

Effects of Moderate UV Radiation Enhancement on Photosynthetic Characteristics and Medicinal Active Components of *Dictamnus dasycarpus* (Postprint)

Authors: Su Yuhang, Song Xiaoqian, Zheng Jingwen, Cao Meng, Zhonghua Zhang, Tang Zhonghua

Date: 2022-05-21T20:03:12+00:00

Abstract

Environmental regulation of secondary metabolites constitutes the theoretical and practical foundation for high-quality cultivation of medicinal plants. However, to date, research on the effects of short-term ultraviolet induction on the accumulation of medicinal active components remains relatively limited. This study employed the light-environment-sensitive plant *Dictamnus dasycarpus* as the research subject to investigate the inductive effects of short-term ultraviolet (UV) radiation enhancement at different intensities (low and moderate doses) on four active constituents—obacunone, fraxinellone, dictamnine, and limonin—in its roots, stems, and leaves. The results demonstrated: (1) Under both low- and moderate-dose UV-A and UV-B radiation conditions, the maximum photochemical quantum yield (F_v/F_m) of Photosystem II (PS II) in *Dictamnus dasycarpus* leaves exceeded 0.76; the actual photosynthetic quantum yield of PS II $Y(II)$, quantum yield of regulated energy dissipation $Y(NPQ)$, photochemical quenching coefficient (q_L), and non-photochemical quenching coefficient (NPQ) showed no significant differences compared with the control (without UV radiation treatment); both low- and moderate-dose UV-B radiation significantly increased the quantum yield of non-regulated energy dissipation $Y(NO)$ of PS II in *Dictamnus dasycarpus*. (2) Moderate short-term UV radiation enhancement could induce rapid accumulation of medicinal active components in *Dictamnus dasycarpus*, with the four active constituents in the roots increasing by up to 51%, primarily accumulating in the roots of *Dictamnus dasycarpus*. Among these treatments, moderate-dose UV-A radiation and low-dose UV-B radiation exhibited the most pronounced effects, not only significantly elevating the four active constituents—obacunone, fraxinellone, dictamnine, and limonin—in the roots, but also promoting the accumulation of dictamnine and fraxinellone in

the stems and leaves. In summary, these findings indicate that short-term UV radiation enhancement can effectively induce the accumulation of medicinal active components in *Dictamnus dasycarpus* and improve its tolerance to light intensity by enhancing the non-photochemical efficiency of PS II.

Full Text

Effects of Moderate Ultraviolet Radiation Enhancement on Photosynthetic Characteristics and Medicinal Active Components of *Dictamnus dasycarpus*

SU Yuhang^{1,2}, SONG Xiaoqian^{1,2}, ZHENG Jingwen^{1,2}, CAO Meng^{1,2}, ZHANG Zhonghua^{1,2*}, TANG Zhonghua^{1,2}

¹Key Laboratory of Forest Plant Ecology, Ministry of Education, Northeast Forestry University, Harbin 150040, China

²College of Chemistry, Chemical Engineering and Resource Utilization, Northeast Forestry University, Harbin 150040, China

Abstract

Environmental regulation of secondary metabolic components forms the theoretical and practical foundation for high-quality cultivation of medicinal plants. However, research on the accumulation effects of short-term ultraviolet (UV) induction on medicinal active ingredients remains relatively limited. This study investigated the inductive effects of short-term enhanced UV radiation at different intensities (low and moderate doses) on four active ingredients—obacunone, fraxinellone, dictamnine, and limonin—in the roots, stems, and leaves of *Dictamnus dasycarpus*, a plant sensitive to light environments. The results showed: (1) Under both low- and moderate-dose UV-A and UV-B radiation, the maximum photochemical quantum yield of photosystem II (Fv/Fm) in *D. dasycarpus* leaves remained above 0.76. Compared with the control (without UV radiation treatment), no significant differences were observed in the actual photosynthetic quantum yield of PS II Y(II), regulated energy dissipation quantum yield Y(NPQ), photochemical quenching coefficient (qL), and non-photochemical quenching coefficient (NPQ). Both low- and moderate-dose UV-B radiation significantly increased the non-regulated energy dissipation quantum yield Y(NO) of *D. dasycarpus* PS II. (2) Appropriate short-term UV radiation enhancement induced rapid accumulation of medicinal active components in *D. dasycarpus*, with the four active ingredients in roots increasing by up to 51%, primarily accumulating in the roots. Moderate-dose UV-A and low-dose UV-B radiation showed the most pronounced effects, significantly increasing the four active components (obacunone, fraxinellone, dictamnine, and limonin) in roots while also promoting dictamnine accumulation in stems and fraxinellone accumulation in leaves. In summary, these findings demonstrate that short-term enhanced UV radiation effectively induces accumulation of medicinal active com-

ponents in *D. dasycarpus* and enhances its light intensity tolerance by improving the non-photochemical efficiency of PS II.

Keywords: ultraviolet radiation, *Dictamnus dasycarpus*, secondary metabolism, medicinal ingredients, photosynthetic characteristics

Dictamnus dasycarpus is a perennial herbaceous plant in the Rutaceae family, and its root bark (*Dictamni Cortex*) is a commonly used traditional Chinese medicine and major medicinal material in China. The primary pharmacological substances are alkaloids and limonoids, which are bioactive secondary metabolites. The four most important compounds are obacunone ($C_{26}H_{30}O_7$), fraxinellone ($C_{14}H_{16}O_3$), dictamnine ($C_{12}H_9NO_2$), and limonin ($C_{26}H_{30}O_8$). The first two are mandatory testing items specified in the *Pharmacopoeia of the People's Republic of China* (2020 edition), requiring minimum contents of 0.15% for obacunone and 0.05% for fraxinellone based on dry weight. The content of these primary active components is a critical indicator of *D. dasycarpus* quality. Although wild *D. dasycarpus* exhibits high medicinal quality, its long growth cycle and difficult harvesting have led to decreasing wild resources due to large-scale collection. Moreover, in traditional practice, only the root bark is used medicinally while the aboveground parts are discarded, causing substantial resource waste. Therefore, improving resource utilization and quality of *D. dasycarpus* has become an urgent issue. Zhao et al. (2020) found that artificially cultivated *D. dasycarpus* in some regions fails to meet pharmacopoeia standards, with obacunone content at only 0.10% and fraxinellone at 0.033%. Production conditions and environmental factors affect *D. dasycarpus* quality. To improve medicinal material quality, utilizing environmental factors to interfere with plant growth and regulate metabolic pathways has become a research hotspot, with studies demonstrating that environmental modification effectively enhances secondary metabolite accumulation in *D. dasycarpus* (Du et al., 2005; Liu et al., 2016). Consequently, research on environmental factor effects on medicinal components is needed to guide artificial cultivation and enhance active ingredient content through environmental induction.

Light is an essential environmental factor for plant photosynthesis, affecting plant development through intensity and quality, and serves as a primary regulator of both primary and secondary metabolism while controlling various metabolic signaling processes (Porto et al., 2020). Solar radiation includes ultraviolet, visible, and infrared bands, with different wavelengths acting on plants through photosynthesis, receptor activation, and damage induction (Christie & Briggs, 2001; Ahmad et al., 2002; Flint & Caldwell, 2003). Previous studies indicate that UV radiation can influence plant secondary metabolite accumulation by 10%–300% (Kakani et al., 2003). Higher plants have evolved defense mechanisms against UV damage, including wax formation and trichomes on stems and leaves, synthesis of UV-absorbing substances such as flavonoids and phenols (Barnes et al., 2016; Valenta et al., 2020), and repair of damaged DNA via antioxidant and enzyme systems (Bornman et al., 2015). UV-A determines

plant sensitivity to UV-B, with blue light receptors including phytochrome A, cryptochromes, and phototropins absorbing certain UV-A radiation (Krizek, 2004). UV-A exerts both positive and negative effects on plant growth, biomass allocation, and synthesis of secondary metabolites like phenols and flavonoids (Valenta et al., 2020). Plant photosynthesis and medicinal component responses to radiation depend on radiation intensity, plant species, and environmental conditions (Yue et al., 2005). Li and Yue (2005) found that *Fritillaria thunbergii* showed good growth and significantly increased alkaloid content under moderate UV-B radiation, while Fu et al. (2017) reported that enhanced UV radiation significantly increased secondary metabolites such as genipin and flavonoids. Appropriate UV-B intensity can promote accumulation of various medicinal active components, including flavonoids, alkaloids, and terpenoids (Zhang & Björn, 2009).

Advances in UV LED technology and habitat suitability analysis have made directional induction of medicinal active components via light quality feasible for field production, though specific control parameters remain scarce. Currently, artificially cultivated plants in China exhibit far lower medicinal efficacy than wild plants. Solving this critical issue through directional light quality induction is crucial for protecting wild plant resources. Therefore, to improve active component content in cultivated *D. dasycarpus*, this study used two-year-old *D. dasycarpus* plants for cultivation experiments under different UV radiation intensities to explore responses of photosynthetic characteristics and four primary active components to short-term UV radiation enhancement. The study addresses three questions: (1) Does *D. dasycarpus* suffer damage under short-term different UV radiation conditions? (2) Is utilization efficiency improved? (3) How do medicinal components in various organs respond to UV radiation? The findings reveal UV radiation effects on medicinal component accumulation and provide technical support for high-quality cultivation and industrial development of *D. dasycarpus*.

1.1 Experimental Materials and Treatment Conditions

One hundred fifty two-year-old potted *D. dasycarpus* plants with uniform growth were selected, using forest understory black soil as the cultivation substrate with three plants per pot. The plants were divided into five groups of 30 plants each. Pre-cultivation was conducted in an artificial climate chamber using white LED light sources (NVC Lighting Technology Co., Ltd., Huizhou) at $400 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ intensity with a $10 \text{ h} \cdot \text{d}^{-1}$ photoperiod until plants developed four fully expanded leaves. Five different light treatment groups were then established: (1) Control group (CK) with the same light intensity and photoperiod as pre-cultivation; (2) Low-dose UV-A radiation enhancement group (UVAL) with $2 \text{ W} \cdot \text{m}^{-2}$ UV-A added to CK; (3) Moderate-dose UV-A radiation enhancement group (UVAM) with $4 \text{ W} \cdot \text{m}^{-2}$ UV-A added to CK; (4) Low-dose UV-B radiation enhancement group (UVBL) with $0.25 \text{ W} \cdot \text{m}^{-2}$ UV-B added to CK; (5) Moderate-dose UV-B radiation enhancement group (UVBM) with $0.50 \text{ W} \cdot \text{m}^{-2}$

UV-B added to CK.

These UV radiation intensities were determined through preliminary experiments, with moderate dose defined as the intensity causing no obvious leaf burn and low dose set at half that intensity. Specific intensities were achieved by adjusting the distance between plants and UV LED light sources. The UV-B LED source (36 W) was produced by Beijing Lighting Research Institute, and the UV-A LED source (40 W) by Dongguan Senxia Electronic Technology Co., Ltd. To reduce cumulative damage from prolonged UV-B radiation, intermittent radiation was applied (15 min radiation every 30 min) for a total daily UV-B radiation time of 2 h. UV-A radiation cycle matched the visible light photoperiod at $10 \text{ h} \cdot \text{d}^{-1}$. Soil moisture was supplemented every 2 days during the treatment period to maintain maximum water content, ensuring no water inhibition occurred within 2 days. Photosynthesis measurements and active component analysis were performed after 7 days of treatment.

1.2 Photosynthesis Measurement

After 7 days of treatment, on a clear morning between 8:00–10:00, fully expanded leaves at the first consistent leaf position from the shoot tip were selected for photosynthesis measurement without dark adaptation. During measurement, air temperature (T) was 25°C , relative humidity (RH) was 60%, and CO_2 concentration was $400 \text{ mol} \cdot \text{mol}^{-1}$. Light response curves were measured using a Li-6400 portable photosynthesis system (Li-Cor, USA) with photosynthetically active radiation (PAR) set at 2,000, 1,600, 1,200, 800, 600, 200, 100, and $0 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Light intensity decreased from high to low, with approximately 5 min equilibrium at each gradient. Measured parameters included net photosynthetic rate (P), respiration rate (R), and transpiration rate (T), with five replicates per leaf and averages used for statistical analysis.

The light response curve fitting model used an exponential function: $P = P_{\max} (1 - e^{-\alpha I}) - R$ (the exponential model has no extreme values, requiring estimation of light saturation intensity. Following Wang et al. (2006), light saturation intensity was assumed as the intensity corresponding to $0.9P_{\max}$ or $0.99P_{\max}$, with $\alpha=0.05$, $P_{\max}=20$, $R=1$). Chlorophyll fluorescence characteristics were measured using a PAM-2000 portable modulated chlorophyll fluorometer (Walz, Germany). After 20 min dark adaptation, minimum fluorescence yield (F_0) and maximum fluorescence yield (F_m) were measured, followed by light-adapted fluorescence (F_t), maximum fluorescence (F_m'), and minimum fluorescence (F_0') at $600 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ intensity without adaptation. PS II maximum photochemical quantum yield (F_v/F_m), actual photosynthetic quantum yield $Y(\text{II})$, non-photochemical quenching coefficient (NPQ), “lake model”-based photochemical quenching coefficient (qL), non-regulated energy dissipation quantum yield $Y(\text{NO})$, and regulated energy dissipation quantum yield $Y(\text{NPQ})$ were calculated using the fluorometer’s built-in formulas: $F_v/F_m = (F_m - F_0)/F_m$; $Y(\text{II}) = (F_t - F_0)/F_t$; $\text{NPQ} = (F_m - F_m')/F_m'$; $qL = (F_m' - F_0)/(F_m' - F_0') \times (F_t'/F_t)$; $Y(\text{NO}) = F_t/F_t$; $Y(\text{NPQ}) = 1 - Y(\text{II}) - Y(\text{NO})$.

1.3 Active Component Content Detection

After 7 days of treatment, 10 plants per group were sampled and separated into roots, stems, and leaves. Each sample was ground with 8 mL methanol, ultrasonically extracted for 1 h (100 W power, 40 kHz frequency, 40 °C temperature), centrifuged at $8,000 \text{ r} \cdot \text{min}^{-1}$ for 10 min, and the supernatant was concentrated to dryness using a vacuum rotary evaporator at 40 °C. The residue was redissolved in 2 mL chromatographic-grade methanol, centrifuged again at $8,000 \text{ r} \cdot \text{min}^{-1}$ for 10 min, and the supernatant was stored at -20 °C for chromatographic analysis.

Contents of obacunone, fraxinellone, dictamnine, and limonin were determined following the method established by Cao et al. (2018) using an e2695-2998 HPLC system (Waters, USA) with a Waters Symmetry® C18 column (4.6 mm × 250 mm, 5 μm). The mobile phase consisted of acetonitrile (A) and ultrapure water (B) with gradient elution (0–20 min, 45.0%–55.0% A) at $1.0 \text{ mL} \cdot \text{min}^{-1}$ flow rate, 35 °C column temperature, and injection volume of 10 μL. Detection wavelengths were 210 nm and 236 nm.

1.4 Data Analysis

Significance analysis and t-tests between groups were performed using the ggstats package in R 4.1.2 to determine statistical significance of differences in photosynthetic characteristics and active component contents among treatments. Figures were generated using the ggplot2 package.

2.1 Effects of Short-term UV Radiation Enhancement on Photosynthetic Characteristics of *D. dasycarpus*

Short-term UV-A and UV-B radiation enhancement had distinct effects on photosynthetic characteristics of *D. dasycarpus* (Fig. 1). The PS II maximum photochemical quantum yield (F_v/F_m) significantly increased in the UVAL group but decreased significantly in UVBL and UVBM groups. No significant differences were observed among treatment groups in PS II actual photosynthetic quantum yield $Y(II)$, regulated energy dissipation quantum yield $Y(NPQ)$, photochemical quenching coefficient (q_L), or non-photochemical quenching coefficient (NPQ). The primary effect of UVBL and UVBM treatments on photosynthetic quantum yield was a significant increase in non-regulated energy dissipation quantum yield $Y(NO)$.

Although UV-A treatment increased net photosynthetic rate (P_n), the difference was not significant compared with CK. UVBM treatment significantly inhibited P_n . No significant differences were observed among groups in respiration rate (R_d). UVAM treatment significantly increased transpiration rate (T).

** and * indicate significant differences at 0.01 and 0.05 levels, respectively; NS indicates no significant difference. CK: white LED light control; UVAL: CK + $2 \text{ W} \cdot \text{m}^{-2}$ UV-A radiation; UVAM: CK + $4 \text{ W} \cdot \text{m}^{-2}$ UV-A radiation; UVBL:

CK + 0.25 W · m⁻² UV-B radiation; UVBM: CK + 0.5 W · m⁻² UV-B radiation. Black dots in the figure represent outliers. The same below.

Fig. 1 Effects of short-term enhanced ultraviolet radiation on photosynthesis of *Dictamnus dasycarpus*

2.2 Effects of Short-term UV Radiation Enhancement on Active Component Accumulation in *D. dasycarpus*

Different UV qualities and intensities differentially affected obacunone, fraxinellone, dictamnine, and limonin contents in roots, stems, and leaves of *D. dasycarpus* (Figs. 2, 3, and 4). UVAM and UVBL significantly increased obacunone content in roots, reaching 1.61- and 1.54-fold of CK, respectively. Fraxinellone showed strong induction in UVBM, UVBL, and UVAM groups, averaging 1.5-fold of CK. UVAM, UVBL, and UVBM significantly induced limonin accumulation, reaching 1.61-, 1.54-, and 1.16-fold of CK, respectively. UVAL and UVAM significantly induced dictamnine accumulation in roots, with UVAL achieving 1.56-fold of CK.

All four UV radiation enhancement treatments significantly affected total content of the four key active components in roots, with the UVAM treatment group showing the highest active component content at 3.86 mg · g⁻¹. In this group, limonin content increased 1.46-fold and dictamnine increased approximately 1.5-fold. Regarding the pharmacopoeia-required components, obacunone showed the greatest enhancement while fraxinellone increased over 1.5-fold. The UVBL treatment group ranked second with 3.61 mg · g⁻¹, while UVBM and UVAL groups showed lower contents at 3.19 and 2.94 mg · g⁻¹, respectively, compared with 2.56 mg · g⁻¹ in CK. This represents a maximum increase of 51% in total content compared with CK.

Active component contents in stems were relatively low (Fig. 3). Except for UVAM significantly promoting dictamnine content, other treatments had no significant effects on the four main active components in stems.

Fig. 2 Effects of short-term enhanced ultraviolet radiation on four active ingredients in *Dictamnus dasycarpus* roots

Fig. 3 Effects of short-term enhanced ultraviolet radiation on four active ingredients in *Dictamnus dasycarpus* stems

Among the four UV radiation enhancement treatments, only fraxinellone content in leaves was significantly affected, showing obvious induced accumulation under UVBL (Fig. 4). No significant effects were observed on obacunone, dictamnine, or limonin contents in leaves.

Fig. 4 Effects of short-term enhanced ultraviolet radiation on four active ingredients in *Dictamnus dasycarpus* leaves

3 Discussion

The PS II maximum photochemical quantum yield (F/F_m) is an important parameter for measuring PS II activity under various environmental stresses and reflects the degree of plant damage (Zhang & Scheller, 2004). Under non-stress conditions, plant PS II maximum photochemical quantum yield (F/F_m) generally ranges between 0.75–0.85 (Kitajima & Butler, 1975; Genty et al., 1989). Research indicates that when F/F_m falls below 0.75, plant damage becomes irreversible, and when F/F_m drops below 0.44, PS II reaction centers lose activity (Schansker & Rensen, 1999). This study found that under both moderate- and low-dose UV-A radiation, F/F_m in *D. dasycarpus* leaves remained stable above 0.8, indicating no UV-A stress effects. However, under low- and moderate-dose UV-B radiation, F/F_m decreased significantly, suggesting PS II photodamage, though the minimum value of 0.76 indicated reversible effects on photosynthetic capacity. The four short-term UV radiation enhancement treatments caused no irreversible damage to *D. dasycarpus*.

When photochemical energy conversion and protective regulatory mechanisms cannot fully dissipate excess light energy, PS II photoinhibition occurs. Plant leaves can mitigate negative effects of photoinhibition through PS II photodamage defense mechanisms (Pascal et al., 2005). Photosynthetic apparatus can alleviate photoinhibition through xanthophyll cycle energy dissipation (Demmig-Adams & Adams, 1992), photorespiration (Osmond & Grace, 1995), and the Mehler reaction (Flexas et al., 1999). This study revealed different energy allocation strategies under different UV radiation types. Under UV-A radiation, non-regulated energy dissipation quantum yield $Y(NO)$, PS II actual photosynthetic quantum yield $Y(II)$, and regulated energy dissipation quantum yield $Y(NPQ)$ remained stable with increasing radiation intensity. Under UV-B radiation, $Y(NO)$ increased significantly, indicating increased energy directed to non-photochemical reactions (Kramer et al., 2004) and tendency toward photosystem damage (Goss & Jakob, 2010; Jahns & Holzwarth, 2012). Although damage may not have occurred yet, continued UV irradiation would cause injury.

Non-regulated energy dissipation quantum yield $Y(NO)$ represents electrons transferred to PS II that neither participate in photochemical reactions nor undergo regulated heat dissipation mediated by the xanthophyll cycle, but are dissipated through photorespiration, Mehler reaction, or transferred to oxygen for reactive oxygen species formation (Wang et al., 2009). This indicates that *D. dasycarpus* can enhance its photosynthetic system non-photochemical efficiency and avoid damage through self-regulation by increasing $Y(NO)$. Additionally, all treatments left photochemical quenching coefficient (q_L) and non-photochemical quenching coefficient (NPQ) unchanged. The q_L reflects plant light energy conversion capacity, while NPQ represents light energy absorbed by PS II antenna pigments that cannot be used for photosynthetic electron transport and is dissipated as heat—a self-protection mechanism for photosynthetic apparatus (Kramer et al., 2004). This suggests that *D. dasycarpus* restored normal PS II

reaction center electron transport activity by increasing Y(NO).

Plant secondary metabolites vary with growth environment (Li et al., 2012), and regulating UV radiation intensity can increase contents of certain medicinally valuable secondary metabolites (Wu et al., 2012). Among the main active components in *D. dasycarpus*, dictamnine is an alkaloid, while obacunone, limonin, and fraxinellone are limonoid compounds (Cao, 2019). Limonoids are highly oxidized tetranortriterpenoids, with fraxinellone being a degraded limonoid and obacunone and limonin being limonoid aglycones. This study found strong induction effects of moderate UV-A and low UV-B on obacunone, limonin, and fraxinellone, with UV radiation promoting triterpenoid synthesis and consequently affecting limonoid content in *D. dasycarpus*. Since obacunone and limonin are upstream of fraxinellone synthesis (Cao, 2019), UV radiation may promote obacunone and limonin synthesis, thereby increasing fraxinellone content. UV radiation primarily controls synthesis of these three limonoid compounds by altering expression of related enzyme genes in the mevalonic acid (MVA) and 2-methylerythritol-4-phosphate (MEP) pathways. Current research on *D. dasycarpus* metabolic pathways is limited, and the mechanism of active component response to UV radiation requires further investigation.

Studies have confirmed that *D. dasycarpus* active substances are synthesized in leaves and stems but accumulate in roots (Zhou et al., 2017), explaining why root active component contents were significantly higher than those in stems and leaves, consistent with Mao et al. (2015). This study found that moderate UV-A radiation significantly promoted dictamnine accumulation in stems, while low UV-B radiation significantly promoted fraxinellone accumulation in leaves, improving utilization efficiency of stems and leaves. Active component content in *D. dasycarpus* increases with growth years (Liu et al., 2015). Using two-year-old plants, UV radiation treatment increased medicinal component content by 1.5-fold, suggesting that treatment of mature plants could more readily elevate cultivated *D. dasycarpus* quality above pharmacopoeia standards. This approach offers promising development prospects and provides a theoretical basis for efficient production of active medicinal components and sustainable development of *D. dasycarpus*.

4 Conclusion

This study investigated the induced accumulation effects of four medicinal active components (dictamnine, obacunone, fraxinellone, and limonin) under short-term, moderate UV-A and UV-B radiation enhancement. The results demonstrated that under experimental conditions, *D. dasycarpus* could avoid damage through self-regulation by enhancing PS II non-photochemical efficiency. Moderate UV radiation enhancement increased medicinal active component content, with the highest content in roots. Moderate UV-A and low UV-B radiation showed the most pronounced induction effects on the four active components. Therefore, in field production, appropriate UV radiation treatment one week before harvest can not only enhance root active component content but also im-

prove utilization efficiency of stems and leaves, achieving the goal of elevating key active component content in cultivated *D. dasycarpus*. This approach is significant for promoting sustainable utilization of *D. dasycarpus* resources.

References

- AHMAD M, GRANCHER N, HEIL M, et al., 2002. Action spectrum for cryptochrome-dependent hypocotyl growth inhibition in Arabidopsis[J]. Plant Physiol, 129(2): 774-785.
- BARNES PW, TOBLER MA, KEEFOVER-RING K, et al., 2016. Rapid modulation of ultraviolet shielding in plants is influenced by solar ultraviolet radiation and linked to alterations in flavonoids[J]. Plant Cell Environ, 39(1): 222-230.
- BORNMAN JF, BARNES PW, ROBINSON SA, et al., 2015. Solar ultraviolet radiation and ozone depletion-driven climate change: effects on terrestrial ecosystems[J]. Photochem Photobiol Sci, 14(1): 88-107.
- CAO M, 2019. Effect of ultraviolet radiation on *Dictamnus dasycarpus* Turcz growth and accumulation of medicinal components[D]. Harbin: Northeast Forestry University: 1-48.
- CAO M, TANG ZH, ZHANG ZH, 2018. Simultaneous determination of five components in cortex *Dictamnus dasycarpus* Turcz by HPLC dual wavelength method[J]. Chin Med Mat, 41(12): 2608-2610.
- CHRISTIE JM, BRIGGS WR, 2001. Blue light sensing in higher plants[J]. J Biol Chem, 276(15): 11457-11460.
- DEMMIG-ADAMS B, ADAMS WW. 1992. Photoprotection and other responses of plants to high light stress[J]. Ann Rev Plant Physiol Plant Mol Biol, 43(1): 599-626.
- DU CF, YANG XX, TU PF, 2005. Studies on chemical constituents in bark of *Dictamnus dasycarpus*[J]. Chin J Chin Mat Med, 30(21): 23-26.
- FLEXAS J, BADGER M, CHOW WS, et al., 1999. Analysis of the relative increase in photosynthetic O₂ uptake when photosynthesis in grapevine leaves is inhibited following low night temperatures and/or water stress[J]. Plant Physiol, 121(2): 675-684.
- FLINT SD, CALDWELL MM, 2003. A biological spectral weighting function for ozone depletion research with higher plants[J]. Physiol Plantum, 117(1): 137-144.
- FU JY, YANG C, LI DW, et al., 2017. Effects of elevated UV-B radiation on photosynthesis and contents of active substance of *Eucommia ulmoides* plantation[J]. J Anhui Agric Sci, 45(26): 6-10.
- GENTY B, BRIANTAIS JM, BAKER NR, 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll

fluorescence[J]. BBA-Gen Subjects, 990(1): 87-92.

GOSS R, JAKOB T, 2010. Regulation and function of xanthophyll cycle-dependent photoprotection in algae[J]. Photosynth Res, 106(1-2): 103-122.

JAHNS P, HOLZWARTH AR, 2012. The role of the xanthophyll cycle and lutein in photoprotection of photosystem II[J]. BBA-Bioenergetics, 1817(1): 182-193.

KAKANI VG, REDDY KR, ZHAO D, et al., 2003. Field crop responses to ultraviolet-B radiation: a review[J]. Agric For Meteorol, 120(1-4): 191-218.

KITAJIMA M, BUTLER WL, 1975. Quenching of chlorophyll fluorescence and primary photochemistry in chloroplasts by dibromothymoquinone[J]. Biochim Biophys Acta, 376(1): 105-115.

KRAMER DM, JOHNSON G, KIIRATS O, et al., 2004. New fluorescence parameters for the determination of QA redox state and excitation energy fluxes[J]. Photosynth Res, 79(2): 209-218.

KRIZEK DT, 2004. Influence of PAR and UV-A in determining plant sensitivity and photomorphogenic responses to UV-B radiation[J]. Photochem Photobiol, 79(4): 307-315.

LI Y, ZHOU XD, LOU ZH, et al., 2012. Review of plant secondary metabolites and the factors that influence its accumulation[J]. S Chin For Sci, 40(3): 54-60.

LI YM, QUE M, 2005. Effects of supplemental UV-B radiation on *Fritillaria thunbergii* growth and photosynthesis[J]. Acta Bot Boreal-Occident Sin, 25(4): 740-744.

LIU L, GUO LN, YU CL, et al., 2016. Research progress on chemical constituents and pharmacological activities of *Dictamnus dasycarpus* peel[J]. Chin Tradit Pat Med, 30(21): 23-26.

LIU LJ, ZHANG GH, SUN WY, et al., 2015. Variation laws of the content of obacunone and fraxinellone in Dictamni Cortex at different growth stages[J]. J NE For Univ, 43(4): 131-133.

MAO SL, ZHOU YF, WANG YC, et al., 2015. Anatomical structures of vegetable organs of *Dictamnus dasycarpus* and dictamine accumulation[J]. Acta Bot Boreal-Occident Sin, 35(6): 1135-1141.

OSMOND CB, GRACE SC, 1995. Perspectives on photoinhibition and photorespiration in the field: quintessential inefficiencies of the light and dark reactions of photosynthesis?[J]. J Exp Bot, 46(290): 1351-1362.

PASCAL AA, LIU ZF, BROESS K, et al., 2005. Molecular basis of photoprotection and control of photosynthetic light-harvesting[J]. Nature, 436(7047): 134-137.

- PORTO DD, MATSUUR HN, HENRIQUES AT, et al., 2020. The alkaloid brachycerine contributes to protection against acute UV-B damage in *Psychotria*[J]. Ind Crop Prod, 147(2): 112254.
- QUE XG, HAN F, SHI SB, et al., 2005. Effects of UV-B radiation of different intensity on the photosynthesis and the dark respiration of alpine plant *Gentiana straminea*[J]. Acta Bot Boreal-Occident Sin, 25(2): 231-235.
- SCHANSKER G, RENSEN JJS, 1999. Performance of active photosystem II centers in photoinhibited pea leaves[J]. Photosynth Res, 62(2): 175-184.
- VALENTA K, DIMAC-STOHL K, BAINES F, et al., 2020. Ultraviolet radiation changes plant color[J]. BMC Plant Biol, 20(1): 253.
- WANG LJ, LOESCHER W, DUAN W, et al., 2009. Heat acclimation induced acquired heat tolerance and cross adaptation in different grape cultivars: relationships to photosynthetic energy partitioning[J]. Funct Plant Biol, 36(6): 516-526.
- WANG ML, FENG YL, LI X, 2006. Effects of soil phosphorus level on morphological and photosynthetic characteristics of *Ageratina adenophora* and *Chromolaena odorata*[J]. Chin J Appl Ecol, 17(4): 602-606.
- WU Y, FANG MF, YUE M, et al., 2012. Advances in influence of UV-B radiation on medicinal plant secondary metabolism[J]. Chin J Chin Mat Med, 37(15): 2247-2251.
- XING AB, CUI HF, YU XP, et al., 2018. Effect of nutrient components on growth of *Pholiota adiposa*[J]. N Hort, 42(3): 163-172.
- ZHANG J, WEI SL, LI J, et al., 2021. Study on impact of different growing ages and harvesting time of medicinal material: *Fagopyrum dibotrys* on yield and quality[J]. Mod Chin Med, 23(3): 501-505.
- ZHANG SP, SCHELLER HV, 2004. Photoinhibition of photosystem I at chilling temperature and subsequent recovery in *Arabidopsis thaliana*[J]. Plant Cell Physiol, 45(11): 1595-1602.
- ZHANG WJ, BJORN LO, 2009. The effect of ultraviolet radiation on the accumulation of medicinal compounds in plants[J]. Fitoterapia, 80(4): 207-218.
- ZHAO LL, WEN BO, WEN LY, et al., 2020. Analysis of quality status of Dictamn Cortex in Jilin Province[J]. Guid Chin Med, 18(25): 40-42.
- ZHOU YF, MAO SL, LI SF, et al., 2013. Advance on biology and chemical constituents of *Dictamnus dasycarpus*[J]. Chin Agric Sci Bull, 29(7): 65-69.
- ZHOU YF, MAO SL, SHI XW, et al., 2017. Histochemistry of obacunone and fraxinellone in vegetative organs of *Dictamnus dasycarpus* and the content changes in different growth stages[J]. J NW For Univ, 32(1): 239-243.

Note: Figure translations are in progress. See original paper for figures.

Source: ChinaXiv –Machine translation. Verify with original.