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RESEARCH

Compensatory growth under leaf damage of herbal vine *Aristolochia contorta* depends on the light availability

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Background: There is a wide range of phenotypic plasticity in plants that respond to tissue damage. Compensatory growth after physical damage may function as a part of tolerance to herbivory, which is affected by resource limitations and/or damage properties.
Results: Under different light availability (unshaded and shaded) and damaged leaf ontogeny (control, young leaf- and mature leaf-damaged), compensatory growth was examined for the herbal vine *Aristolochia contorta*. Under the unshaded treatment, compensatory growth on leaf and branch emergence was strongly induced compared to the shaded treatment. Damage to young leaves induced leaf emergence more strongly than damage to old leaves.
Conclusions: It appears that light availability acted as a limiting factor in the compensatory growth of *A. contorta* after the damage despite its vigorous growth under the shade treatment. Under the shade, leaf damage led to altered biomass allocation as indicated by a decrease in specific leaf area and an increase in root mass fraction. The present study contributes to the understanding of the phenotypic plasticity of vine species under different environmental conditions and damaged tissue, which may differ depending on the species' habitat range.

Keywords: herbal vine, leaf ontogeny, over-compensation, phenotypic plasticity, resource availability

Introduction

Plants are exposed to diverse risks of stress and damages from their biotic/abiotic environmental factors (Berens et al. 2019; Nguyen et al. 2016). Physical damage could occur by herbivory, which leads to the loss of the plant tissue and could negatively affect the Darwinian fitness. Plants have their own phenotypic plasticity in response to changes in biotic and abiotic environmental change (Barton 2008; Schlichting 1986). Plants respond to the tissue damage including herbivory by diverse defense mechanisms. Herbivory defense mechanisms are commonly classified into resistance and tolerance (Núñez-Farfán et al. 2007; Strauss and Agrawal 1999). Resistance to the herbivory usually accompanies the change in chemical and/or structural composition of plant tissues to avoid the further herbivory. Tolerance, which refers the capacity to reduce the effect of tissue damage after herbivory, usually presented as the phenotypic plasticity and/or regrowth after damage (Fornoni 2011; Stowe et al. 2000).

Regrowth after damage could compensate the damage, however, not always fully compensate the damage of plant tissues (Fornoni 2011). In some cases, plant could "over-compensate" the damage to cope with the competition for resource availability (Järemo et al. 1996). In the other cases, moderate leaf damage by herbivory could stimulate the compensatory growth, which could enhance the vigorous growth of plant individual even than the undamaged individual (McNaughton 1979). Even with the same level of physical damage, properties of damaged tissue could make difference in the result of plant defense, such as leaf ontogeny (Barton and Boege 2017). Level of compensatory growth is affected by resource limitation and damage level (Wise and Abrahamson 2005). Resource availability also could be limiting factor of compensatory growth after damage, yet the relationship between resource availability and compensatory growth response is unclear (Ballina-Gómez et al. 2010). Light availability is one of major limiting factor to plant resource acquisition and allocation (Ågren 1985). Response to herbivory stress of plant is also affected by light availability (Hough-Goldstein and LaCoss 2012; Lentz and Cipollini 1998). Therefore, differences in compensatory growth by damaged tissue might depend on the light availability.

Compensatory growth in response to herbivory damage can impact both plant and herbivore communities, influenced by the quantitative and/or qualitative traits of tissue regrowth relative to herbivory pressure (Fornoni 2011). Response to herbivory of vine species among light availability is known to vary by specific optimal range (Gianoli et al. 2007). In case of vine species, they are exposed to various light availability conditions which depend on the life-form and/or morphological characteristics of host (Park et al. 2019). Family Aristolochiaceae have distinct secondary metabolites, which allows only a few specialist leaf herbivore species (Miller 1987). *Aristolochia contorta* is one of the Aristolochiaceae vine species which have the specialist herbivore butterfly, *Sericinus montela* (dragon swallowtail; Hong et al. 2014). Vigorous growth of *A. contorta* was shown under shade than without damage (Park et al. 2019). As well as the growth without damage, compensatory growth response of *A. contorta* against herbivory is related to the maintenance of *S. montela* population. The growth response of the *A. contorta* under herbivory and/or leaf damage stress has been poorly understood.

In this study, we tried to assess the phenotypic plasticity to the leaf damage of *A. contorta* under different light availability in the experimental field. Light availability was manipulated by artificial shade and leaf damage treatment was applied to two different leaf ontogeny groups (young leaf and old leaf). Result of this study could enhance the fundamental understanding of the environment-dependent plant phenotypic plasticity to physical damage.

Materials and Methods

Plant growth condition and treatment

Aristolochia contorta is a non-parasitic perennial vine found in East Asia and Russia. It has heart-shaped leaves measuring 4–10 cm in length and 4–8 cm in width. The stem can grow up to 1.5 m, but may extend longer depending on the host plant. Inflorescences appear on plants over three years old from July to August (Korea National Arboretum 2024; Park et al. 2019). *Aristolochia contorta* seeds were collected from a population which located in Gapyeong, Gyeonggi Province, Republic of Korea at December 2017. Seeds were delivered to laboratory and germinated in greenhouse located in Gwanak-gu, Seoul (37°27'N 126°57'E) at May 2018. In June 2018, a total of 120 seedlings with about 5 cm of shoot height were individually transplanted in the pots (15 cm diameter × 20 cm depth) filled with mix of sand and topsoil (2:1 in v/v, Super EXTN-1; Farmhannong, Seoul, Korea). Physical support of plastic stake (0.3 cm diameter × 1.3 m height) was added in each pot.

One week after transplanting (early July), two relative light availability treatments (relative light intensity, RLI; unshaded = 100% of RLI to outside; shaded = 50% of RLI) were applied to 60 individuals for each. 100% and 50% of RLI represented *A. contorta* under herb (or no) host and tree host, respectively (Park et al. 2019). Half level of RLI (in case of shade treatment) was provided by layered black mesh 2.5 m above the steel structure, which have shown as the half level of the photosynthetically active radiation (PAR) at outside (Park et al. 2019). Since there was a forest surrounding the experimental plot, PAR at noon under the unshaded and the shaded treatments were 1,303 μmol m^{-2} s^{-1} and 654 μmol m^{-2} s^{-1}, respectively. Individuals of *A. contorta* were acclimated under each light availability treatment for one month and used to the following leaf damage treatment.

In each light availability condition, leaf damage treatments were applied two times (15th August and 15th September) to mimic the temporal emergence of the larvae of *S. montela* (Kim and Kwon 2010). Three leaf damage treatments were applied for each light availability treatment as follow: control (undamaged), mature leaves damaged, and young leaves damaged. The treatment “mature leaves damaged” by damage using hole puncher (6 mm diameter) was applied to the 25% of the lowermost leaves in each individual, which cause the loss of 50% in area of damaged leaves. The treatment “young leaves damaged” was applied as same as “mature leaves damaged” to the uppermost leaves (25% of total leaves). Individuals were additionally grown for four weeks after the second treatment.

Measurement of growth characteristics

Plants were harvested at October, four weeks after the second leaf damage treatment. Following characteristics were measured: number of primary branches, number of leaves, total leaf area, stem length, and dry weight of stem, leaf, and root. Total leaf area of each individual was measured using portable leaf area meter (LI-3000C, LI-COR Bioscience, Lincoln, NE, USA). Internode length and petiole length of the representative middle parts (n = 3 for each individual) were also measured using digital caliper (Mitutoyo, Kanagawa, Japan). Chlorophyll contents were quantified from the average of the three leaf replicates at the mid-shoot in each individual using chlorophyll meter (SPAD-502, Konica Minolta, Tokyo, Japan). Total dry weight was calculated as the sum of the dry weight of stem, leaves, and root. The specific leaf area (SLA) for each individual was calculated based on their total leaf area and leaf dry weight. Due to the excessively low leaf dry weight, four excessively high SLA values (more than 100 mm^2 mg^{-1}) were discarded from the further analysis.

Calculation of phenotypic plasticity

To compare the phenotypic plasticity between two light availability treatments to the leaf damage, a relative distance plasticity index (RDPI) of each growth parameter was calculated. The RDPI was calculated by averaging the relative differences between the trait values of the control and the treated individuals (Valladares et al. 2006). Because of the discontinuity of the leaf damage treatment, relative distances under each leaf damage treatment (mature- and young-) from control treatment under each light availability treatment were calculated as below:

$$RDPI = \left(\sum \frac{d_{ctrl,i \rightarrow treatment,j}}{x_{ctrl,i} + x_{treatment,j}}\right)/n$$

where n is the total number of distances.

Statistical analysis

Significances of light availability, leaf damage treatments, and interaction between the light availability and leaf damage were examined by two-way analysis of variance (ANOVA) using R version 4.0.2 (R Core Team 2020). Significance of the difference between group means was determined by Duncan's post-hoc test using R package "agricolae."

Results

Growth characteristics under different light availability and leaf ontogeny

From the result of two-way analysis of variance, morphological traits significantly differed by the light availability and leaf damage treatment, mainly by light availability (Table 1). There was a significant effect of light availability on overall growth traits ($p < 0.05$), with the exception of chlorophyll content of representative leaves and root dry weight. The leaf damage treatment significantly affected number of primary branches and leaves, SLA (ratio between the leaf area and dry weight), root dry weight, shoot dry weight, and total dry weight ($p < 0.05$). Interaction of the light availability and leaf damage treatment was significant in total leaf area, average leaf area, chlorophyll content, leaf mass fraction (LMF), root mass fraction (RMF), and leaf dry weight (Table 1).

Both stem and internode length were higher under the shade treatment, than the unshaded treatment (Fig. 1A, B). Number of branches and leaves were higher under the unshaded treatment than the shaded treatment (Fig. 1C, D). Under the shade treatment, however, total leaf area and average single leaf area were higher than under the unshaded treatment (Fig. 1E, F). In the absence of leaf damage, SLA was higher in the shaded treatment than in the unshaded (Fig. 1G). Petiole length was also greater under the shaded treatment than under the unshaded (Fig. 1H). Chlorophyll contents of representative leaf did not show the significant difference under two light availability treatments (Fig. 1I). The total biomass (in dry weight) under the shade was slightly higher than under the unshaded (Fig. 2A). Compared to the unshaded treatment, the dry weight of aboveground parts (leaves and shoots) was higher under the shade treatment, whereas the root dry weight did not differ under the two light availability treatments (Fig. 2D-F). Plants grown under the unshaded showed lower LMFs and higher RMFs than plants grown under the shade, except when mature leaves were damaged (Fig. 2B, C).

Some of growth characteristics were affected by the leaf damage treatment regardless of the light availability. Number of branches and leaves seemed to increase under the leaf damage treatment, young leaf damaged treatment in

Table 1 Two-way analysis of variance results for growth traits of *Aristolochia contorta, F* statistics are shown. The two treatments were light intensity (unshaded and shaded) and leaf damage (control, mature leaf damaged, and young leaf damaged). *df* = 1, 2, 114 for each treatment. Significant effects are shown in asterisk (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

	Light	Damage	Light × damage
Stem length (cm)	69.521^{***}	1.111	1.985
Internode length (cm)	61.478^{***}	0.102	0.061
No. of primary branches	36.147^{***}	11.926^{***}	2.272
Total leaf area (cm^2)	35.476^{***}	1.422	4.948^{**}
No. of leaves	6.274^{*}	8.168^{***}	2.553
Single leaf area (cm^2)	104.625^{***}	2.233	4.374^{*}
Specific leaf area (mm^2 mg^{-1})	0.618	7.275^{**}	0.507
Petiole length (mm)	58.085^{***}	0.063	2.836
Chlorophyll content (SPAD)	1.637	0.358	11.175^{***}
Total dry weight (g)	6.546^{*}	3.299^{*}	1.014
Leaf mass fraction (g g^{-1})	19.460^{***}	1.088	7.822^{***}
Root mass fraction (g g^{-1})	32.605^{***}	1.609	7.297^{**}
Root dry weight (g)	0.451	3.387^{*}	0.606
Shoot dry weight (g)	23.991^{***}	3.329^{*}	1.834
Leaf dry weight (g)	11.876^{***}	2.792	3.521^{*}

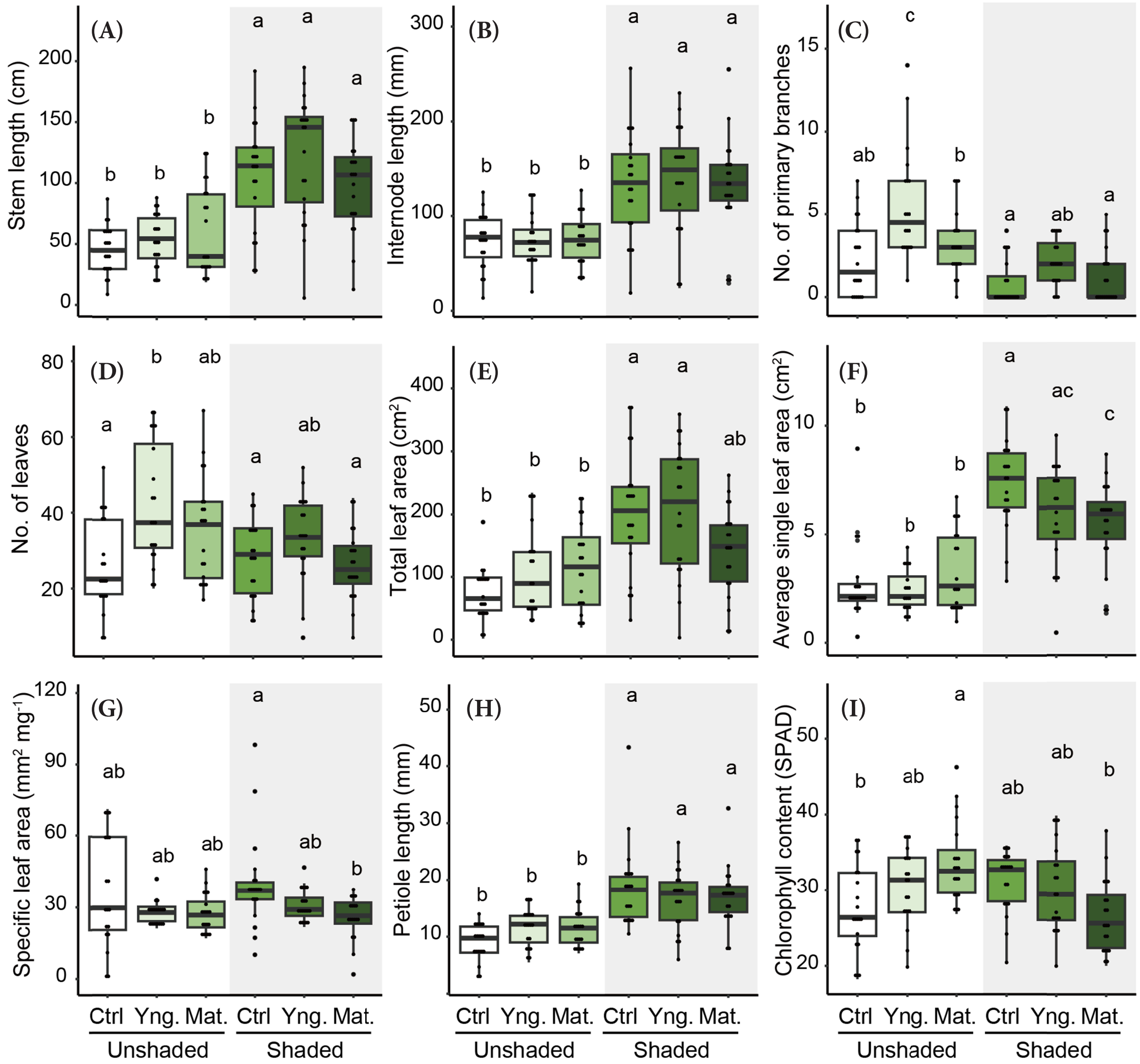

Fig. 1 Variations in morphological traits among treatments in the mesocosm experiment. (A) Stem length; (B) internode length; (C) number of primary branches; (D) number of leaves; (E) total leaf area; (F) average single leaf area; (G) specific leaf area; (H) petiole length; (I) chlorophyll content. Lower case alphabets on graph represent statistically different groups by Tukey's post-hoc test (< 0.05 level). Unshaded = 100% relative light intensity; Shaded = 50% relative light intensity; Ctrl = control; Yng. = young leaf damaged; Mat. = mature leaf damaged.

particular (Fig. 1C, D). Total dry weight was also higher under the leaf damage treatment (Fig. 2A). On the other hand, several growth responses to leaf damage treatment were differed by light availability. Total leaf area of damaged individuals was higher than the undamaged individuals under the unshaded, while individuals of mature leaves damaged treatment showed lower total leaf area than the undamaged individual under shade (Fig. 1E). Average single leaf area was decreased after the damage treatment only under the shade treatment (Fig. 1F). Chlorophyll content of representative leaves of damaged individuals showed the higher level than the undamaged individuals under the unshaded condition, while lower chlorophyll content level was showed in damaged individuals under the shaded condition (Fig. 1I). Leaf damage treatment induced the decrease of SLA only under the shaded condition (Fig. 1G). Response in leaf dry weight was similar to the total leaf area, which showed the partial overcompensation of leaf dry weight under shade only to the young leaf damaged treatment (Fig. 2A).

Phenotypic plasticity against leaf damage under different light condition

Calculated RDPI showed the difference in phenotypic plasticity to the leaf damage among two light availability treatments (Fig. 3). Total leaf area, leaf number, average single leaf area, petiole length, and chlorophyll content showed the higher plasticity under the unshaded treatment than the shade treatment (Fig. 3D-J). Under the unshaded treatment, the total dry weight as well as the leaf and root dry weights showed higher plasticity (Fig. 3J, M, O). A higher level of plasticity was observed under the shade

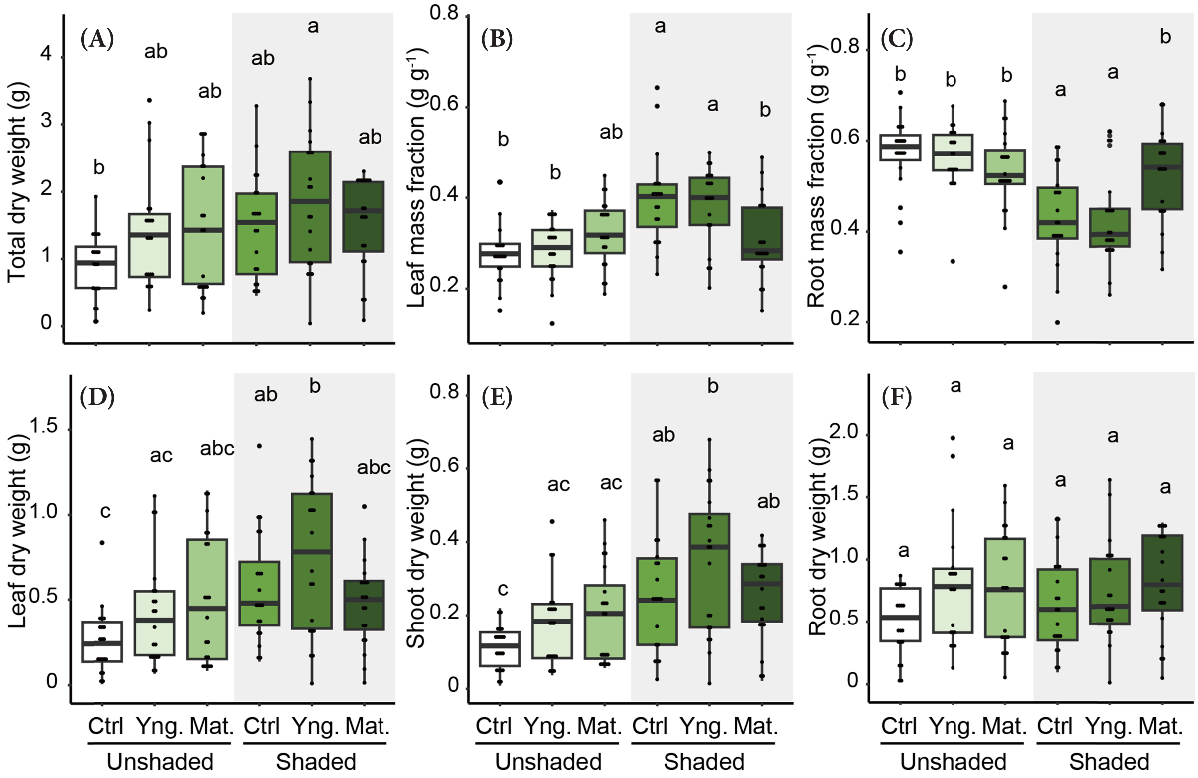

Fig. 2 Variations in biomass allocation among treatments in the mesocosm experiment. (A) Total biomass; (B) leaf mass fraction; (C) root mass fraction; (D) leaf biomass; (E) shoot biomass; (F) root biomass. Lower case alphabets on graph represent statistically different groups by Tukey's post-hoc test (< 0.05 level). Unshaded = 100% relative light intensity; Shaded = 50% relative light intensity; Ctrl = control; Yng. = young leaf damaged; Mat. = mature leaf damaged.

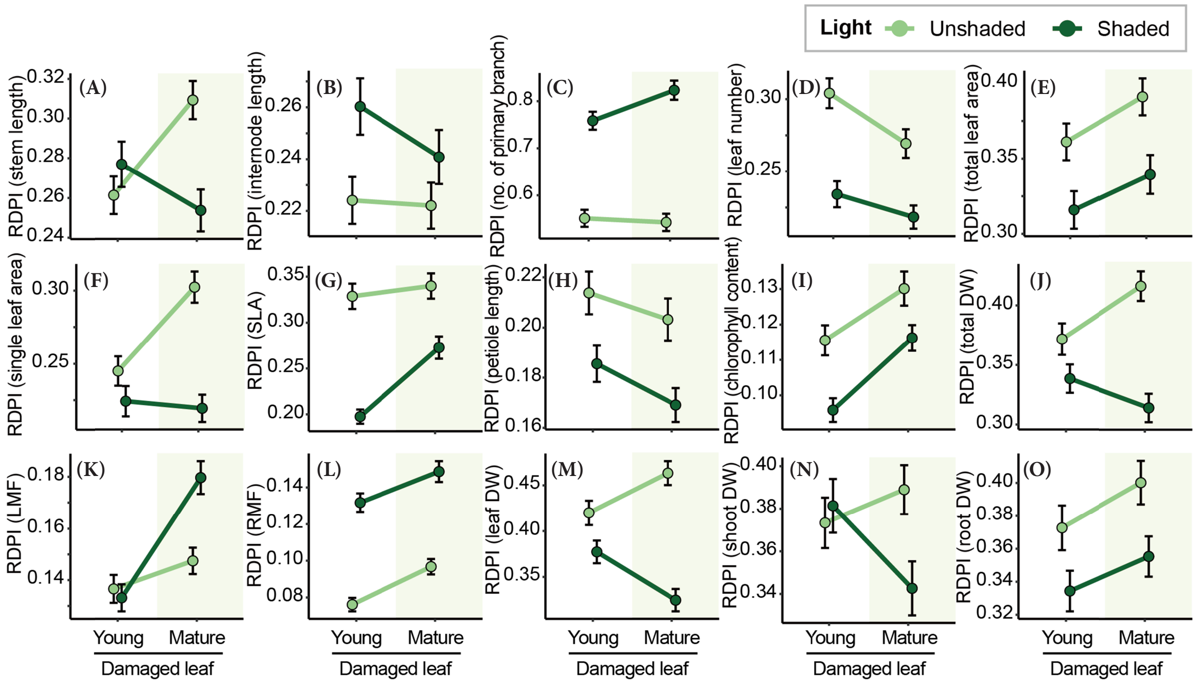

Fig. 3 Relative distance plasticity index (RDPI) of morphological traits under different light conditions. RDPI of (A) stem length; (B) internode length; (C) number of primary branches; (D) leaf number; (E) total leaf area; (F) average single leaf area; (G) specific leaf area; (H) petiole length; (I) chlorophyll content (SPAD); (J) total biomass; (K) leaf mass fraction; (L) root mass fraction; (M) leaf biomass; (N) shoot biomass; (O) root biomass. Unshaded = 100% relative light intensity; Shaded = 50% relative light intensity; Young = young leaf damaged; Mature = mature leaf damaged. Vertical bars represent the standard error.

treatment compared with the unshaded treatment in terms of the length of internodes, the number of primary branches, and the RMF (Figs. 3B, C, L).

The total leaf area, chlorophyll content, RMF, and root dry weight were found to be higher with mature leaf damaged treatments compared to young leaf damaged treatments (Fig. 3D, I, L, O). The higher light availability induced the higher RDPI of stem length and average single leaf area with mature leaf damaged treatment, yet not with young leaf damaged treatment (Fig. 3A, F). Phenotypic plasticity of total dry weight and leaf dry weight was higher under the unshaded treatment than the shaded treatment, especially with mature leaf damaged treatment than young leaf damaged treatment (Fig. 3J). SLA and LMF under the shade treatment showed the higher plasticity by damage on the mature leaf than the young leaves (Fig. 3G, K).

Discussion

Many of the growth characteristics of *A. contorta* showed an increase under the leaf damage treatment. For example, biomass under the leaf damage treatment was higher than under the undamaged treatment (Fig. 2A). Under leaf damage treatment, *A. contorta* also displayed over-compensatory traits, such as the increase in new leaves, branches and primary productivity, implying rapid recovery and re-occupation of resources.

Compensatory response to herbivory stress in plants has been studied in diverse plant species (Strauss and Agrawal 1999; Trumble et al. 1993). Some vine plant species with climbing life-form showed compensatory response to herbivory (Gianoli et al. 2007; Rausher et al. 1993; Schierenbeck et al. 1994). In case of vine species, light availability is mainly determined by host plant species. *Aristolochia contorta* showed the higher shoot growth and the larger leaf area under the tree host, than the shrub and herb host plant (Park et al. 2019). In the former study, 3-year-old *A. contorta* individuals showed the relatively vigorous growth under shade with the larger leaf and the longer stem than full sunlight (Park et al. 2019). Similar to the 3-year-old *A. contorta* individuals, 1-year-old *A. contorta* individuals in the present study also showed the longer stem, larger leaf area, and higher biomass production under the shade treatment (Figs. 1 and 2). Excessive solar radiation could cause heat, dehydration and UV irradiation, which could inhibit the plant growth (Valladares and Niinemets 2008).

On the other hand, *A. contorta* seemed to respond to the leaf damage differently depend on the light availability. Light availability could role as limiting factor for compensatory growth (Hough-Goldstein and LaCoss 2012; Lentz and Cipollini 1998). Vine species could respond to the leaf damage differently by the light availability (Gianoli et al. 2007). Particularly, some phenotypic plasticity indices on the aboveground parts, such as leaf number, total leaf area, and leaf dry weight, were higher under the unshaded than the shaded treatment (Fig. 3). In contrast, the SLA of damaged individuals under the shaded treatment decreased at a similar rate to that of those under the unshaded treatment (Fig. 1G). The SLA tends to be higher under shade, which could be an adaptive strategy to maximize the amount of light harvested (Stotz et al. 2022; Yuan et al. 2016). While leaf damage on the *A. contorta* individual under the shade did not induce an increase in the total dry weight, damage on mature leaves under the shade treatment altered the allocation, such as an increase in the RMF and a decrease in the LMF, which could be interpreted as a potential resource limitation. The resource requirements for compensatory growth of *A. contorta* appeared to be affected by both the ontogeny of the damaged leaves as well as the light conditions.

Damage to young leaves further affected the growth characteristic parameters than the damage of mature leaf. Newly emerging leaves are considered to have the higher nutritional value from the higher photosynthesis rate and nitrogen concentrations (Field and Mooney 1983). Therefore, phytophagous insects commonly prefer the new leaves than the mature leaves, which could make the physical damage mainly to the younger leaves (Bazzaz et al. 1987; Cranshaw and Radcliffe 1980). Damage of newly emerging leaves could make the apical dominance weaker, which trigger the emergence of new leaf or shoot (Aarssen 1995). In the present study, damage of young leaves more induced the emergence of new leaves and branches, therefore more new leaves could re-emerge. Thus, *A. contorta* seemed to quickly respond to damage of young leaves by rapid compensatory regrowth, while the regrowth was weaker when mature leaves were damaged. Research on several species has shown that the younger leaves are more resistant to herbivory or pathogen infection (Berens et al. 2019; Ohnmeiss and Baldwin 2000). According to our results, compensatory growth against leaf damage is also affected by leaf ontogeny, which could be interpreted as a plant that optimizes both regrowth and resistance.

Conclusions

Compensatory growth could be regarded as a part of tolerance to the physical damage. Herbal vine species *A. contorta* showed compensatory growth under leaf damage, depends on the leaf ontogeny and light availability. The previous study had shown that *A. contorta* grows well under shade, but compensatory growth was greater under the unshaded treatment following leaf damage. As shown by the plasticity of leaf and RMFs, light availability also affected the allocation of resources after leaf damage. As a result, *A. contorta* optimizes its compensatory growth as a resource-dependent process against leaf damage. To assess the variation in tradeoff between tolerance and the other traits in *A. contorta* more precisely, resistance against herbivory should be assessed in the further study.

Abbreviations

RLI: Relative light intensity
PAR: Photosynthetically active radiation
SLA: Specific leaf area
RDPI: Relative distance plasticity index
LMF: Leaf mass fraction
RMF: Root mass fraction

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Author's contributions

SHP conceived the ideas, conducted the field study and the data collection and analysis, and wrote the original manuscript. BEN conducted the data collection and analysis, and wrote and edited the manuscript. JGK conceived the ideas, secured the funding, and edited the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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