (Timac Agro, USA). Two independent portable greenhouses of metallic frames (175 cm width × 250 cm length × 150 cm height) were covered with either clear polyester or low-density polyethylene to set the minus UV-B and supplemental UV-B treatments, respectively (see below); and positioned longitudinally along the north-south axis. The north and south sides of the portable greenhouses were left open to favour air circulation. To avoid early morning and late afternoon solar UV exposure, 100 cm long curtains with the same plastic films were installed on the east and west sides. The plants (see number of replicates in Table 1) were labelled with numbers and randomized with random function in excel. Then, the plants were placed within the portable greenhouses described above following a completely randomized design (CRD) with a factorial arrangement of treatments (UV-B x POP).

The minus UV-B (-UV-B) treatment was set by covering one portable greenhouse with a clear polyester (100 µm) that filters 95% of solar UV-B (Oeste Aislante, Buenos Aires, Argentina). The UV-B filter also absorbed *ca.* 30% of solar UV-A and 15% of PAR. The supplemental UV-B (+UV-B) treatment was produced by adding UV-B to the solar radiation with irradiances of 10 µW cm^{-2} over a 7 h period (from 10:00 to 17:00 h) using two UV-B fluorescent lamps (TL 100 W/01; Philips, Nieuwegein, the Netherlands) suspended 50 cm above plants within the

other portable greenhouse along its longitudinal axis. The UV-B lamps emitted at the narrow waveband of 310–315 nm with a maximum at 311 nm, and are commonly used to treat psoriasis [30]. To minimize the environmental differences between −UV-B and +UV-B treatments, a low-density polyethylene (40 μm) that transmitted most of the solar radiation (*ca.* 75% of UV-B, 80% of UV-A and 85% of PAR) was used to cover the portable greenhouse of the +UV-B treatment. UV-B irradiance in +UV-B treatment was 11% higher than those measured at 2393 m a.s.l., the *S. kurtzianum* upper altitude limit so far described in VNR [28]. Irradiances of UV-B and PAR fluence rate were measured with a PMA2102 erythemally-weighted UV-B detector (Solar Light Company, Glenside, PA) and a LI-190SA quantum sensor (LI-COR, Lincoln, NE), respectively. Mean values of UV-B and PAR are shown in Fig. 1A.

2.2.2. Altitudinal experiment with natural contrasting UV-B and other environmental conditions: genotype level analysis

Two mountain EG were established in the VNR, one located at 1141 m a.s.l. (EG-1141; S 32°34'39.57", W 68°56'45.65") and the other at 2113 m a.s.l. (EG-2113; S 32°35'6.47", W 69°56.85"). In both EG, clones from three genotypes (G-1141-1, G-1935-2 and G-2166-3; Table 1) were cultivated on 10 L pots filled with compost, previously autoclaved for sterilization. Six biological replicates (*i.e.* clones obtained from tubers) per genotype were used in each EG (n = 6). Plants were weekly irrigated and fertilized with Fertiliser KSC II PHYT-actyl (Timac Agro, USA). The experiment started on 14 January and finished on 2 September, 2015. The plants were labelled with numbers and randomized with random function in excel. Then, the plants were placed within the EG following a CRD, with a factorial arrangement of treatments (EG x GEN). Mean values of UV-B and PAR registered at elevational gradient of about 1100 m within VNR are shown in Fig. 1B.

2.2.3. Germination assay

Seven sets of seeds were evaluated: two obtained from the UV-B experiment (+UV-B and −UV-B, respectively) and five collected in 2011 from natural population along the altitudinal gradient (Table 1). Seeds were soaked in 96% ethanol for 1 min and then with pure and sterilized water for 5 min. In this assay, as the aim was to evaluate natural seed germination, gibberelic acid was not used to break seed dormancy. Then, 30 seeds were placed on Petri dishes with a 0.8% (w/v) water-agar solution and incubated in a growth chamber under white fluorescent day light (PAR 133.8 μmol m^{-2} s^{-1} and UV-B 0.13 μW cm^{-2}) with a 16-h photoperiod at 25 °C constant temperature. Five Petri dishes (n = 5) per set of seeds were used. Also, seeds were screened for light sensitivity since there were no reports about the light influence on seed germination (photoblasticity) for *S. kurtzianum*. Thus a replicate germination assay was performed in darkness.

2.3. Sampling of leaves

Two fully expanded (6th and 7th from the base) leaves per plant were collected 35 and 47 days after the treatments began for UV-B and altitudinal experiments, respectively. Each leaf was severed in the field, covered with aluminium foil and immediately frozen with liquid nitrogen, transported to the laboratory and kept at −20 °C until further analysis.

2.4. Analysis of photosynthetic and photoprotective pigments, terminal leaflet area and thickness

The chlorophylls (Chl *a* and Chl *b*), carotenoids (Car), total chlorophyll (TChl) and UVAC were determined in the leaflets, as previously described by Berli et al. [31]. Terminal leaflet area (LA) was assessed by using a portable area meter (LICOR 3000, LI-COR Biosciences, Lincoln, NE, USA). Photosynthetic and photoprotective pigments were calculated on a leaf area basis. Leaflet thickness was estimated through leaflet area and weight. Thus, 1 cm^2 leaflet discs were dried at 40° C to constant weight.

2.5. Tuber and fruit production

Total number of tubers, total tubers weight and mean tubers weight per plant were determined at the end of UV-B and altitudinal experiments. For the UV-B experiment, fruits formed through open pollination in the +UV-B and −UV-B treatments were collected separately. Then, all fruits collected in each treatment were disaggregated and the seeds pooled and stored at 4° C.

2.6. Seed germination capacity and seedling growth

The number of germinated seeds per day was registered and seven days old seedling were collected and stored at 4° C. Seedlings were divided into hypocotyl and radicle, weighed and photographed, to measure its lengths with AxioVison software (AxioVision Viewer 4.8, Carl Zeiss MicroImaging GmbH, Jena, Deutschland). Also, UVAC was determined in hypocotyls and radicles as previously described (see 2.4 section) and the seedling vigour index (SVI) was calculated by seedling length (hypocotyl + radicle length) x germination percentage at seventh day according to Muthusamy et al. [32].

2.7. Statistical analysis

For the UV-B and EG experiments, the effects of UV-B, altitude, population, genotype, and their interactions in each measured parameter were determined by two-way ANOVA and LSD Fisher's comparison, with a significance level of $P \leq 0.05$ using InfoStat (InfoStat version 2009 software; Grupo InfoStat, Córdoba, Argentina). The GraphPad software (GraphPad Prism 5.02, California, USA) was used to make all the graphics. For germination assay, germination percentage was assessed with a generalized linear mixed-model approach with random effect(s) to account for serial correlation among measures within plots at each development stage, using InfoStat. The parameters measured in seedlings were compared by one-way ANOVA and Fisher's LSD test also with InfoStat.

3. Results

The results would be presented in a way that allow comparing and contrasting the manipulative UV-B (*UV-B experiment*) and the elevational (*Altitudinal experiment*) approaches to assess in which extent the artificial experimental conditions reflect the reality on natural conditions. Also, it is important to highlight that the results have to be interpreted with caution since there were no replicates either for the light manipulation in the UV-B experiment or for natural condition assayed in the EG.

3.1. Light environment

The maximum UV-B irradiance utilised in the supplemented UV-B treatment was about 18 times higher than in filtered UV-B treatment (43.42 and 2.31 μW cm^{-2}, respectively), with minor differences in PAR fluence rate (1980 and 1915 μmol m^{-2} s^{-1}, respectively; Fig. 1A).For the altitudinal experiment, the maximum irradiance value of solar UV-B registered during a mid-January day in the VNR increased by 11.6% from 1231 m a.s.l. to 2100 m a.s.l. and 15% to 2393 m a.s.l. (32.48, 36.11 and 37.4 μW cm^{-2}, respectively), while PAR varied 1.6 and 2.64% for the same comparisons (2162.77, 2197.59 and 2219.97 μmol m^{-2} s^{-1}, for 1231, 2100 and 2393 m a.s.l., respectively; Fig. 1B).

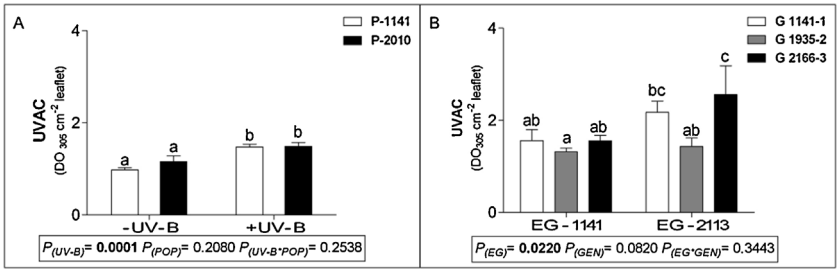

Fig. 2. UV-absorbing phenolic compounds (UVAC) per leaflet area in *Solanum kurtzianum* plants collected along an altitudinal range. (A) Responses to supplemented UV-B (+UV-B) and filtered UV-B (-UV-B) treatment in populations collected at 1141 and 2010 m a.s.l. (B) Response in clones of three genotypes (G-1141-1, G-1935-2 and G-2166-2) cultivated in mountain experimental garden at 1141 m a.s.l. (EG-1141) and 2113 m a.s.l. (EG-2113). Values are means obtained from *n* replicates presented on Table 1. $P_{(UV\text{-}B)}$, $P_{(POP)}$, $P_{(UV\text{-}B*POP)}$, $P_{(EG)}$, $P_{(GEN)}$, and $P_{(EG*GEN)}$: effects of UV-B, population and they interaction, EG, genotypes and their interaction, respectively. Error bars show SE; different letters indicate statistically significant difference ($P \leq 0.05$).

3.2. Photoprotective pigments

For the UV-B experiment, the UVAC in leaves were increased by +UV-B (Fig. 2A). The UVAC accumulations in +UV-B *vs.* −UV-B were, on average, 39.43% higher than in −UV-B.

Altitudinal experiment showed that higher altitude EG (EG-2113) increased UVAC (Fig. 2B). The amounts of UVAC were, on average, 38.49% higher in EG-2113 than those obtained in the +UV-B treatment at 940 m a.s.l.

3.3. Photosynthetic pigments

The +UV-B treatment induced an increase in the concentration of Car and chlorophylls with differences among populations and significant factor interactions. The increases in Car in +UV-B respect to −UV-B treatments were higher in P-1141 than in P-2010 (64.48% and 21.05%, respectively), with an average of 42.67% (Fig. 3A). Chl *a* increased on average 54.24% and Chl *b* 48.35% comparing +UV-B vs. −UV-B, and the rise in Chl *b* was greater in P-2010 than in P-1141 (significant interaction; Table 2). Also, factors interact for the ratio of total chlorophyll (TChl) to Car being significantly reduced for P-2010 in −UV-B treatment (Fig. 3B).

In the altitudinal experiments, EG affected the concentration of Car and TChl/Car ratio, with differences among genotypes (Fig. 3C, 3D). Car concentration was higher in G-1935-2 and a reduction of 14.59% on average was observed in EG-2113 (Fig. 3C). Thus, the TChl/Car ratio increased, on average, 11.08% (Fig. 3D). Chl *a* and *b* were differentially accumulated in the genotypes (*i.e.* Chl *a* was greater in G-1935-2; while Chl *b* was higher in G-2166-3), without EG effects (Table 2).

3.4. Leaflet area and thickness

In the UV-B experiment, UV-B affected terminal leaflet area and thickness, with differences between populations (Fig. 4A and B). In

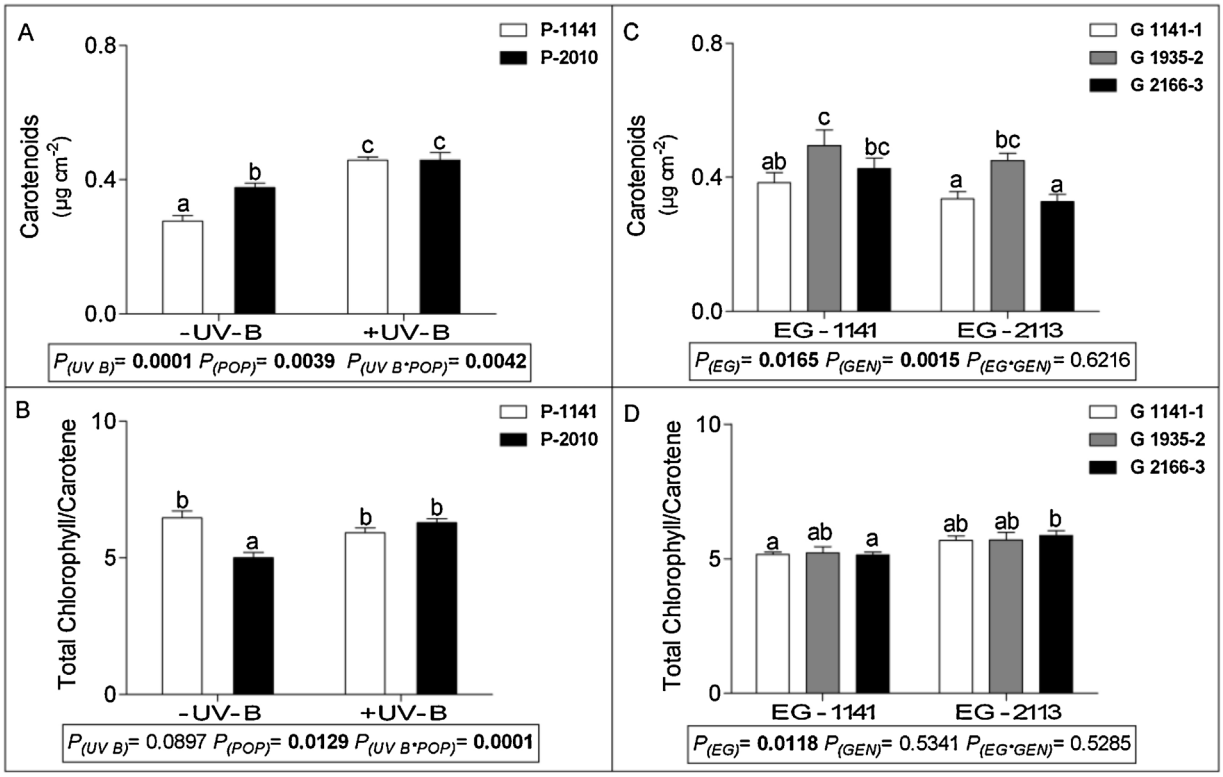

Fig. 3. Photosynthetic pigments per leaflet area of *Solanum kurtzianum* plants collected along an altitudinal range. Carotenoids (A) and Total Chlorophyll/Carotenoids ratio (B) of populations collected at 1141 and 2010 m a.s.l. and cultivated in filtered UV-B (-UV-B) and supplemented UV-B (+UV-B). Carotenoids (C) and Total Chlorophyll/Carotenoids ratio (D) in clones of three genotypes (G-1141-1, G-1935-2 and G-2166-3) cultivated in mountain experimental gardens at 1141 (EG-1141) and 2113 (EG-2113) m a.s.l. Values are means obtained from *n* replicates presented on Table 1. $P_{(UV\text{-}B)}$, $P_{(POP)}$, $P_{(UV\text{-}B*POP)}$, $P_{(EG)}$, $P_{(GEN)}$, and $P_{(EG*GEN)}$: effects of UV-B, population and they interaction, EG, genotypes and their interaction, respectively. Error bars show SE; different letters indicate statistically significant difference ($P \leq 0.05$).

Table 2
Photosynthetic pigments per leaflet area (μg cm^{-2}) of *Solanum kurtzianum* plants growing under contrasting UV-B conditions, artificially by lamps and filters (+UV-B and −UV-B, respectively) or naturally by cultivating in mountain experimental garden located at 1141 and 2113 m a.s.l. in the same hill region (EG-1141 and EG-2113, respectively). Values are means ± SE obtained from *n* genotypes/clones presented on Table 1. $P_{(UV\text{-}B)}$, $P_{(POP)}$, $P_{(UV\text{-}B*POP)}$, $P_{(EG)}$, $P_{(GEN)}$, and $P_{(EG*GEN)}$: effects of UV-B, population and they interaction, EG, genotypes and their interaction, respectively. Mean with different letters show significance difference ($P \leq 0.05$).

Cultivation conditions	Population/ Genotype	Photosynthetic pigments	
		Chlorophyll a	Chlorophyll b
−UV-B	P-1141	1.27 ± 0.07a	0.47 ± 0.02a
	P-2010	1.44 ± 0.08a	0.44 ± 0.03a
+UV-B	P-1141	2.07 ± 0.07b	0.62 ± 0.02b
	P-2010	2.11 ± 0.07b	0.73 ± 0.02c
p(UV-B)		**0.0001**	**0.0001**
p(POP)		0.1544	0.0770
*p(UV-B*POP)*		0.3893	**0.0029**
EG-1141	G-1141-1	1.48 ± 0.15a	0.50 ± 0.04a
	G-1935-2	1.93 ± 0.15b	0.58 ± 0.04ab
	G-2166-3	1.61 ± 0.15ab	0.70 ± 0.04b
EG-2113	G-1141-1	1.43 ± 0.15a	0.47 ± 0.04a
	G-1935-2	1.93 ± 0.15b	0.49 ± 0.04a
	G-2166-3	1.42 ± 0.15a	0.63 ± 0.04b
p(EG)		0.4928	0.0933
p(GEN)		**0.0059**	**0.0005**
*p(EG*GEN)*		0.8114	0.7537

P-values in bold show significance difference at $P \leq 0.05$.

+UV-B treatment, terminal leaflet area decreased 30.61% on average and terminal leaflet thickness increased on average 25.83%.

In the altitudinal experiment, no differences in terminal leaflet area were observed (Fig. 4C). However, terminal leaflet thickness mean value increased on average 29.12% in EG-2113 (Fig. 4D). Fig. 4 also shows different morphological leaflets characteristics between the experiments; the leaves were more expanded and thinner when exposed to natural conditions in the altitudinal experiment, as compared with the artificial UV-B exposure.

3.5. Tuber production

Artificial UV-B conditions in the UV-B experiment did not induce changes in the number of tubers produced per plant; however, differences were observed between populations (Fig. 5A). UV-B and populations significantly interact ($P \leq 0.05$ level) for the total tuber weight, *i.e.* tuber yield (Fig. 5B); without affecting mean tuber weight (Fig. 5C). The tuber yield increased in P-1141 exposed to −UV-B treatment (Fig. 5B).

Similarly to the observed in UV-B experiment, the cultivation at different altitudes did not induce changes in the number of tubers produced per plant, although there were differences among genotypes (Fig. 5D). Significant differences induced by EG were observed in total tuber weight, where total tuber yield declined 28.39% on average by increased altitude (Fig. 5E). There were differences in the mean tuber weight between altitudes and among genotypes. On average, mean tubers weight in EG-2113 decreased 40.74% respect to EG-1141 (Fig. 5F). Among genotypes, the G 1141-1 produced a greater number of tubers, but of a smaller size (Fig. 5D and 5F). In addition, the weight of each tuber and the tuber yield was greater in the altitudinal experiment, as compared with the artificial UV-B exposure.

3.6. Seed germination and seedling growth

The mean germination percentage was significantly higher in light than in darkness conditions (29.55% *vs.* 8.29%, respectively; $P \leq 0.05$). Thus, only germination results in light conditions are presented.

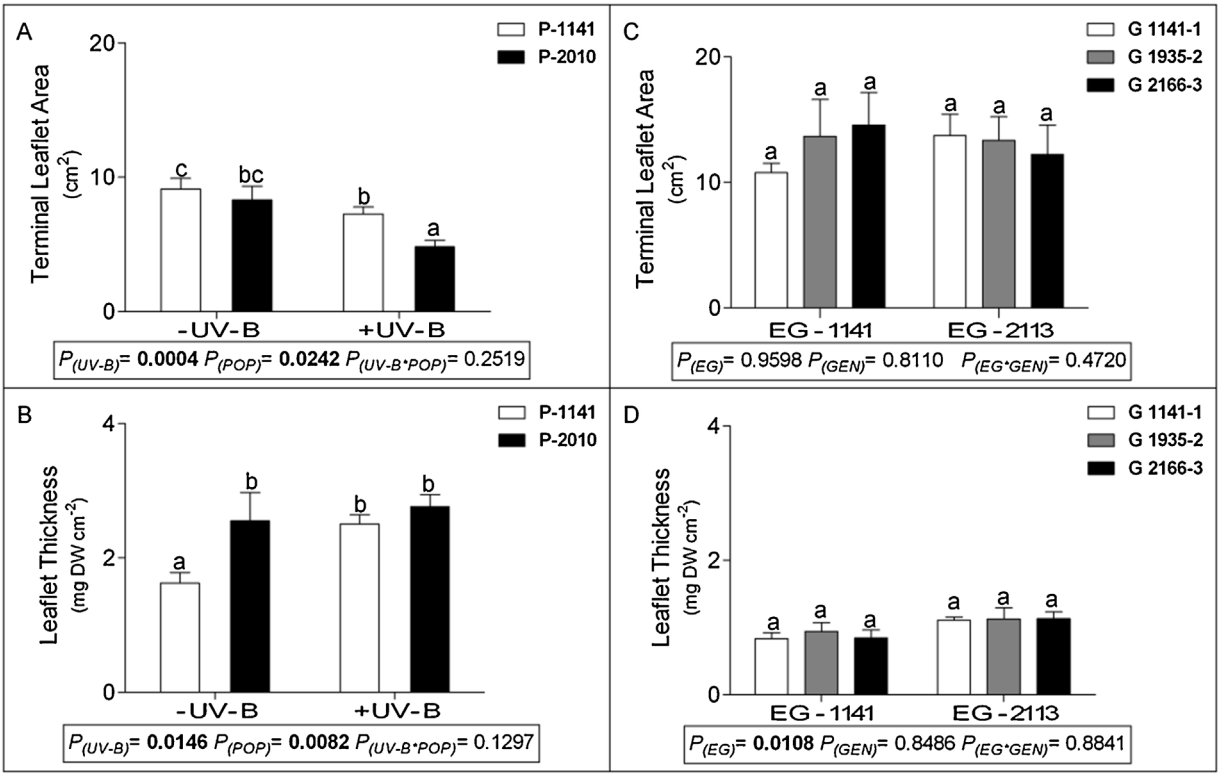

Fig. 4. Terminal leaflet area and thickness in *Solanum kurtzianum* plants collected along an altitudinal range. Terminal leaflet area (A) and thickness (B) of populations collected at 1141 and 2010 m a.s.l. and cultivated in filtered UV-B (-UV-B) and supplemented UV-B (+UV-B). Terminal leaflet area (C) and thickness (D) in clones of three genotypes (G-1141-1, G-1935-2 and G-2166-3) cultivated in experimental gardens at 1141 (EG-1141) and 2113 (EG-2113) m a.s.l. Values are means obtained from *n* replicates presented on Table 1. $P_{(UV\text{-}B)}$, $P_{(POP)}$, $P_{(UV\text{-}B*POP)}$, $P_{(EG)}$, $P_{(GEN)}$, and $P_{(EG*GEN)}$: effects of UV-B, population and they interaction, EG, genotypes and their interaction, respectively. Error bars show SE; different letters indicate statistically significant difference ($P \leq 0.05$).

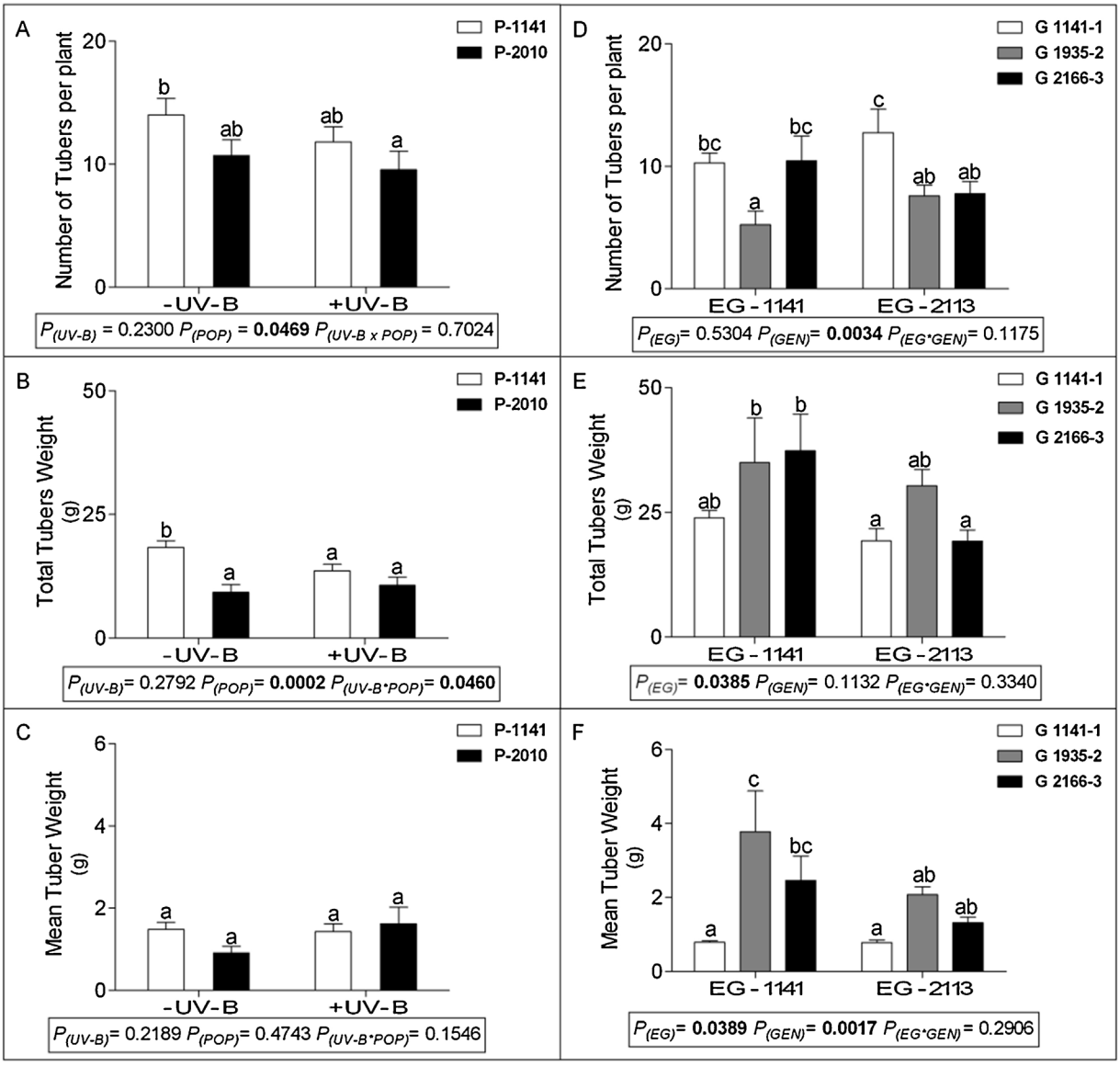

Fig. 5. Number and weight of tubers produced in *Solanum kurtzianum* plants collected along an altitudinal range. (A) Number, (B) total fresh weight and (C) mean tuber weight of tubers produced per plant from populations collected at 1141 and 2010 m a.s.l. and cultivated in supplemented UV-B (+UV-B) and filtered UV-B (-UV-B). (D) Number, (E) total fresh weight and (F) mean tuber weight of tubers produced per plant of three genotypes (G-1141-1, G-1935-2 and G-2166-3) cultivated in mountain experimental gardens at 1141 (EG-1141) and 2113 (EG-2113) m a.s.l. Values are means obtained from *n* replicates presented on Table 1. $P_{(UV\text{-}B)}$, $P_{(POP)}$, $P_{(UV\text{-}B*POP)}$, $P_{(EG)}$, $P_{(GEN)}$, and $P_{(EG*GEN)}$: effects of UV-B, population and they interaction, EG, genotypes and their interaction, respectively. Error bars show SE; different letters indicate statistically significant difference ($P \leq 0.05$).

Table 3
Germination percentage and seedling growth of *Solanum kurtzianum* seeds. Length (mm), fresh weight (FW; mg) and UV-absorbing phenolic compounds (UVAC) on 7-day old hypocotyl and radicle per seedling and seedling vigour index (SVI). Seed collected from UV-B treatment or from 5 natural populations grown in chamber whit white fluorescent day light at 25 °C constant temperature. Values are means ± SE (n = 5). $P_{(UV\text{-}B)}$ and $P_{(POP)}$: effects of UV-B and population, respectively. Mean with different letters show significance difference ($P \leq 0.05$).

Treatment/ Population	Germination percentage	Hypocotyl/Seedling			Radicle/Seedling			SVI
		Length	FW	UVACs	Length	FW	UVACs	
−UV-B	87.64 ± 2.06	2.27 ± 0.07	22.56 ± 2.50	0.09 ± 0.02	22.30 ± 1.66	27.32 ± 8.97	0.06 ± 0.02	2166.34 ± 173.94a
+UV-B	85.64 ± 2.06	2.17 ± 0.07	22.56 ± 2.50	0.11 ± 0.02	19.27 ± 1.66	24.12 ± 8.97	0.08 ± 0.02	2184.64 ± 173.94a
p(UV-B)	0.5296	0.3792	0.9999	0.2952	0.2320	0.8072	0.4836	0.9425
P-1200	15.95 ± 4.47b	1.68 ± 0.23a	3.20 ± 2.49a	0.12 ± 0.03	17.75 ± 3.24	3.55 ± 3.05a	0.06 ± 0.04	417.43 ± 122.78a
P-1300	24.77 ± 4.47ab	1.89 ± 0.23a	5.45 ± 2.49a	0.20 ± 0.03	22.78 ± 3.24	5.12 ± 2.73a	0.07 ± 0.04	686.86 ± 122.78ab
P-1713	32.62 ± 4.47a	1.75 ± 0.23a	8.54 ± 2.49ab	0.12 ± 0.03	19.80 ± 3.24	7.36 ± 2.73a	0.13 ± 0.04	802.78 ± 122.78b
P-1900	36.77 ± 4.47a	2.68 ± 0.23b	13.50 ± 2.49b	0.09 ± 0.03	17.55 ± 3.24	16.50 ± 2.73b	0.05 ± 0.04	804.87 ± 122.78b
P-2000	37.64 ± 4.47a	2.23 ± 0.23ab	15.16 ± 2.49c	0.12 ± 0.03	26.29 ± 3.24	21.44 ± 2.73b	0.05 ± 0.04	1274.32 ± 122.78c
p(POP)	**0.0186**	**0.0388**	**0.0088**	0.1494	0.3022	**0.0007**	0.5513	**0.0018**

P-values in bold show significance difference at $P \leq 0.05$.

UV-B treatments did not affect the% of germination, the length, fresh weight (FW) and UVAC of hypocotyl and radicles (Table 3). However, in the seeds collected from the altitudinal gradient, differences among populations were observed in the germination%, hypocotyl length and FW, and radicle FW. The populations from lower altitudes presented the lesser% of germination and SVI (Table 3). No significant differences among populations in radicle length and UVAC of hypocotyl and radicle were observed (Table 3).

4. Discussion

The most common plant response to UV-B tolerance at increased UV-B levels is the biosynthesis of UVAC [9,33]. These secondary metabolites, mainly phenolic compounds as flavonoids and hydroxycinnamic acids in the leaf tissues, absorb the photon energy of UV-B radiation [5]. This kind of response has also been observed in the cultivated potato *S. tuberosum* growing under supplementary UV-B radiation, being mainly flavonoids [21]. In our experiments, +UV-B changed the concentration of photoprotective compounds in *S kurtzianum*. A trend towards higher increases in UVAC was observed in the population collected from lower altitude (*i.e.* P-1141) when exposed to +UV-B treatment. This result coincides with that obtained by Ziska et al. [34] in which lower-altitude plants presented higher increases in UVAC compounds than plants from higher elevations.

Chl and Car per leaf area basis were increased by UV-B, and the P-1141 population presented lesser TChl to Car ratio, indicating that the increase of Car was higher than the TChl. Also, there was an increase in Chl *b* in both populations, but it was greater in P-2010 than P-1141. Carotenoids are photosynthetic pigments that also act as photoprotection pigments under stress conditions [35], quenching excited Chl *a* molecules and scavenging reactive oxygen species [36]. Vyšniauskiene and Rančeliene [22] reported that 5 Lithuania-bred *S. tuberosum* cultivars treated with 6 kJ m^{-2} d^{-1} UV-B doses for 8 days did not show changes in Chl *a* and *b* and Car. Several studies reported decreases in Chl in various crops, which may indicate oxidative damage to the photosynthetic pigments [37]. However, increases in Chl content in *Arabidopsis* plants growing under UV-B-enriched conditions has been described [38].

Decreases in leaf area and increases of leaf thickness are expected in response to UV-B [39–41]. These morphological modifications are effective mechanisms to reduce the transmittance of UV-B to the inner leaf cells layers, protecting the chlorophylls [41,42]. In *S. kurtzianum* the P-2010 population responds mainly by decreasing the area of terminal leaflet, while the P-1141 population responds mostly by increasing the leaf thickness. This behavior suggests that to reduce UV-B interception, less adapted plants change both leaf morphological parameters, while the more adapted plants only modify leaf expansion. Robson et al. [40] have shown that UV-B produces a short-term disruption in leaf development of non-acclimated plants, and that the effects are transient. Differential responses observed between populations in our experiment could be also transient UV-B effects, but this need to be proved.

In potato, decrease in tubers production after UV-B exposure has been reported [23], showing reductions in number, FW, biomass and starch content of tubers in plants submitted to 9.6 kJ m^{-2} of UV-B during 120 days. In our work with *S. kurtzinaum,* the +UV-B treatment did not induce changes, neither in the number of tubers, nor in the tubers weight. However, in the P-1141 population, reductions in total tuber aweight in the +UV-B treatment was observed, suggesting that this population may be vulnerable to high UV-B levels.

It has been reported that increased UV-B radiation delayed seedling emergence and affected seed formation by reducing pollen germination and pollen tubes growth of several crops [37]. There were not differences between UV-B treatments in seed germination, SVI, and seedling UVAC concentration of *S. kurtzianum*, which suggest that sexual organs and fruits development in *S. kurtzianum* were not affected by UV-B and viable seeds can be produced. On the other hand, seeds collected from natural populations along an altitudinal gradient, presented differences in seed germination and seedling growth. These results could be explained by genetic differences among population and/or by maternal environmental effects. Although previous researches using neutral SSR and AFLP markers and evaluating different *S. kurtzianum* populations have demonstrated that the higher percentage of genetic variation was within populations [29,43], it cannot rule out that adaptive genes remain differentiated among populations. On the other hand, the results obtained in the UV-B experiment indicate that the UV-B could have a marginal impact respect to other environmental factors if the maternal effects were operating in the observed differences among seeds collected from natural populations. Because of in *S. kurtzianum,* botanical seeds play a key role on population establishment [29], the reduction in germination percentage and SVI in lower-altitude populations may explain the difficulty to find *S. kurtzianum* populations below 1100 m a.s.l. in the VNR [28]. This response observed in the lower-altitude populations, in which maternal effects could play a role, unlikely is the only factor determining the lower altitudinal limit of *S. kurtzianum* in the VNR. Within this Reserve, it has been demonstrated long dispersal distance of seeds through storm water channels [29], mechanisms that would enable the germination of higher-altitude seeds in lower altitudes sites. An experiment in which seeds collected from the whole altitudinal range so far described for *S. kurtzianum* were *in situ* assayed for seed germination and seedling growth at lower altitudes (*e.g.* the EG-1141 used in this study) can illuminate what is the key factor limiting the lower limit species distribution.

Although the UV-B levels in +UV-B treatment was 20.24% higher than those registered at 2100 m a.s.l. in the VNR (43.42 *vs.* 36.11 μW cm^{-2}), the mean UVAC concentration in EG-2113 was 39.48% higher than in +UV-B. The increase in UVAC concentration in this EG may be also affected by other environmental factors like UV-A, cloudiness and temperature. Other studies have shown increases in phenolic compounds with altitude, a response related to increased UV-B levels [44]. However, Bernal et al. [45] have sampled leaves of *Buxus sempervirens* L. along an altitudinal gradient and also, conducted an *in situ* exclusion UV-B experiment at the lowest and highest altitudes. They have shown that increased phenolic compounds (phenolic acids) with altitude were not due to UV-B and conclude that other factors rather than UV-B are acting. The temperature, light quantity and quality and their interactions can affect UVAC accumulation [46,47].

Singh et al. [23] found a reduction in tuber yield of *S. tuberosum* cultivated with UV-B supplementation. In our experiment there was not effect of UV-B treatment on tuber yield. Our results indicate that in *S. kurtzianum* the activation of protective mechanism did not interfere in tuber production. In the altitudinal experiment there was a clear reduction in tuber yield in EG- 2113, pointing out that other factors than UV-B influence tubers development, and possibly could constraint the altitudinal distributional range of this species. Despite that the total tuber weight in altitudinal experiment was higher than in UV-B experiment, these differences may be explained because pots of major size were used in the former.

It is important to acknowledge that in the present work the variation among populations within elevations was not studied and that the evaluated genotypes and populations may not be representative of the variability present at each elevation. In summary, the experimental UV-B conditions assayed in this study suggest that natural populations from low and high altitude of *S. kurtzianum* are adapted to UV-B and may be challenged to increased levels of UV-B due to the upward shift projected by climatic change models. However, this approach, in which we compared artificial contrasting UV-B radiation and natural contrasting altitudes, highlights the complex interactions among multiple environmental factors. Thus, in order to advance with the *in situ* conservation program implemented in the VNR, further molecular and physiological studies in field conditions with other climatic factors and, also, the

interaction among them are necessary. The EG used in the present work could be useful as an intermediate approach between observational and experimental studies and could contribute to estimate plant distribution and adaptation to high altitude environments.

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