

Principal component analysis of intraspecific responses of tartary buckwheat to UV-B radiation under field conditions

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Abstract

Fifteen populations of tartary buckwheat (*Fagopyrum tataricum* Gaertn.) occurring in habitats with different natural UV-B levels were sampled, and the plants were exposed to enhanced UV-B radiation under field conditions simulating 25% depletion of the stratospheric ozone layer. The experimental design was a 2×15 factorial, with two levels of UV-B radiation (ambient and enhanced UV-B radiation) and plants from 15 populations. The responses of plants in growth, morphology, productivity and in the composition of photosynthetic pigments were measured. The results demonstrated that there were significant differences among populations in responses to UV-B radiation: some populations exhibited a positive effect while others were negatively affected. The UV-B effects on plant traits were correlated with the constitutive values. A principal component analysis (PCA) was used to evaluate the overall sensitivity of responses to UV-B radiation. Our results suggest that the sensitivity of plants to UV-B radiation is not only associated with the ambient UV-B level in natural habitats but also with the relative growth rate and other factors.

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1. Introduction

Reductions in the ozone column primarily due to anthropogenic discharge of chlorofluorocarbons (CFCs) have led to a substantial increase in UV-B radiation on the Earth's surface (Madronich et al., 1998; WMO, 1999). As CFCs can remain in the upper atmosphere with a half-life ranging from 50 to 150 years, decreased ozone levels will not be recovered to the pre-1970 levels until 2050 (Dentener et al., 2001; UNEP, 2002). During the last few decades, numerous investigations concerning the influence of enhanced UV-B radiation on different plant species have been conducted. The majority of plant species are affected negatively (Kakani et al., 2003; Yang et al., 2005; Ren et al., 2007; Lu et al., in press), although neutral and positive effects

have also been reported in some species (Papadopoulos et al., 1995). Great intraspecific variation in the responses of plants to UV-B radiation has been observed in different species, e.g., wheat (Li et al., 2000), maize (Correia et al., 1998), cucumber (Murali and Teramura, 1986), soybean (Li et al., 2002) and rice (Dai et al., 1994). However, the basis of intraspecific responses and the mechanisms of plant adaptation need to be further elucidated.

Nowadays, due to a reborn-interest, buckwheat is becoming one of the most important alternative crops for health food (Halbrecq et al., 2005). Tartary buckwheat (*Fagopyrum tataricum* Gaertn.) is mainly cultivated in the alpine regions and on the high plateau of Asia, and also in some countries of Central Europe (Bonafaccia et al., 2003; Fabjan et al., 2003). In some regions, it suffers from high doses of UV-B radiation during the growth season. Previous studies have shown that tartary buckwheat is sensitive to ambient and enhanced UV-B radiation (Yao et al., 2006a). Therefore, there is an urgent need to improve the

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UV-B resistance and to reveal the underlying adaptation mechanism of the tartary buckwheat. Tartary buckwheat occurs in a range of locations and is exposed to various levels of ambient UV-B radiation. Thus, as a result of long-term adaptation and evolution in their natural habitats, different populations of tartary buckwheat may possess different levels of UV-B tolerance.

In our study, 15 populations of tartary buckwheat occurring in different natural habitats were sampled, and the seeds were sown in the field to observe the crop's responses in growth, development, yield and the composition of leaf photosynthetic pigments under enhanced UV-B radiation. The values for each trait and each population were established from measurements on plants grown with and without enhanced UV-B radiation. The resulting population \times trait value matrix (control and treatment) was subjected to a principal components analysis (PCA). Our aims were as follows: (1) to characterize the extent of responses to UV-B radiation for different plant traits, and to evaluate the sensitivity of populations with PCA to characterize the overall UV-B response and (2) to determine whether populations from natural habitats with higher ambient UV-B radiation are more tolerant to UV-B radiation when compared to other populations.

2. Materials and methods

2.1. Plant material and growth conditions

In our study, 15 populations of tartary buckwheat (*F. tataricum* Gaertn.) from locations in China with different natural UV-B levels were sampled (Table 1). Of the 15 populations, 4 populations (nos. 1–4) occurred in a habitat with a low level of UV-B radiation, 5 populations (nos. 5–9) in a habitat with a medium level of UV-B radiation, and 6 populations (nos. 10–15) in a habitat with a high level of UV-B radiation. Populations 1–8 are prevalently cultivated populations selected by plant breeders. On the other hand, populations 9–15 are cultivated within a small area and they were randomly selected for the study to represent different origins. The field experiment was conducted

in upland red soil in Kunming (25°04'N, 102°73'E, elevation 2020 m), Southwest China. All populations were sown on 10 March 2004, and they were harvested depending on the time of grain maturity. Population 14 was harvested on 6 June, populations 11–13 and 15 on 12 June, populations 5–10 on 20 June, and populations 1–4 on 26 June. The soil contained 2.56% organic matter, 120.78 mg kg⁻¹ available N, 36.08 mg kg⁻¹ available P and 130.70 mg kg⁻¹ available K with pH 7.15. All treatments received 40 kg N ha⁻¹ as ammonium nitrate, 40 kg P₂O₅ ha⁻¹ as superphosphate and 40 kg K₂O ha⁻¹ as potassium chloride. The fertilizer was applied at tillage. The experimental design was a 2 \times 15 factorial, with two levels of UV-B radiation (ambient and enhanced UV-B radiation) and plants from 15 populations of tartary buckwheat. Three replicated plots (1.5 m \times 1.5 m) per population in each UV-B treatment (ambient or enhanced UV-B radiation) were arranged randomly. In total, 90 plots were used. In each plot, three border rows were marked on each side to minimize heterogeneity in the microclimate. The tartary buckwheat was planted in rows spaced 0.15 m apart with a final density of 130 seedlings m⁻². Buckwheat farming represents a common practice in the Kunming region.

2.2. UV-B radiation

Enhanced UV-B radiation in the field was provided by filtered UV fluorescent lamps (ranging from 275 to 380 nm and peaking at 308 nm, Beijing Electronic Resource Inc., Beijing, China), as described by Yao et al. (2006a). Lamps were suspended above, perpendicular to the planted rows, and filtered with either 0.13-mm thick cellulose diacetate (transmission down to 290 nm) for enhanced UV-B radiation or 0.13-mm thick polyester plastic films (absorbs all radiation below 315 nm) as a control (Sullivan and Teramura, 1990). Six lamps were installed above each plot. Plants were irradiated for 7 h daily, beginning from day 15 after seedling emergence, centered around solar noon. The height of the lamps above the plants was adjusted weekly to maintain a distance of 0.45 m between the lamps and the top of the canopy, with 6.30 kJ m⁻² day⁻¹ effective UV-B radiation (UV-B_{BE}) added.

Table 1
Geographical locations of the 15 populations of tartary buckwheat and the ambient UV-B radiation intensities in their habitats

Population no.	Location	Latitude (N)	Longitude (E)	Altitude (m)	UV-B radiation (kJ m ⁻² day ⁻¹)
1	Guangku 1	32°28'	105°51'	600	5.3
2	Fenghuang	28°06'	109°16'	740	4.8
3	Yu 6–21	38°17'	109°45'	950	4.6
4	Jiujiang	29°21'	115°37'	450	4.2
5	Zhenba	32°56'	107°91'	1231	7.0
6	Eluow	27°55'	102°16'	1760	6.6
7	Laoya	28.66'	102°49'	1900	6.3
8	Bier	28°03'	102°51'	2200	7.3
9	Meigu	28°33'	103°14'	1800	7.6
10	Yaoran	25°04'	101°24'	1885	10.8
11	Jiantang	27°78'	99°72'	3228	10.0
12	Wangdui	26°86'	100°25'	2600	9.3
13	Gesang	30°03'	101°58'	2800	10.3
14	Qingku3	36°38'	101°45'	2530	8.3
15	Qingku 4	36°41'	94°09'	2700	8.2

The UV-B radiation levels are the average values of sunny summer days after year 2000, as determined by local meteorological stations.

This supplemental level was similar to that experienced in Kunming with a 25% stratospheric ozone reduction during a clear day around summer solstice ($10.00 \text{ kJ m}^{-2} \text{ UV-B}_{\text{BE}}$) according to a mathematical model by Madronich et al. (1995). The UV-B radiation was determined at the plant level by USB2000 Fiber Optic spectrometer (Ocean Optics Inc., USA). The spectral irradiance was weighted with the generalized plant response action spectrum (Caldwell, 1971) and normalized at 300 nm to obtain UV-B_{BE} .

2.3. Pigment quantification

Thirty-five days after planting (DAP), the second and third leaves from the top of the plants were plucked off for a photosynthetic pigment analysis. The chlorophyll was measured as described by Lei et al. (2006) and Ren et al. (2006), and the carotenoid content was determined as described by Wellburn (1994).

2.4. Growth measurements

At the end of the experiment, the plant height and the diameter of the main stem were measured. The aboveground parts of the plants in each plot were randomly sampled from a $1.0 \text{ m} \times 1.0 \text{ m}$ area and partitioned into different organs, branches, stems, leaves and seeds. The different parts were oven-dried at 105°C for 15 min, followed by incubation at 80°C for 24 h to a constant weight. Before oven-drying, the seeds in each sample area were completely mixed, and the ratio of mature seeds (hard and filled seeds) to the green seeds was measured to denote seed ripeness, as described by Yao et al. (2006a). After heat incubation, the thousand-grain weight (mature seeds) was also determined. The leaf area was measured by a CI-202 scanning planimeter (CID Inc., USA). The specific leaf weight (SLW) of 10 seedlings, randomly selected from each plot, was calculated by dividing the total leaf dry weight by the total leaf area.

2.5. Data analysis

Analyses were performed with the software SPSS 11.5 for Windows. Data were log-transformed when necessary to ensure assumptions of normality and homogeneity of variances. The effect of the UV-B treatments on each trait in each population was tested using pair-samples *t*-tests. The effects of UV-B radiation and population on the traits were tested using two-way ANOVAs. The population changes in each trait were regressed against their control values. The whole original data set of 90 field plots (30×3 replicates) was subjected to a principal component analysis (PCA) using the Varimax method. This analysis allows the identification of interrelated variables. The mean values for the PC scores of replicated plots were calculated for each population. The change of PC scores by the enhanced UV-B radiation in each population was also calculated.

3. Results

3.1. The effects of UV-B radiation on plant growth, morphology, productivity and the composition of photosynthetic pigments

There were significant population differences in the growth traits of plants (e.g., height and stem diameter) among the 15 populations ($P < 0.001$, Table 2), with plant height ranging from 31.4 to 90.9 cm, and stem diameter ranging from 3.1 to 5.2 mm at the ripening stage. The effects of UV-B radiation on growth traits were negatively related to their control values ($P < 0.001$, Table 3). Enhanced UV-B radiation caused significant reductions in plant height in eight populations (nos. 1, 3, 4, 9, 11, 12, 14 and 15), whereas, stimulative effects were detected in four populations (nos. 6, 7, 8 and 10) and no effects in three populations (nos. 2, 5 and 13) (Table 2). Similar effects of UV-B radiation on stem diameter were also observed, with significant reductions in seven populations (nos. 2, 3, 6, 9, 11, 14 and 15) and no effect in the other populations. In response to enhanced UV-B radiation, the specific leaf weight (SLW) increased in eight populations (nos. 5, 6, 8, 9, 11, 12, 14 and 15), six populations (nos. 1–4, 10 and 13) were not affected, and it decreased only in population 7, which possessed the highest SLW value among the 15 populations.

Significant differences in aerial biomass and yield were also detected among the 15 populations ($P < 0.001$, Table 2). The highest values of biomass and yield were found in population 3, about 4.5 and 5.2 times as much as the lowest values observed in population 13. The populations with higher values of aerial biomass and yield among the 15 populations were most strongly affected by enhanced UV-B radiation ($P < 0.01$ and $P < 0.05$, Tables 2 and 3). As shown in Table 2, aerial biomass and yield decreased in six populations (nos. 1–3, 9, 12 and 14) and increased in three populations (nos. 4, 13 and 15), while no effect was found in the remaining three populations (nos. 5, 7 and 11). On the other hand, yield was significantly enhanced with little effect on aerial biomass in two populations (nos. 6 and 8). In population 10, only aerial biomass was reduced. The different changes in aerial biomass and yield in populations 6, 8 and 10 were consistent with an increase in thousand-grain weight (TGW). TGW decreased in six populations (nos. 2–3, 4, 11–12 and 14), whereas, UV-B radiation had no effect on this trait in the other six populations (nos. 1, 5, 7, 9, 13 and 15). In addition, there were different UV-B effects on seed ripeness: eight populations (nos. 1, 3, 4, 7, 11–14) had a delay in seed ripening, whereas this process was accelerated in five populations (nos. 2, 5, 8, 10 and 15) and not affected in populations 6 and 9.

Photosynthetic pigments were negatively affected by UV-B radiation under field conditions. The total chlorophyll content decreased in 12 populations, and the total carotenoid content decreased in nine populations (Table 2). In our study, the decreases in the amount of photosynthetic pigments were observed in young leaves 35 days after planting (DAP), while the changes were not pronounced in the old leaves (data not shown). The interactive effect of the population and UV-B radiation on the total chlorophyll content was significant ($P < 0.001$).

Table 2
The traits of the 15 populations of tartary buckwheat as affected by enhanced UV-B radiation

Population no.	Treatment	Plant height (cm)	Stem diameter (mm)	SLW (g dm ⁻²)	Aerial biomass (g/10 plants)	Yield (g/10 plants)	TGW (g)	Ripeness	Chlorophyll (mg g ⁻¹)	Carotenoids (mg g ⁻¹)
(1)	C	90.9(2.7)	4.48(0.2)	0.495(0.05)	63.4(7.1)	20.8(0.6)	26.9(0.2)	0.71(0.01)	32.2(0.1)	4.17(0.04)
	UV-B	79.5(1.7) -12.5%**	4.11(0.2) -8.1%	0.513(0.05) 3.6%	30.4(2.9) -52.1%**	9.7(1.0) -53.3%***	27.8(0.6) 3.4%	0.53(0.02) -24.8%	22.7(0.9) -29.4%***	4.00(0.14) -4.0%
(2)	C	76.7(2.4)	5.24(0.2)	0.504(0.06)	54.2(3.5)	31.4(0.7)	16.5(0.2)	0.36(0.02)	30.4(0.8)	4.95(0.1)
	UV-B	71.4(2.1) -6.87%	3.86(0.2) -26.4%***	0.475(0.03) -5.9%	39.5(2.7) -27.0%*	20.6(1.0) -34.4%***	14.9(0.2) -9.3%**	0.56(0.01) 55.0%**	24.8(0.7) -18.7%**	4.45(0.1) -10.0%*
(3)	C	61.3(3.6)	4.97(0.1)	0.463(0.02)	89.2(4.5)	52.1(1.4)	22.7(0.3)	0.72(0.00)	33.4(0.3)	5.2(0.06)
	UV-B	49.9(2.6) -18.6%*	4.12(0.1) -17.1%***	0.502(0.06) 8.3%	48.4(4.6) -45.8%**	28.6(0.9) -45.1%***	17.4(0.6) -23.4%**	0.43(0.01) -40.6%***	24.6(0.6) -26.4%***	4.1(0.20) -22.5%*
(4)	C	65.5(2.8)	3.47(0.1)	0.468(0.02)	32.3(1.6)	18.4(0.4)	23.8(0.3)	0.36(0.03)	26.2(0.5)	4.24(0.08)
	UV-B	59.7(1.6) -8.9%	3.59(0.2) 3.3%	0.435(0.02) -7.1%	39.6(2.7) 22.7%	24.5(1.0) 33.1%**	16.1(0.5) -32.2%***	0.30(0.0) -15.2%	19.2(0.7) -26.6%***	3.53(0.09) -16.7%**
(5)	C	31.4(2.1)	4.42(0.2)	0.459(0.05)	53.1(6.1)	30.2(1.0)	16.9(0.5)	0.55(0.02)	25.2(0.2)	4.18(0.03)
	UV-B	37.6(3.2) 19.5%	4.14(0.2) -6.3%	0.526(0.11) 14.6%	52.8(1.8) -0.6%	31.0(0.8) 2.4%	17.2(0.4) 1.6%	0.68(0.00) 23.2%*	22.9(0.5) -9.1%*	3.43(0.05) -18.0%***
(6)	C	36.2(2.2)	4.16(0.1)	0.370(0.01)	43.5(2.8)	10.9(1.0)	17.9(0.2)	0.69(0.01)	27.0(1.0)	4.30(0.10)
	UV-B	49.8(1.8) 37.8%***	3.79(0.2) -8.9%	0.414(0.01) 11.8%**	45.2(2.8) 3.9%	19.0(1.9) 74.8%**	19.3(0.3) 8.1%*	0.72(0.02) 4%	24.0(0.5) -11.1%*	4.17(0.12) -2.8%
(7)	C	45.8(1.3)	3.40(0.2)	0.460(0.05)	30.0(2.0)	17.4(0.9)	18.6(0.2)	0.69(0.01)	25.4(0.3)	4.05(0.02)
	UV-B	54.8(1.8) 19.6%***	3.75(0.3) 11.4%	0.378(0.02) -17.8%	27.6(2.5) -8.0%	18.1(0.9) 3.8%	18.8(0.4) 1.1%	0.59(0.00) -14.4%*	20.8(0.2) -18.1%***	3.47(0.03) -14.4%*
(8)	C	51.8(2.7)	3.74(0.2)	0.442(0.02)	28.6(4.3)	8.4(0.5)	15.9(0.5)	0.21(0.02)	25.6(1.6)	3.61(0.13)
	UV-B	66.0(2.2) 27.3%***	3.90(0.3) 4.1%	0.569(0.08) 28.8%*	29.7(5.2) 4.0%	11.9(0.5) 41.5%**	19.3(0.5) 21.7%**	0.34(0.01) 66.5%*	23.4(0.5) -8.5%	3.63(0.12) 0.5%
(9)	C	74.3(3.0)	5.49(0.2)	0.343(0.01)	61.5(3.0)	37.5(0.8)	18.9(0.3)	0.68(0.01)	29.3(1.0)	3.81(0.22)
	UV-B	53.0(2.1) -28.7%***	3.67(0.2) -33.2%***	0.513(0.03) 49.6%**	54.5(3.2) -11.3%	26.4(0.8) -29.6%***	18.3(0.2) -3.1%	0.70(0.01) 2.9%	22.2(0.4) -24.2%**	4.02(0.09) 5.7%
(10)	C	37.7(2.1)	3.11(0.1)	0.404(0.04)	46.5(2.0)	17.3(0.6)	16.0(0.2)	0.37(0.01)	26.7(0.6)	4.23(0.02)
	UV-B	45.6(2.0) 21.0%**	2.92(0.1) -6.2%	0.437(0.02) 8.2%	35.8(1.2) -22.9%**	17.8(0.5) 3.0%	18.5(0.5) 15.3%*	0.46(0.00) 26.8%**	21.7(0.6) -18.9%**	3.53(0.26) -16.7%*

(11)	C	71.8(3.2)	4.68(0.2)	0.369(0.06)	36.6(1.7)	16.1(0.6)	24.4(0.6)	0.76(0.00)	31.8(0.3)	4.97(0.03)
	UV-B	60.2(2.7)	4.15(0.2)	0.415(0.04)	36.9(1.8)	15.7(0.9)	22.0(0.8)	0.68(0.02)	20.5(0.2)	3.53(0.08)
		-16.2%**	-11.3%*	12.4%	0.7%	-3.0%	-9.8%	-11.4%*	-35.5%***	-28.9%***
(12)	C	51.4(1.7)	3.90(0.2)	0.380(0.01)	36.6(3.5)	13.4(0.5)	18.4(0.3)	0.65(0.00)	32.8(1.4)	5.06(0.18)
	UV-B	45.4(1.9)	3.51(0.2)	0.425(0.01)	21.0(1.7)	7.2(0.6)	14.7(0.2)	0.29(0.01)	23.3(0.4)	4.26(0.06)
		-11.7%*	-10.0%	11.7%	-42.8%**	-46.7%***	-20.1%***	-55.8%***	-28.8%**	-15.8%*
(13)	C	45.9(2.0)	3.74(0.1)	0.356(0.01)	20.0(1.8)	9.9(0.9)	17.9(0.2)	0.55(0.01)	24.8(0.6)	4.23(0.11)
	UV-B	54.7(3.6)	3.67(0.1)	0.343(0.01)	24.8(1.6)	12.5(0.9)	18.7(0.3)	0.46(0.02)	24.7(0.7)	3.84(0.12)
		19.2%	-1.9%	-3.6%	24.1%	26.2%	4.9%	-16.4%	0.0%	-9.2%
(14)	C	88.5(3.2)	3.87(0.2)	0.463(0.02)	56.3(6.6)	21.3(1.3)	19.3(0.5)	0.40(0.01)	35.1(0.6)	5.17(0.58)
	UV-B	68.8(2.5)	3.10(0.2)	0.537(0.03)	21.0(1.5)	7.5(0.4)	15.0(0.5)	0.26(0.01)	27.8(0.8)	5.03(0.22)
		-22.5%***	-19.9%***	15.9%*	-62.8%**	-65.0%***	-22.5%**	-35.3%**	-20.7%***	-2.7%
(15)	C	91.3(3.0)	4.74(0.2)	0.450(0.03)	43.6(4.0)	18.6(0.5)	17.8(0.1)	0.45(0.01)	27.82(0.5)	4.39(0.29)
	UV-B	75.2(2.6)	3.93(0.2)	0.560(0.1)	49.3(2.6)	21.4(0.5)	17.1(0.3)	0.64(0.01)	28.07(1.0)	4.94(0.21)
		-17.6%***	-17.1%**	24.4%	13.1%	15.0%**	-3.8%	42.4%**	0.9%	12.6%
Analyses of variance	Population effect	***	***	**	***	***	***	***	**	**
	UV-B effect	***	***	***	***	***	***	***	***	**
	Population × UV-B	**	**	*	***	***	*	**	***	*

The percentages indicate the changes in plants grown with enhanced UV-B radiation (UV-B) compared with the control plants (C), expressed as $((UV-B - C)/C) \times 100\%$. The asterisks indicate the presence of significant differences between the UV-B treatment and control according to a paired-samples t-test, or the presence of significant UV-B and population effects according to two-way ANOVAs. *, **, *** Significant differences at $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively. The values are means of three replicates with standard error in parentheses.

Table 3
Correlations between plant traits and their changes under enhanced UV-B radiation

	<i>r</i>	<i>P</i>
Plant height	−0.815	0.000***
Stem diameter	−0.806	0.000***
Specific leaf weight	−0.555	0.0328*
Aerial biomass	−0.657	0.008**
Yield	−0.539	0.041*
Seed ripeness	−0.622	0.013*
Thousand grain weight	−0.467	0.079
Chlorophyll	−0.641	0.01*
Carotenoid	−0.43	0.109

The percentages of the changes (Table 2) in the 15 populations induced by enhanced UV-B radiation in each plant trait were regressed against their mean control values.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Populations with high total chlorophyll content encountered a greater reduction than the other populations did when exposed to enhanced UV-B radiation ($P < 0.05$, Table 3).

3.2. PCA of plant responses to UV-B radiation

The control and treatment values of each population were subjected to a principal component analysis. The first four components accounted for the majority of variation in the data set (82.6%). Of the variation, 28.0% could be explained by the first principal component (PC1), 23.6% by the second principal component (PC2), 17.2% by the third principal component (PC3), and 13.7% by the fourth component (PC4). As seen in Table 4, PC1 explains the majority of variance in aerial biomass, yield, stem diameter and seed ripeness, and PC2 explains the majority of variance in the photosynthetic pigments of leaves, while PC3 as well as PC4 separately explains the majority of variance in thousand grain weight (TGW) and specific leaf weight (SLW). The variance of plant height is loaded on PC2, PC3 and PC4, and the variance of seed ripeness is loaded on PC1 and PC3.

The PCA score plots of the populations with and without UV-B radiation are shown in Fig. 1. As seen in Fig. 1a (PC1–PC2 side), the populations with high values of biomass, yield and stem diameter are located toward the positive end of the PC1 axis, and the populations with high values of photosynthetic pigments and plant height are located toward the positive end of the PC2 axis. All populations treated with UV-B radiation had smaller PC2 scores than their controls did, and they are located toward the negative ends of the PC2 axis. In general, populations from a low UV-B level (nos. 1–3) possessed high control scores in the PC1 axis, except for population 4, while populations from a high UV-B level (nos. 10–15) had low control scores in the PC1 axis. The populations originating from a middle UV-B level (nos. 5–9) had low PC2 control scores. Fig. 1b (PC3–PC4 side) also shows that the populations with higher values of TGW and seed ripeness are located toward the positive end of the PC3 axis. The buckwheat populations treated with UV-B had higher values of SLW and PC4 scores than their controls did, and they

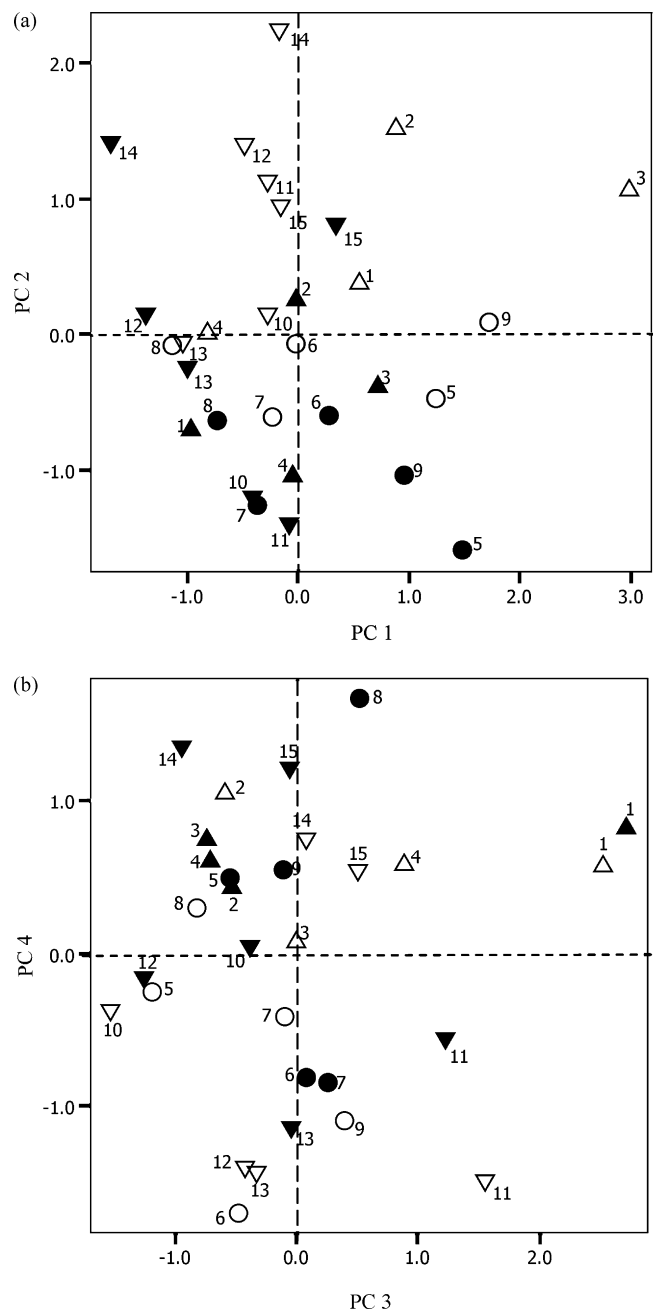


Fig. 1. The principal components analysis (PCA) of the 15 populations of tartary buckwheat. (a) The scatter plot of tartary buckwheat on the PC1 and 2 side; (b) the scatter plot of tartary buckwheat on the PC3 and 4 side. Open (Δ , \circ and ∇) and solid symbols (\blacktriangle , \bullet and \blacktriangledown) denote tartary buckwheat populations under control condition and enhanced UV-B radiation, respectively. Triangle (Δ and \blacktriangle), circle (\circ and \bullet) and reversed triangle (∇ and \blacktriangledown) denote tartary buckwheat population originating from natural habitats with a low, medium and high level of UV-B radiation, respectively. Each symbol represents the mean values for the PC scores of the three replicates in each population.

were located towards the positive end of the PC4 axis except for population 7.

To clarify the comparison in the changes of the PC scores caused by UV-B radiation in different populations, the PC1 score change ($PC1_{(UV-B)} - PC1_{(Control)}$) as well as the PC2 score change ($PC2_{(UV-B)} - PC2_{(Control)}$) are shown in Fig. 2. Two population groups were observed. The PC scores of the

Table 4
Correlation coefficients for plant attributes linked to the first four principal components (PCs)

	PC1	PC2	PC3	PC4
Yield	0.946***	0	0	0
Biomass	0.914***	0.257*	0	0
Diameter	0.625***	0.350**	0.348**	-0.178
Ripeness	0.546***	0.123	0.404***	-0.457***
Carotenoid	0.119	0.908***	0	0
Chlorophyll	0.268*	0.885***	0.152	-0.100
Thousand grain weight (TGW)	0.118	0	0.916***	0
Plant height	0	0.543***	0.625***	0.329**
Specific leaf weight (SLW)	0	0	0	0.924***

Plant trait values (control and UV-B treatment) were regressed against the scores of PC1–4. The attributes are ranked by correlation coefficients.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

group including populations 1–3, 9, 12 and 14 were markedly decreased by enhanced UV-B radiation (as also indicated in Fig. 1a), while the PC scores of the group including populations 6–8, 11, 13 and 15 had a modest change when exposed to enhanced UV-B radiation. The UV-B responses of the other populations ranged between the values detected in these two population groups. The PC1 scores of the populations from low UV-B levels (nos. 1–3) markedly decreased except for population 4, and the populations from medium UV-B levels (5–8) showed little change in PC1 scores except for population 9, whereas populations 10–15 originating from high UV-B levels or high elevations expressed various PC1 changes when exposed to enhanced UV-B radiation.

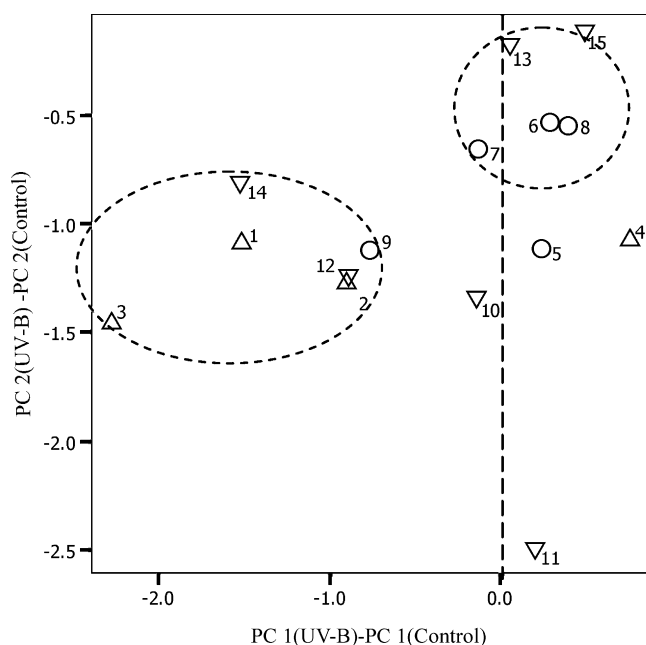


Fig. 2. The PC1 and PC2 score changes in 15 populations of tartary buckwheat when exposed to enhanced UV-B radiation. Triangle (Δ), circle (\circ) and reversed triangle (∇) denote tartary buckwheat population originating from natural habitats with a low, medium and high level of UV-B radiation, respectively. The dotted circles represent the two population groups, the big circle representing the group with high PCs changes and the small circle the group with modest PCs changes.

4. Discussion

In this study, we identified intraspecific responses to UV-B radiation in terms of growth, morphology, productivity and the composition of photosynthetic pigments among 15 populations of tartary buckwheat (Table 2). Indeed, considerable variation in responses existed among the different populations, as it has been previously reported for soybean (Li et al., 2002), wheat (Li et al., 2000), rice (Dai et al., 1994) and maize (Correia et al., 1998). We observed that the UV-B-induced changes in plant traits were negatively correlated with their constitutive values, particularly in the case of plant height and stem diameter (Table 3). Cooley et al. (2001) have also reported that the UV-B sensitivity of *Arabidopsis* was positively correlated with the growth rate: cultivars with a higher level of biomass were more inhibited when exposed to UV-B radiation, and other traits, e.g., the leaf area, lamina length and width, displayed the same effect. Recently, Hofmann et al. (2003) observed that the UV-B sensitivity of white clover populations was positively related to the constitutive productivity. In the study on the nutrient stress of plants, Shipley and Keddy (1988) reported that susceptibility to environmental stress was positively correlated with relative growth rate.

A positive effect of UV-B radiation on the height and yield of plants was detected in some tartary buckwheat populations (Table 2), which confirms results obtained in studies on perennial forage crops (Papadopoulos et al., 1995) and wheat (Al-Oudat et al., 1998). Nevertheless, the underlying reason for such an improvement still remains unclear. The contrasting effects of UV-B radiation on different populations suggest that there exist abundant genetic resources for selecting tolerant and sensitive populations of tartary buckwheat. Our results imply that a future effort to conduct selection breeding in order to develop cultivars, which are more tolerant to enhanced UV-B radiation, is feasible in tartary buckwheat.

In our study, the majority of trait variances were extracted into four principal components by a PCA approach (Table 4, Fig. 1). The most important dimension (PC1) comprised the important agronomic traits, e.g., aerial biomass and yield. Also the stem diameter, which is closely related to bearing or biomass, was included in PC1 (Table 4, Fig. 1a). The total biomass represents a long-term integration of all biochemical, physiological

and growing process, while yield is the primary aim of agronomic activity. In general, the population-wise PC1 scores were reduced by enhanced UV-B radiation. This observation signified that UV-B radiation negatively affects those agronomic traits, and it also supports previous studies showing that UV-B radiation causes reductions in biomass and yield in many crop species, e.g., the tartary buckwheat (Yao et al., 2006a), common buckwheat (Gaberščik et al., 2002) and other crop species (Kakani et al., 2003). The second dimension (PC2) was comprised of photosynthetic pigments and plant height (Table 4, Fig. 1a). Decreases in the amount of photosynthetic pigments have been evident in most crop species when exposed to UV-B radiation (Kakani et al., 2003). Similar results were also found in our study. The pronounced decrease in the amount of photosynthetic pigments could affect photosynthesis and reduce both biomass accumulation and economic yield (Jansen et al., 1998; Yao et al., 2006b). The third dimension (PC3) was related to seed traits, e.g., seed ripeness and thousand-grain weight (Table 4, Fig. 1b). Different populations expressed contrary changes in PC3 scores under enhanced UV-B radiation, which indicates that the plants' reproductive processes respond differently to UV-B radiation. Moreover, the SLW value of the tartary buckwheat populations extracted by PC4 increased when exposed to enhanced UV-B radiation (Table 4; Fig. 1b). This result is consistent with previous reports by Yao et al. (2006a) and Gaberščik et al. (2002). Increased leaf thickness, indicated as a greater SLW value, could serve as a protective response to UV-B radiation (Nagel et al., 1998).

The important agronomic traits, including growth, development and production, could be integrated in PC1 and PC2 (Table 4). It follows that changes in PC1 and PC2 reflect the overall sensitivity of tartary buckwheat populations to enhanced UV-B radiation (Fig. 2). In this study, we found the presence of both sensitive populations (nos. 1–3, 9, 12 and 14) and tolerant populations (nos. 6–8, 13 and 15). The sensitive populations had higher constitutive plant attributes as well as higher control PC scores than did the other populations, on average 39.2, 18.6, 62.1, 79.9 and 20.5% greater height, stem diameter, aerial biomass, yield and total chlorophyll content, respectively, than in other populations (Table 2). Our results are consistent with the report by Cooley et al. (2001) proposing that plants with more vigorous growth are more susceptible when they are exposed to environmental stress. A change in PC1 was related to sensitivity to UV-B radiation concerning biomass accumulation and final yield (Fig. 2). Among the eight prevalently cultivated populations (nos. 1–8), generally the populations originating from low elevation (1–3) were more sensitive to UV-B radiation regarding biomass accumulation and yield than were those from middle elevation (nos. 5–8). This could be due to long-term adaptation to UV-B radiation in the natural habitats and also due to different agronomic selection. The populations prevalently cultivated in low-elevation habitats have been selected mainly based on their yield potential under favorable agronomic conditions, while the populations prevalently cultivated in middle-elevation habitats have been selected for yield stability and stress resistance under more unfavorable agronomic conditions.

In conclusion, significant variation in UV-B sensitivity exists among tartary buckwheat populations, which is apparently due to inherent genotypic differences. Therefore, a future effort to breed for more tolerant cultivars may be possible. Our study proved that the UV-B effect on different plant traits was negatively correlated with their constitutive values. In the tartary buckwheat populations, the sensitivity to UV-B radiation was not only associated with the ambient UV-B level in natural habitats but also correlated with the relative growth rate and other factors. As tartary buckwheat is mainly grown at high elevation locations that suffer from strong doses of ambient UV-B radiation, the clarification of the adaptation mechanism to ambient and enhanced UV-B radiation is very important. Further studies are needed to improve our understanding of the various UV-B effects on the agronomic traits.

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