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Functional Plant Biology

Parental UV-B radiation regulates the habitat selection of clonal *Duchesnea indica* in heterogeneous light environments

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ABSTRACT

Habitat selection behaviour is an effective strategy adopted by clonal plants in heterogeneous understorey light environments, and it is likely regulated by the parental environment's ultraviolet-B radiation levels (UV-B) due to the photomorphogenesis of UV-B and maternal effects. Here, parental ramets of *Duchesnea indica* were treated with two UV-B radiation levels [high (UV5 group) and low (UV10 group)], newborn offspring were grown under a heterogeneous light environment (ambient light vs shade habitat), and the growth and DNA methylation variations of parents and offspring were analysed. The results showed that parental UV-B affected not only the growth of the parent but also the offspring. The offspring of different UV-B-radiated parents showed different performances. Although these offspring all displayed a tendency to escape from light environments, such as entering shade habitats earlier, and allocating more biomass under shade (33.06% of control, 42.28% of UV5 and 72.73% of UV10), these were particularly obvious in offspring of the high UV-B parent. Improvements in epigenetic diversity (4.77 of control vs 4.83 of UV10) and total DNA methylation levels (25.94% of control vs 27.15% of UV10) and the inhibition of shade avoidance syndrome (denser growth with shorter stolons and internodes) were only observed in offspring of high UV-B parents. This difference was related to the eustress and stress effects of low and high UV-B, respectively. Overall, the behaviour of *D. indica* under heterogeneous light conditions was regulated by the parental UV-B exposure. Moreover, certain performance improvements helped offspring pre-regulate growth to cope with future environments and were probably associated with the effects of maternal DNA methylation variations in UV-B-radiated parents.

Keywords: clonal plants, DNA methylation, *Duchesnea indica*, foraging behavior, maternal effect, shade avoidance syndrome (SAS), UV-B radiation.

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Introduction

Sunlight is of primary importance to sessile plants, both as an energy source to fuel photosynthesis and as an informational signal that influences their entire life cycle (Rizzini *et al.* 2011). Plants living in dense communities or underneath a leaf canopy experience a strong reduction in light intensity and changes in light quality because of light absorption and reflection by surrounding vegetation (Gommers *et al.* 2013). Furthermore, the light in these environments is extremely heterogeneous due to the influence of cloud cover, movement of leaves by wind, and composition of canopies (Küppers *et al.* 1996). These factors obviously increase the difficulty of accessing light resources for plants.

As an intrinsic part of the solar spectrum, ultraviolet-B (UV-B, 280–315 nm) light has a major effect on plant growth and development, although it accounts for less than 1% of the total solar spectrum (Liu *et al.* 2015). For many plants underneath the canopy, their shade avoidance syndrome (SAS) response is strongly inhibited by UV-B radiation (Mazza and Ballaré 2015; Fraser *et al.* 2016, 2017). SAS responses are observed for many species

under the canopy because of the low red to far-red light ratios (R:FR), and they include rapid hypocotyl growth, internode and petiole elongation, upward leaf movement, and apical dominance, which help plants capture more light (Courbier and Pierik 2019; Ma and Li 2019). However, this SAS response is inhibited by UV-B radiation due to the inhibitory effect of UV-B on auxin and gibberellin biosynthesis (Hayes *et al.* 2014; Tavridou *et al.* 2020). Therefore, UV-B radiation greatly complicates the growth of plants in the understorey, especially under a background of increases in UV-B radiation with ozone depletion.

Clonal plants are dominant species in many habitat types. In heterogeneous light environments, clonal plants preferentially colonise newborn ramets in patches with appropriate light resources, as has been reported in numerous studies (Luo and Dong 2001; Chen *et al.* 2004; Xiao *et al.* 2006; Wang *et al.* 2016; Latzel and Münzbergová 2018). This selective placement of ramets is known as 'foraging behaviour' or 'habitat selection', which can not only maximise the plant's resource acquisition but also balance the risk in heterogeneous environments, ultimately contributing to enhancing the competitiveness of clonal plants (Chen *et al.* 2019). Thus, clarifying the regulatory mechanisms of habitat selection behaviour helps us understand the environmental adaptability of clonal plants.

In addition to the present environment, the growth behaviour of plants is also regulated by the environment of their parents. The 'maternal effects' of the parental environment can persist across offspring generations and influence the phenotype and fitness of progeny (Galloway 2005; Louâpre *et al.* 2012; González Besteiro and Ulm 2013; González *et al.* 2017; Dong *et al.* 2018, 2019). Because of the asexual reproduction of clonal plants, they have a greater ability than nonclonal plants to 'remember' the environmental events of their parent (Zhang *et al.* 2021). Therefore, maternal effects induced by the parental environment have been reported for several clonal plants in recent years. In these studies, the offspring ramets of stressed parents displayed adapted growth or increased fitness in the same environment as their parent (Herman and Sultan 2016; González *et al.* 2018; Baker *et al.* 2019; Dong *et al.* 2019). In the study of the environmental adaptability of clonal plants, the environment of the parent is a nonnegligible factor that plays an important role in regulating the growth behaviour of clonal plants.

The effect of parental UV-B on the growth of offspring ramets in a heterogeneous UV-B environment was investigated in our previous studies on *Glechoma longituba* (Quan *et al.* 2021; Zhang *et al.* 2021). The results suggested that parental UV-B exposure strongly influenced the growth and foraging behaviour of clonal offspring. By regulating epigenetic variation and phenotypical plasticity, the offspring of UV-B-stressed parents adopt an 'escape strategy' to avoid environments with UV-B radiation. Considering the effect of UV-B radiation on the photomorphogenesis of understorey species, the effect of parental UV-B radiation on the habitat selection behaviour of clonal plants in patchy light environments is an important question that remains to be resolved.

In our study, the parental ramets of clonal *Duchesnea indica* (Andr.) Focke were grown under two different UV-B conditions (5 and 10 μW cm^{-2}), and their newborn offspring ramets were subjected to a heterogeneous light environment (ambient light vs shade habitat). After 45 days of vegetative propagation, the growth and epigenetic variation of parent and offspring ramets were explored. The following questions were addressed: first, how does the parental UV-B environment influence the habitat selection of clonal offspring in a heterogeneous light environment? Second, do the selection results vary based on the parental UV-B intensity? Third, are the SAS responses of offspring ramets in shade habitat affected by the parental UV-B radiation? Finally, what is the role of parental epigenetic variations in the selection of habitat for clonal offspring?

Materials and methods

Plant material and propagation

Duchesnea indica (Andr.) Focke is a perennial herb belonging to Rosaceae that produces long over-ground stolons with rooted ramets on its nodes, and it is commonly employed in clonal plant research due to its high phenotypic plasticity. Its clonal growth pattern is shown in Fig. 1. Additionally, as a clonal plant with a sympodial branching pattern, *D. indica* is a good material for habitat selection research (Quan *et al.* 2018). The *D. indica* plants used in our experiment were collected from the campus of Northwest University in Xi'an (397 m a.s.l., 34.3°N, 108.9°E). To reduce the impact of the previous environment on plant materials, *D. indica* from the same genet were propagated for at least three generations in a greenhouse before this experiment. Then, ramets of equal genotype and similar size (0.56 ± 0.17 g) were selected as the parental ramets and transferred to square plastic containers for 45 days of growth. Vermiculite and loam (1:3, v/v) were mixed and utilised as the culture soil of *D. indica*.

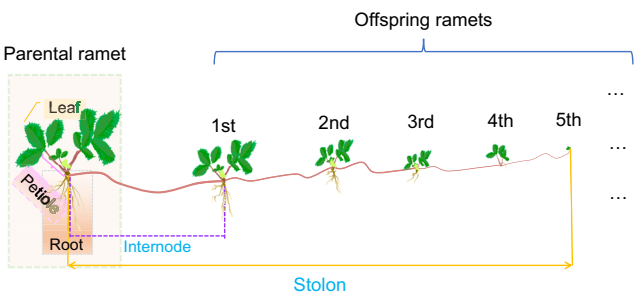

Fig. 1. Clonal growth pattern diagram of *Duchesnea indica*.

The greenhouse conditions were a 23/18°C day/night temperature cycle, a 12/12 h light/dark cycle, and 360 μmol m^{-2} s^{-1} photosynthetic photoflux density (PPFD) during daytime hours. PPFD levels were measured with a Quantum Metre (LQS-QM, Apogee Instruments Inc., USA). The relative humidity of the greenhouse was maintained at 60%. Ramets were watered every 2 days to prevent water stress.

Experimental design

The experiment was conducted in the greenhouse of Northwest University from September 2, 2019, to October 17, 2019. There were three treatments in our study: control, UV5 and UV10 (Table 1). We used a randomised block design. Each treatment was designed with six replicates. At the beginning of the experiment, 18 parental ramets were randomly assigned to one of the treatments and planted in the centre of a square plastic container (100 cm long × 40 cm wide × 20 cm high). Two groups of parental ramets were separately exposed to different levels of UV-B radiation (5 and 10 μW cm^{-2}). During the 45 days of the experiment, the newborn offspring ramets experienced a heterogeneous light environment, which means that one side of the growth container was the ambient light habitat and the other was a shade habitat. The shade habitat was achieved with a sunshade net, the nets were covered 0.6 m above the plant canopy, and approximately 30% of ambient light was transmitted and reached the canopy. Furthermore, during the experiment, to screen the offspring ramets from their parental UV-B light and avoid the interference from UV-B radiation on the offspring environment (ambient light or shade habitat), two transparent polyester films (0.3-mm, Dongguan Linuo Plastic Insulation Material Co. LTD, China) were placed vertically on both sides of parental ramets separately to ensure that the bottom of the films did not affect the growth of the offspring ramets (Fig. 2).

Table 1. Different treatments in the study.

Treatments	Interpretation
Control	Parental ramets received background light in a greenhouse for 45 days, there was little UV-B radiation in greenhouse
UV5	Parental ramets were exposed to an additional 5 μW cm^{-2} UV-B radiation for 45 days
UV10	Parental ramets were exposed to an additional 10 μW cm^{-2} UV-B radiation for 45 days

UV-B radiation treatment

The UV-B doses used in the experiment were set as follows: 5 μW cm^{-2} UV-B radiation was added to the parental ramets of the UV5 group based on the ratio of visible to UV-B light at noon in the natural environment of our campus and according to the PPFD of our greenhouse; and 10 μW cm^{-2} was added to the parental ramets of the UV10 group as a stressed UV-B dose

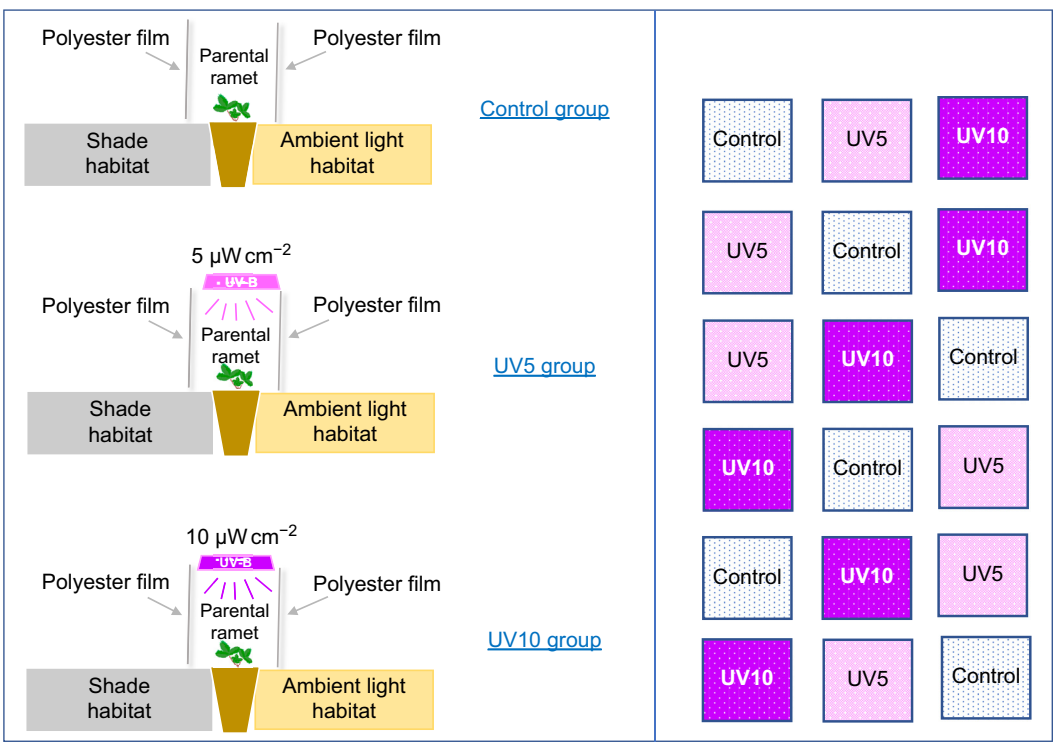

Fig. 2. Experimental layout and schematic representation of the three treatments. Each treatment was replicated six times, as shown in the layout to the right.

based on the stress effect of enhanced UV-B radiation demonstrated by our previous experience.

UV-B radiation was provided by square-wave UV-B fluorescent lamps (central wavelength 313 nm, 36 W, Beijing Lighting Research Institute, Beijing, China) by the procedure described in Liu *et al.* (2015). The UV-B irradiation treatment was carried out for 8 h per day from 09:00 to 17:00 h and continued for 45 days. For the UV-B radiation groups (UV5 and UV10 groups), a 0.13-mm cellulose acetate film (Grafix plastics, Cleveland, Ohio, transmission to 290 nm) was used to filter out a small amount of UV-C in the UV-B lamp spectrum. To avoid the effect of photodegradation of UV-B radiation on the film, the cellulose acetate film was replaced regularly every 5 days. The UV-B lamps were suspended directly above the parent ramets, and the two radiation levels (5 and 10 μW cm^{-2}) were controlled by adjusting the distance between the top of the plant canopy and the lamps. The level of UV-B radiation was measured by a UV radiometer (Handy, Beijing, China) every other day.

Measurement of growth parameters

After 45 days of growth, some growth parameters of each group were recorded before harvest, such as the number of offspring ramets in different light habitats (ambient light or shade); in addition, the stolon length between the parental ramet and the offspring ramet that first bent to the shade was also measured to analyse the difference in the sequence of habitat selection in different groups.

Then, the genets of different treatments were harvested carefully and the growth parameters of parental ramets, offspring ramets, and the whole genets were measured as follows: first, the leaf area, petiole length, petiole biomass, and biomass of parental ramets were measured; second, the length and biomass of the longest primary stolon, length of the internode, and total biomass of the ramets of the offspring ramets in different environments (ambient light or shade habitat) were measured; finally, the branching intensity, total number of offspring ramets, the biomass of over-ground parts (leaf and stolon) and total biomass of the whole clonal genet were recorded.

The length of the stolons was measured with Vernier callipers, and the mean internode length (MIL) was calculated by the ratio of the stolon length to the number of internodes. The leaf area and petiole length were obtained as follows: fresh leaves were scanned with a scanner (EPSON Perfection V19, EPSON, China), the leaf area was calculated by Motic software (Motic Images Plus 2.0. Ink, Motic, China), and the petiole length was calculated by Image-Pro software (Image-Pro Plus 6.0, Image-Pro, China). Moreover, the leaf blade and petiole were dried separately at 75°C for 48 h to a constant weight and the dry mass was weighed using an electronic balance (Sartorius BT25S, Beijing, China). The specific petiole length (SPL) was calculated by the ratio of petiole length to petiole biomass. The ratio of stolon length to stolon biomass was calculated as the specific stolon length (SSL). Leaf biomass allocation (or stolon biomass allocation) of the genet was calculated by the ratio of the leaf biomass (or stolon biomass) to the total biomass of the genet.

Analysis of DNA methylation variation

DNA methylation variation in *D. indica* was detected using the methylation-sensitive amplification polymorphism method (MSAP). The leaf samples were scrubbed gently with 75% ethanol to minimise contamination by microorganisms and then dried in silica gel for the subsequent extraction of DNA. Total genomic DNA was extracted from the above 30 mg dry leaves using a DNA Kit (BioTeKe, China). The DNA quality was examined by electrophoresis in agarose gel (1% w/v), and the DNA concentration and purity were examined spectrophotometrically using a nucleic acid protein detector (BioSpec-nano, Shimadzu, Japan). The concentration of DNA was adjusted to 100 ng μL^{-1} with eluent for subsequent experiments.

A total of 500 ng genomic DNA was cut with 1 μL *Eco*RI (NEB, Ipswich, USA) and 1 μL of the frequent-cutting methylation sensitive restriction enzyme *Msp*I (NEB, Ipswich, USA) or 1 μL *Hpa*II (NEB, Ipswich, USA), 2 μL Cutsmart Buffer and 11 μL double distilled water in a 20 μL reaction (NEB, Ipswich, USA) at 37°C for 6 h. *Eco*RI + *Msp*I enzymes were inactivated at 65°C for 20 min, and *Eco*RI + *Hpa*II enzymes were inactivated at 80°C for 20 min. Next, 30 μL of ligation mixture was prepared, which containing 5 pM of *Eco*RI-related adapter and 50 pM of *Hpa*II/*Msp*I-related adapter, 3 μL 10 × T_4 ligase buffer (NEB, Ipswich, USA) and 0.5 μL of T_4 DNA ligase (NEB, Ipswich, USA), this ligation mixture was incubated at 16°C for 12 h. Preamplification was performed in a total volume of 25 μL, including 3 μL of ligated DNA, 17.5 μL 2 × *Taq* PCR master mix (Baosai, China), 0.5 μL of *Eco*RI preselective primer (10 μM) and 0.5 μL H-M preselective primer (10 μM), and 8.5 μL double distilled water respectively. The preamplification conditions were as follows: initial denaturation at 94°C for 2 min; followed by 20 cycles at 94°C for 30 s, 56°C for 30 s and 72°C for 1 min; and a final elongation step at 72°C for 10 min and 4°C to pause. The samples were then examined by electrophoresis in agarose gel (2% w/v).

A selective amplification step was carried out with 10 *Eco*RI/*Hpa*II selective primer combinations: 5′-AAC/TCT-3′, 5′-ACT/TTG-3′, 5′-ACT/TAA-3′, 5′-AGC/TTG-3′, 5′-AGG/TGA-3′, 5′-AGG/TCC-3′, 5′-AGG/TTG-3′, 5′-AGG/TTC-3′, 5′-AGT/TTA-3′, 5′-AGT/TTG-3′. The preamplification products were diluted 25 times as a selective amplification template. Selective amplification was performed in a total volume of 50 μL, including 1 μL of preamplified DNA, 25 μL of 2 × *Taq* PCR master mix (Baosai, China), 1 μL of *Eco*RI preselective primer (10 μM) and H-M preselective primer (10 μM), and 22 μL of double distilled water. Selective amplification was

performed under the following conditions: initial denaturation at 94°C for 2 min; followed by 10 cycles at 94°C for 30 s; 65°C for 30 s and 72°C for 1 min (each cycle was decremented by 1°C); 23 cycles at 94°C for 30 s; 56°C for 30 s and 72°C for 1 min; and a final elongation step at 72°C for 10 min and then 4°C on pause. The samples were then examined by electrophoresis in agarose gel (2% w/v). The product was separated by 10% denatured polyacrylamide gel electrophoresis at 260 V for 3.5 h, and the gel was dyed with silver. After that, rinsing, development, and photographing, and band statistical analysis were performed.

Statistical analyses

Growth parameters

Considering the slight difference among the initial biomass of parental ramets, an analysis of covariance (ANCOVA) was performed in our experiment. Before the statistical analyses, to meet the assumptions of homoscedasticity and normality, some data were subjected to logarithmic transformation (leaf area and SPL of parent; offspring ramet number, stolon biomass allocation, and leaf biomass allocation of the whole genet; biomass, ramet number and MIL of offspring ramets in different habitats) or square root transformation (biomass of genets and SSL of offspring ramets). Then, to determine the effect of parental UV-B radiation levels (5 and 10 μW cm^{-2}) on the growth of the parental ramets (biomass, leaf area, petiole length and SPL) and whole clonal genets (biomass, offspring ramet number, branching intensity, leaf biomass allocation, and stolon biomass allocation), one-way ANCOVA was used. Additionally, two-way ANCOVA was performed to analyse the effects of parental UV-B radiation levels and offspring light environments (ambient light vs shade) on the growth parameters of the offspring ramets (biomass, offspring ramet number, stolon length, MIL, SSL). Duncan's test was chosen as the method of multiple comparisons to test the significance among different treatments, and the significance level was set at 0.05. Moreover, the Chi-squared test was performed to analyse the difference in the stolon position when it bent towards the shade habitat in different treatments. All the growth traits were analysed with Statistic 10.0 software (StatSoft Inc, Tulsa, OK, USA).

In addition, the regression relationship between the parental total DNA methylation level and growth parameters of the parent (biomass, leaf area, petiole length, and SPL) and genet (biomass, offspring ramet number, branching intensity, stolon and leaf biomass allocation) were analysed with Origin Pro 8.0 software (OriginLab, USA). All analytical mapping was performed with Origin Pro 8.0 software.

DNA methylation variation

Electrophoretic fragments from approximately 100–500 bp of MSAP were scored. The preliminary statistics on the fragment as present (1) or absent (0) were generated and recorded with Excel 2013 (Microsoft, WA, USA). The DNA methylation status of the restriction sites (5′-CCGG target) was different: the presence of both *Eco*RI–*Hpa*II and *Eco*RI–*Msp*I fragments (1/1) denoted an unmethylated state; the presence of either *Eco*RI–*Hpa*II (1/0) or *Eco*RI–*Msp*I (0/1) fragments indicated methylated states (hemimethylated or internal C methylation); and the absence of both *Eco*RI–*Hpa*II and *Eco*RI–*Msp*I fragments (0/0) was considered an uninformative state (Schulz *et al.* 2013). The total methylation level (%) was calculated by the ratio of the MSAP bands representing the methylated 5′-CCGG sites (differential presence/absence of restricted fragments in *Hpa*II and *Msp*I assays) to the total number of scored bands (Liu *et al.* 2012). Additionally, Shannon's diversity index was analysed with a binary matrix of methylation states via the *vegan* package of R software (RStudio, New Zealand) (Dixon 2003).

Results

DNA methylation level and growth of parental ramets

To understand the DNA methylation variation of parental ramets, the epigenetic diversity (which was represented with Shannon's diversity index) and the total DNA methylation level of parental ramets were analysed. The ANOVA results showed that parental epigenetic variation was influenced only by the parental UV-B environment ($P < 0.05$), and the offspring light environment had no effect on this variation ($P > 0.05$) (Supplementary material Table S1). Shannon's diversity index and total DNA methylation level were significantly improved by high UV-B radiation (10 μW cm^{-2}) ($P < 0.05$). For instance, Shannon's diversity index increased from 4.77 in the control group to 4.83 in the UV10 group, and the total DNA methylation level also improved from 25.94% to 27.15% (Table 2).

The growth traits of parental ramets, such as biomass, leaf area, petiole length and SPL, were significantly influenced by direct UV-B radiation ($P < 0.05$) (Table S2). The leaf area and

Table 2. Shannon's diversity index and total DNA methylation level of parental ramets in different treatments. Different letters indicate significant differences among the treatments, and the same letter indicates no significant differences at the P = 0.05 level. Control, parental ramets received background greenhouse light with little UV-B radiation for 45 days; UV5, parental ramets were exposed to an additional 5 μW cm−2 UV-B radiation for 45 days; and UV10, parental ramets were exposed to an additional 10 μW cm−2 UV-B radiation for 45 days.

Treatments	Shannon's diversity index	Total DNA methylation level
Control	4.77 ± 0.019[b]	25.94 ± 0.51%[b]
UV5	4.79 ± 0.009[b]	26.55 ± 0.24%[b]
UV10	4.83 ± 0.001[a]	27.15 ± 0.47%[a]

petiole length of the parental ramets were significantly decreased by UV-B radiation, and the decrease was increased with improved radiation, but the biomass and SPL of parental ramets were only increased under high radiation or low radiation (Fig. 3).

Habitat selection of *D. indica*

To analyse the effect of parental UV-B radiation on the habitat selection behaviour of *D. indica*, we compared the growth of offspring ramets before and after habitat selection among different treatments. For the clonal *D. indica*, once the stolon began to bend, the habitat that the newborn ramet entered was determined. We analysed the length of stolons between the parent and offspring ramets that first bent to shade in different treatments, and it was obvious that the length was shortened significantly in the UV10 group ($P < 0.05$) (Fig. 4*a*). Moreover, the position of the stolon when it bent towards the shade habitat was also displayed. In all treatments, most bends occurred between the first and second offspring ramets (O_1–O_2) (50.0% of control, 62.5% of UV5 and 40% of UV10) ($P = 0.868$) (Fig. 4*b*).

At the end of the experiment, the growth of offspring ramets in different habitats was examined. There were significant effects of parental UV-B radiation on the growth of the offspring ramets (biomass, ramet number, stolon length, MIL and SSL) ($P < 0.001$). Additionally, except for the ramet number ($P = 0.746$), the growth of offspring ramets was affected by their environment, with the biomass, stolon length, MIL and SSL of the offspring ramets affected by the interaction effect of parent and offspring environments ($P < 0.05$) (Table S3).

The growth of offspring ramets in different habitats (ambient light and shade) is shown in Table 3. In the control, the offspring ramets settled in ambient light habitat had more biomass (66.94%), although this allocation in ambient light was significantly decreased in the UV5 (57.72%) and UV10 (27.27%) groups. Moreover, increases of parental radiation intensity corresponded to less biomass in the ambient light environment, especially in the UV10 group, where most of biomass was distributed to shade habitat (72.73%). Furthermore, regardless of the parental environment, a greater number of ramets settled in the ambient light environment. In addition, the stolon length of *G. indica* in the ambient light habitat in the control was similar to that in the shade habitat (72.20 cm in ambient light vs 72.45 cm in shade; $P > 0.05$), although in the UV5 group, the stolon length in ambient light was increased

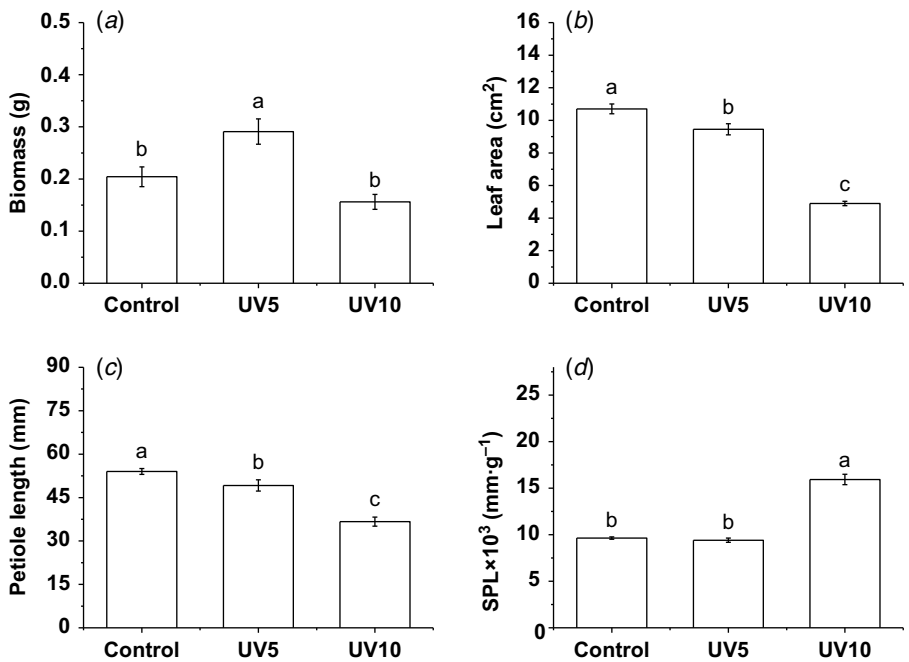

Fig. 3. Growth of parental ramets in different treatments. (*a*) Biomass; (*b*) leaf area; (*c*) petiole length; (*d*) specific petiole length (SPL). Control, parental ramets received background greenhouse light for 45 days, and there was little UV-B radiation in the greenhouse; UV5, parental ramets were exposed to an additional 5 μW cm^{-2} UV-B radiation for 45 days; UV10, parental ramets were exposed to an additional 10 μW cm^{-2} UV-B radiation for 45 days. The different letters are significantly different among the treatments, and the same letter indicates no significant differences at the $P = 0.05$ level with Duncan's multiple range test. Error bars show s.e.

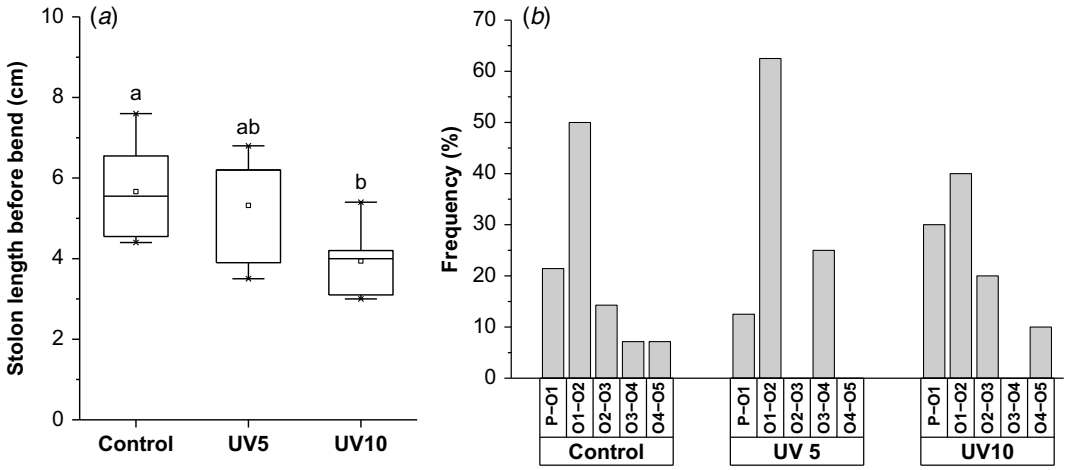

Fig. 4. Stolon length and frequency distribution of the stolon position when it bends towards the shade habitat in different treatments. (*a*) Stolon length between the parent and offspring ramets that first bend towards the shade habitat. (*b*) The frequency distribution of the stolon position when it bends towards the shade habitat. Control, parental ramets received background greenhouse light for 45 days, and there was little UV-B radiation in the greenhouse; UV5, parental ramets were exposed to an additional 5 μW cm^{-2} UV-B radiation for 45 days; UV10, parental ramets were exposed to an additional 10 μW cm^{-2} UV-B radiation for 45 days. P–O1: bend occurs between the parental and first offspring ramets; O1–O2: bend occurs between the first and second offspring ramets; O2–O3: bend occurs between the second and third offspring ramets; O3–O4: bend occurs between the third and fourth offspring ramets; O4–O5: bend occurs between the fourth and fifth offspring ramets. The different letters in Fig. 4*a* are significantly different among the treatments, and the same letter indicates no significant differences at the $P = 0.05$ level with Duncan's multiple range test. Error bars show the s.e.

Table 3. Effect of UV-B environment of the parent (5 and 10 μW cm^{-2}) and light environment of the offspring ramet (ambient light vs shade) on the growth of offspring ramets.

Environment of offspring	Treatments	Biomass (%)	Ramets number (%)	Stolon length (cm)	MIL (cm)	SSL (cm g^{-1})
Ambient light						
	Control	66.94 ± 3.34^{aA}	64.40 ± 3.37^{abA}	72.20 ± 8.04^{bA}	9.39 ± 0.81^{aA}	656.86 ± 46.35^{bB}
	UV5	57.72 ± 3.17^{bA}	52.40 ± 0.23^{bcA}	103.35 ± 8.55^{aA}	9.40 ± 0.08^{aA}	775.77 ± 72.17^{bA}
	UV10	27.27 ± 7.65^{cB}	67.13 ± 5.59^{aA}	58.62 ± 12.92^{bA}	6.94 ± 0.59^{bA}	1141.62 ± 107.12^{aB}
Shade						
	Control	33.06 ± 3.34^{cB}	35.60 ± 3.37^{bcB}	74.25 ± 13.00^{aA}	9.37 ± 0.97^{bA}	799.00 ± 58.48^{bA}
	UV5	42.28 ± 3.17^{bB}	47.60 ± 0.23^{abB}	77.82 ± 16.94^{aB}	10.47 ± 0.84^{aA}	790.70 ± 50.83^{bA}
	UV10	72.73 ± 7.65^{aA}	32.87 ± 5.59^{cB}	20.14 ± 9.25^{bB}	4.27 ± 0.66^{cB}	1563.12 ± 107.56^{aA}

Different letters indicate significant differences among the treatments, and the same letter indicates no significant differences at the $P = 0.05$ level with Duncan's multiple range test. Different lowercase letters indicate significant differences in offspring ramets in the same habitat among different treatments (0, 5 and 10 μW cm^{-2}); and different uppercase letters indicate significant differences in offspring ramets in the same treatment between different habitats (ambient light vs shade).
Control, parental ramets received background greenhouse light with little UV-B radiation for 45 days; UV5, parental ramets were exposed to an additional 5 μW cm^{-2} UV-B radiation for 45 days; and UV10, parental ramets were exposed to an additional 10 μW cm^{-2} UV-B radiation for 45 days; MIL, mean internode length; SSL, specific stolon length.

(103.35 cm), while in the UV10 group, the length in shade was clearly decreased (20.14 cm). In the ambient light habitat, reduced MIL (6.94 cm vs 9.39 cm of control) and increased SSL (1141.62 cm g^{-1} vs 656.86 cm g^{-1} of control) of offspring ramets were observed in the UV10 group, although significant differences were not observed in these two traits between the control and UV5 groups ($P > 0.05$). In shade habitat, the MIL value of offspring in the control group was 9.37 cm, which was significantly improved in the UV5 group (10.47 cm) but decreased in the UV10 group (4.27 cm); moreover, the SSL of offspring ramets was also increased in UV10 (1553.12 cm g^{-1} vs. 799.00 cm $g^{-1}$of control).

The growth of the whole clonal genets was significantly influenced by parental radiation (Table S4). Except for the increase in leaf biomass, other growth traits (biomass, branching intensity, offspring ramet number and stolon biomass allocation) were all decreased by parental UV-B radiation. Moreover, with the increase in parental radiation intensity, the total leaf biomass improved while the stolon biomass and total biomass of the genets were reduced (Fig. 5).

Relationship of parental DNA methylation variation and growth parameters

The regression relationships between the DNA methylation level of parental ramets and their growth traits (biomass, leaf area, petiole length and SPL) are displayed in Fig. 6. Except for the biomass, the leaf area, petiole length, and SPL of the parental ramets all displayed a significant regression relationship with their DNA methylation level. Moreover, some growth parameters of genets (e.g. biomass, branching intensity, stolon, and leaf biomass allocation) displayed regression relationships with the parental DNA methylation levels (Fig. 7).

Discussion

Effects of parental UV-B radiation on the growth of *D. indica*

In our study, the growth of parental ramets was significantly influenced by direct UV-B radiation, as no surprise. Regardless of radiation intensity, the leaf area and petiole length of the parent were decreased by UV-B radiation, and this decrease increased with the enhancement of radiation intensity. The smallest leaf area and the shortest and thinnest petiole appeared under high UV-B radiation conditions (10 μW cm^{-2}). This inhibitory effect on growth was related to the restriction of UV-B radiation on cell division, which inhibited the expansion of the leaf blade and petiole (Wargent *et al.* 2009). Although leaf growth was inhibited, from another perspective, a reduction in leaf

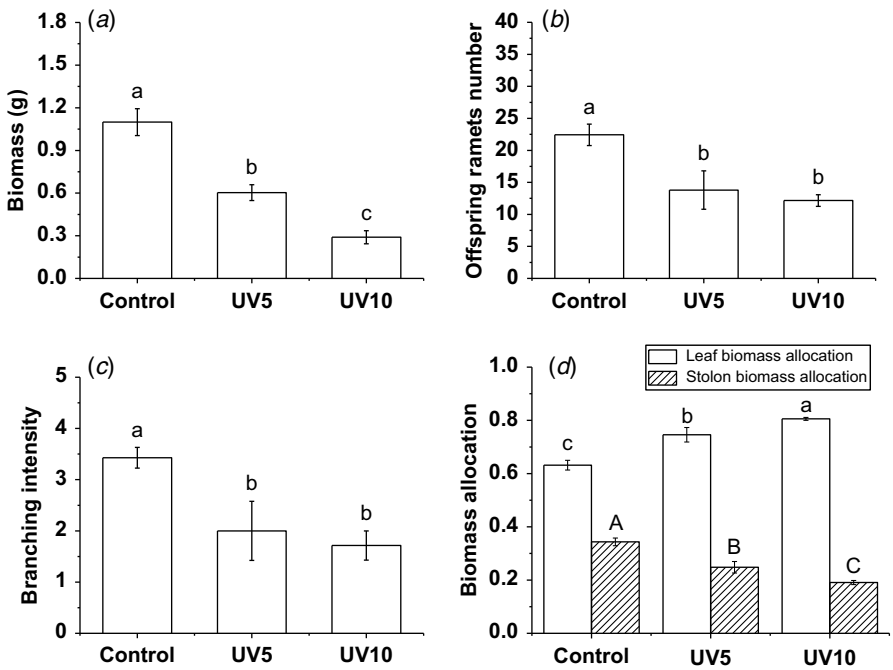

Fig. 5. Growth of clonal genets in different treatments. (*a*) Biomass; (*b*) offspring ramets; (*c*) branching intensity; (*d*) stolon and leaf biomass allocation. Control, parental ramets received background greenhouse light for 45 days, and there was little UV-B radiation in the greenhouse; UV5, parental ramets were exposed to an additional 5 μW cm^{-2} UV-B radiation for 45 days; UV10, parental ramets were exposed to an additional 10 μW cm^{-2} UV-B radiation for 45 days. Different letters indicate significant differences among the treatments, and the same letter indicates no significant differences at the $P = 0.05$ level with Duncan's multiple range test. In Fig. 5*d*, different lowercase letters represent the difference in leaf biomass allocation of genets among different treatments (Control, UV5 and UV10), while different uppercase letters represent the difference in stolon biomass allocation of genets among different treatments (Control, UV5 and UV10). Error bars show the s.e.

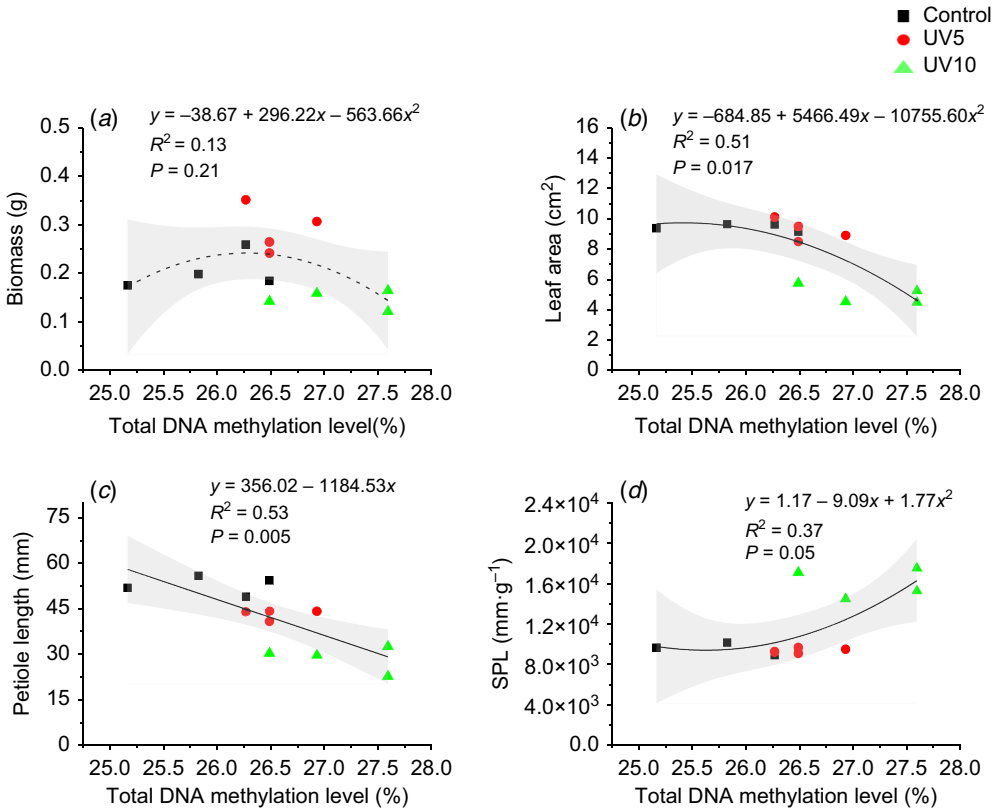

Fig. 6. Regression relationship between parental total DNA methylation level and their growth traits in different treatments. (*a*) Biomass; (*b*) leaf area; (*c*) petiole length; (*d*) specific petiole length (SPL).

area can reduce the absorption of environmental UV-B radiation and thus can avoid UV-B damage, which can be considered a protection strategy for plants in adverse light environments (Mazza *et al.* 2013; Vyšniauskienė and Rančelienė 2014; Chen *et al.* 2016; Roro *et al.* 2017; Yang *et al.* 2018). At the end of the experiment, the biomass of parental ramets was improved by low UV-B radiation (5 μW cm^{-2}), which was related to the eustress effects of low-dose UV-B stress. Eustress is an activating, stimulating stress that is a positive element in plant development; when a plant experiences eustress, its metabolism is adjusted, and the plant acclimates to the new environment (Zhang *et al.* 2021); thus, the parental biomass was increased by this mild, elastic UV-B radiation.

Furthermore, although only parental ramets were exposed to UV-B radiation, the growth of the parent as well as the genets was influenced. Regardless of the dose, UV-B radiation had a negative effect on the growth of offspring ramets, and those genets with radiated parents had less total biomass, fewer ramets and lower branching intensity. With the increase of parental UV-B radiation intensity, the biomass allocated to leaves of offspring ramets was increased but that to stolons was decreased; thus, this kind of biomass distribution between the leaf and stolon was disadvantageous for genets to resist UV-B stress. Therefore, a decrease in the total biomass was observed, and the decrease in the genet biomass was more pronounced in genets with highly radiated parents.

Effect of parental UV-B radiation on the habitat selection of clonal offspring

In heterogeneous patchy environments, the bending of stolons is a key step in the habitat selection behaviour of clonal plants, and the direction of bending determines which patch newborn ramets will enter. Here, we analysed the situation of the stolon that began bending to the shade habitat, and the results showed that more offspring ramets of the highly radiated parent bent to the shade habitat earlier than those of the control group. In addition to the beginning of habitat selection (bend occurrence) of offspring ramets being changed by parental radiation, the results of selection were also influenced. For instance, in the control, more ramets and more biomass settled in the ambient light habitat, which was beneficial for capturing more light under a patchy light environment. Our result was consistent with studies on habitat selection of clonal plants in heterogeneous light environments (Wang *et al.* 2012; Zhao *et al.* 2013; Ye *et al.* 2015; Latzel and Münzbergová 2018). However, the radiation experience of parental ramets significantly

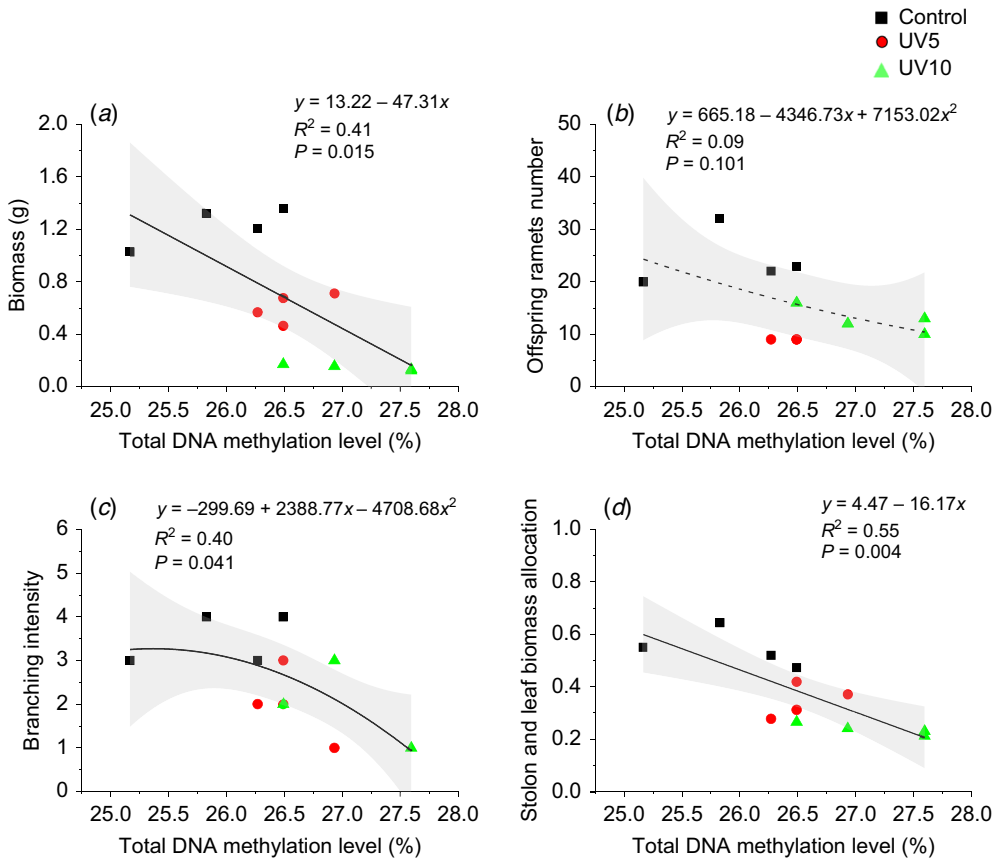

Fig. 7. Regression relationship between parental total DNA methylation level and growth traits of the genets in different treatments. (*a*) Biomass; (*b*) offspring ramet number; (*c*) branching intensity; (*d*) stolon/leaf biomass allocation.

modified this arrangement, and the genets with radiated parents distributed more biomass to shade habitats, especially with highly radiated parents.

Moreover, in the control, the growth pattern (based on stolon length and MIL) of *D. indica* was not significantly different in the ambient light and shade habitats, while that of the genets with the highly radiated parent showed a denser growth pattern, with shorter and thinner stolons (short stolon length and MIL and larger SSL) in the shade habitat. For the genets with the low-radiated parent, the offspring ramets in shade had shorter stolon lengths, while those in the ambient light habitat displayed extended growth patterns with longer and thinner stolons.

Overall, these results showed that offspring ramets seemed to feel the parental environment and adjust their growth in a timely manner. For example, the *D. indica* with a high-radiated parent bent their stolon to the shade habitat earlier and allocated more biomass to the shade habitat. These offspring ramets appear to demonstrate their parental memory of UV-B stress entered the shade environment as a strategy to avoid adverse UV-B radiation. This phenomenon was most likely related to 'maternal effects' and 'transgenerational effect', and it will be discussed below.

Role of parental epigenetic memory in the habitat selection of *D. indica*

Increasing research has proven that the phenotypes of plants are also determined by epigenetic variations induced by the environment; in addition, parental epigenetic variations, such as DNA methylation, can be inherited transgenerationally by offspring and then influence the performance of offspring ramets (Schwaegerle *et al.* 2000; Latzel and Klimešová 2010; Latzel *et al.* 2016; Auge *et al.* 2017; Latzel and Münzbergová 2018). In this study, parental UV-B radiation induced an improvement in their total DNA methylation level and this epigenetic variation was related to the phenotypic variation of the parent, which was accompanied by a decrease in petiole length and leaf area. These phenotypic changes can reduce the adverse effects of UV-B and enhance the resistance of plants to UV-B radiation. Furthermore, parental epigenetic variations were also connected to the growth of the whole genet, which was associated with decreases in biomass, branching intensity and stolon/leaf biomass.

Through maternal effects, offspring ramets can perceive the parental environment and adjust their growth behaviour

according to the parental environment (Schwaegerle *et al.* 2000; Latzel and Klimešová 2010, 2018; Latzel *et al.* 2016; Auge *et al.* 2017). For example, in this study, the growth of offspring ramets in the shade habitat was changed by parental exposure to UV-B radiation. Usually, under shade conditions, many species exhibit SAS by inducing an exaggerated elongation of stems and petioles to capture light (Fritz *et al.* 2018; Ma and Li 2019), while the SAS response can be inhibited by UV-B radiation by antagonising the phytohormones auxin and gibberellin (Hayes *et al.* 2014; Yang *et al.* 2018; Sharma *et al.* 2019; Tavridou *et al.* 2020). For clonal plants, the extension of internodes and stolons in shade can be considered a process of searching for light resources. In the present study, different intensities of parental radiation induced different reactions of offspring ramets in a heterogeneous light environment. For instance, the extension of stolons and internodes in shade habitats was depressed by high UV-B experienced by parental ramets. The clone displayed denser growth with shorter stolons, while the clone with low-radiated parents displayed a more extended growth pattern in ambient light habitats.

Similar effects of the paternal environment on offspring traits have also been found in many studies; for instance, drought stress of parents triggered epigenetic changes in clonal *Trifolium repens*, and most of the induced epigenetic changes were maintained, observed across multiple clonal offspring generations (González *et al.* 2018). Additionally, drought-stressed parents of *Polygonum persicaria* produced drought-adapted offspring, and demethylation treatment of parents removed these adaptive developmental effects (Herman and Sultan 2016). Furthermore, parental shading effects of *Alternanthera philoxeroides* could be transmitted via clonal generation and decreased growth and modified morphology of offspring. These offspring responses were also influenced by DNA methylation levels of parents (Dong *et al.* 2019). Moreover, shaded parents of *P. persicaria* produced offspring with increased fitness in shade as well as a greater competitive impact on plant neighbours (Baker *et al.* 2019). Our previous study also suggested that the parental ramets of clonal *G. longituba* could record their UV-B radiation experience and form epigenetic memory via a decrease in DNA methylation levels, the growth of offspring and genets was clearly affected by parental experience (Zhang *et al.* 2021).

Conclusion

Our results suggested that although only parents were exposed to UV-B radiation, not only the growth and epigenetics of the parent but also the habitat selection behaviour of their offspring ramets and the growth of the whole genet were affected by the parental UV-B environment. In addition, some of these growth traits were controlled by parental epigenetic variation. Interestingly, it appears that offspring ramets were able to sense the high UV-B environment of the parents and then avoid the UV-B environment, as observed by the earlier bending of their stolons to the shade habitat and greater allocation of biomass to the shade habitat. These behaviours could be regarded as a preregulation of clonal offspring to future UV-B stress. Moreover, the performance of offspring differed according to the different radiation intensities of their parents. For instance, with a high UV-B stressed parent, the SAS responses of offspring in shade habitat was inhibited, and they displayed more dense growth with shorter stolons and internodes, while clones with a low-radiated parent showed extensive longer internode lengths in shade. The difference was related to the eustress and stress effects of low and high UV-B radiation, respectively. In conclusion, our results showed that parental environmental information was important to the performance of offspring ramets, which was related to the maternal effect of parental ramets via epigenetic variation. UV-B radiation was a nonnegligible factor in regulating the habitat selection of clonal plants in heterogeneous light environments. Our results will help to understand the strategies and mechanisms of clonal plants in response to complex light environmental information in natural ecosystems.

Supplementary material

Supplementary material is available online.

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Data availability. The original contributions presented in the study are included in the article/supplementary file, further inquiries can be directed to the corresponding author.

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