

Air and Root Zone Temperature for Growth of Coastal Glehnia Seedlings

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Abstract

Coastal glehnia (Korean name: gaet-bang-pung) is a perennial herb belonging to the Apiaceae family and is distributed in harsh environments with high salinity and dry conditions, such as coastal dunes and sandy beaches. Both the shoots and roots of coastal glehnia contain health-promoting phytochemicals, which can be used in functional foods and in the pharmaceutical industry. In this study, the air temperature (AT) and root-zone temperature (RZT) of seedlings under different treatment combinations were evaluated to establish a cultivation protocol for high seedling quality in controlled environments such as greenhouses and plant factories with artificial lighting (PFALs). Two-week-old seedlings were transplanted to deep-flow-technique hydroponic systems and grown for four weeks. In study I, the seedlings were treated with RZTs of 15°C, 20°C, and 25°C, with or without aeration. The RZT of 25°C with aeration significantly increased the shoot fresh and dry weights compared to the other treatments. In study II, the seedlings were treated with ATs and RZTs of 20°C and 25°C along with aeration. The AT 25°C/RZT 25°C treatment improved the shoot and root growth, photosynthetic rate, and electron transport rate compared to the AT 20°C/RZT 20°C treatment. In addition, the mineral content (P, K, S, Mg, Ca, and Fe) per shoot increased significantly at an AT of 25°C with a RZT of 25°C. These results suggest that the combination of an AT of 25°C and RZT of 25°C is the appropriate temperature condition to improve productivity during the seedling stage of coastal glehnia for mass production in PFALs and greenhouses.

Additional key words: controlled environment, medicinal plants, plant factory, seedling quality, temperature management

Introduction

Given the increased interest in food safety and health, the demand for natural health products from medicinal plants is growing rapidly worldwide. Medicinal plants contain various secondary metabolites and are valuable resources for the food and medical supply industries (Kozai and Niu, 2019). However, it is difficult to produce high-quality and stable plant-derived materials in the field owing to climate change, global warming, and soil pollution. Plant factories with artificial lighting (PFALs) are plant production systems that can produce plants on a large scale throughout the year by controlling

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shoot and root zone environmental conditions. PFALs are suitable for the stable production of high-value plants because more precise environmental control is possible in PFALs than in greenhouses or fields (Kozai, 2018).

The medicinal plant coastal *glehnia* (*Glehnia littoralis* F. Schmidt ex. Miq.) is an Apiaceae perennial herb that is mainly distributed in coastal areas (Kim, 2013). Traditionally, its shoots and roots have been used for pharmaceutical purposes, as they contain various health-promoting phytochemicals (Hiraoka et al., 2002). Extracts of coastal *glehnia* are known to have high levels of antioxidant, antitumor, and anti-rheumatic compounds (Hiraoka et al., 2002; Um et al., 2010). For the stable mass production of medicinal plants, stable growing conditions must be established for the entire production process, from seed germination to harvest. In a previous study, dormancy breaking and using the proper germination temperature of coastal *glehnia* seeds were found to shorten the germination time and increase the germination rate (Yeom et al., 2021). The main problem on farms cultivating coastal *glehnia* is the delay in harvesting and the decrease in productivity due to slow seedling growth rate. Therefore, it is necessary to identify the environmental conditions required for seedling growth and development.

Among various environmental factors, the plant temperature, affected by the air and root-zone temperature, is related to enzyme activity in physiological responses, the regulation of photosynthesis, the plant phenology, and growth performance. Accordingly, this factor affects plant metabolic activity, yield, and quality levels (Tuteja and Gill, 2013; Jeon et al., 2022). Plant responses to the air temperature are driven by the minimum, optimum, and maximum cardinal temperatures. The plant growth rate increases linearly with the minimum cardinal-to-optimal temperatures and decreases with the optimum-to-maximum cardinal temperatures, and long-term exposure to excessively low or high temperatures leads to suppressed growth and reduced metabolic activity in plants due to stress (Kozai and Niu, 2019). Low temperatures affect the respiratory process, material movements and inhibit enzyme activity in the cell membrane structure (Criddle et al., 1997). High temperatures of up to 30°C promote plant respiration, whereas higher temperatures of 32–35°C induce a decrease in the respiratory rate due to the denaturation of protoplasmic proteins and inhibit photosynthesis by deactivating photosynthetic enzymes, including Rubisco (Went, 1953; Criddle et al., 1997; Lee et al., 2022). Few studies have concentrated on root-zone responses to different temperatures. Some studies have reported changes in the absorption and transportation of water and minerals, root development, and the root architecture depending on the rhizosphere temperature (Aroca et al., 2002; Koevoets et al., 2016; Inkham et al., 2020; Lee et al., 2022). Because root development is systemically related to shoot growth and development (Leskovar and Stoffella, 1995), proper temperature management of the root zone is important during the cultivation process (Grossnickle, 2005). Moreover, root development at the seedling stage determines vigor and rooting and leads to faster cell division than shoot development; therefore, precise temperature control in the root zone can promote uniform growth (Went, 1953). Thus, this study aimed to determine the suitable temperature conditions for the shoot and root zones at the seedling stage to promote seedling growth in coastal *glehnia*.

Materials and Methods

Plant Material and Growth Conditions

The dormancy of coastal *glehnia* seeds was broken after ten weeks of cold stratification, as recommended by Yeom et al. (2021). The seeds were then sown in seed pouches (CYG seed germination pouch, Mega International, Roseville, MN, USA) and grown in a growth chamber (DS-51GLP; Dasol Scientific, Hwaseong, South Korea) at 20°C, 80% relative

humidity, and $50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux density (PPFD), radiated by white LED light for two weeks. The seedlings were transplanted to a deep-flow-technique (DFT) hydroponic system ($32.5 \times 22 \times 23$ cm, L \times W \times H) and cultivated in a PFAL module ($4 \times 2 \times 3$ m, L \times W \times H) for four weeks. The seedlings were rotated three times a week to ensure uniform light distribution on the leaves. The light conditions of the PFAL module were as follows: $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of PPFD using a LED light source (red:white:blue, 8:1:1) for a 12 h photoperiod. We used the Hoagland/Arnon hydroponic nutrient solution (Hoagland and Arnon, 1950), with electrical conductivity of $1.0 \text{ dS}\cdot\text{m}^{-1}$ and pH of 5.8 ± 0.2 . All treatments were performed immediately after transplanting.

Aeration and Temperature Treatments

In study I, the PFAL module was maintained at an air temperature (AT) of 20°C , and the aeration treatment also involved supplying oxygen to the hydroponic system using a bubble generator (DY104-A, Angelaqua, Guangdong, China) connected to an air supply device (HP-40, Hiblow, Osaka, Japan). No additional oxygen was supplied in the non-aeration treatment. Three root-zone temperatures (RZTs) were used: 15°C , 20°C , and 25°C . For the 15°C treatment, a cooling coil with a coolant flow was placed inside the DFT hydroponic system for the RZT, and a heater (AH-55, Amazon, Zhongshan, China) was installed in the system for the 25°C treatment. The 20°C treatment did not require additional devices. The RZT was continuously monitored in real time using analog and digital thermometers (OKE-6710CF, Sewon Oke, Busan, South Korea).

In study II, for different AT treatments, coastal glehnia seedlings were grown in two PFAL modules at 20°C and 25°C . For the 20°C AT module, the 25°C RZT was maintained using a heater (AH-55, Amazon, Zhongshan, China), whereas the 20°C RZT was maintained without additional devices. For the 25°C AT module, the 20°C RZT was maintained by installing a cooling coil, the 25°C RZT was maintained without additional devices. A bubble generator was installed inside the system to aerate the nutrient solution.

Seedling Growth Parameters

The fresh and dry weights of the shoot and root, the number of leaves, the crown diameter, and the shoot area were measured four weeks after the seedlings were transplanted in both studies I and II. The fresh weights of the shoots and roots were measured using an electronic scale (SI-234, Denver Instruments, Denver, CO, USA), after which the seedlings were dried in a freeze-drier (Alpha 2-4 LSCplus, Christ, Osterode, Germany) for 72 h to measure the dry weight. The crown diameter where the buds were generated was measured using a digital vernier caliper (BD500-300, Bluetec, Yongin, South Korea). The shoot area, including the area of the leaves and petioles, was measured using an area meter (LI-3100C, Li-Cor, Lincoln, NE, USA).

Photosynthetic and Chlorophyll Fluorescence Parameters

The stomatal conductance and photosynthetic rate of the seedlings were measured using a portable photosynthetic system (LI-6800, Li-Cor, Lincoln, NE, USA) with a 1×3 cm leaf sectional chamber (LI-6800-12A, 1×3 SS, Li-Cor, Lincoln, NE, USA). The conditions for the leaf chamber were a relative humidity rate of 60%, reference CO_2 level of $500 \mu\text{mol}\cdot\text{mol}^{-1}$, and airflow of $700 \mu\text{mol}\cdot\text{s}^{-1}$. The block temperature was identical to the AT. The LED light source in the leaf

chamber had a light intensity level of $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, with 60% red light and 40% blue light.

The leaves were dark-adapted for 30 min to measure the maximum quantum yield (Fv/Fm), relative electron transport rate (rETR), steady-state non-photochemical quenching in light (NPQ), and an effective photosystem II quantum yield (QY) using a portable chlorophyll fluorometer (PAM-2000, Heinz Walz GmbH, Effeltrich, Bayern, Germany). The rETR was calculated using the following equation: $\text{rETR} = \text{quantum yield of PS II} \times \text{PAR} \times 0.5 \times 0.84$ (ETR factor). Four seedlings per treatment were measured days before harvest.

Mineral Content

To analyze the mineral content of the seedlings, the dried seedlings were placed in a Teflon beaker and 70% nitric acid was added for 12 h. The sample solutions were heated to 125°C and reacted for 90 min using a heating block (Ecopre 3, OD-98-003, Odlab, Seoul, South Korea). The heated sample solutions were cooled and then catalyzed with 34% hydrogen peroxide, boiled at 200°C , and cooled for 1 d. To resuspend the minerals in the solution, 2% nitric acid was added to the cooled sample solutions, and distilled water was massed up to 70 g. All solutions were filtered using a quantitative filter paper. The minerals (P, K, S, Mg, Ca, and Fe) were analyzed by inductively coupled plasma optical emission spectrometry (ICP-OES, Optimia 7300 DV, Perkin Elmer Inc., Waltham, MA, USA).

Statistical Analysis

Seven and ten seedlings per treatment were used to evaluate the seedling growth characteristics in studies I and II, respectively. Four seedlings with fully expanded leaves were used to measure the photosynthetic and chlorophyll fluorescence parameters. Six dried shoots were used for the mineral analysis. One-way and two-way ANOVA were conducted for both studies, and the means of the treatments were compared using Tukey's range test with SAS software (Statistical Analysis System, 9.4 Version, SAS Institute, Cary, NC, USA).

Results

Growth Characteristics

In study I, aeration and RZT were used to accelerate the growth of the coastal glehnia seedlings, with the growth characteristics examined four weeks after transplanting (Fig. 1 and Table 1). Aeration and non-aeration treatments did not significantly affect seedling growth, but different RZT treatments significantly affected the shoot fresh and dry weights and the shoot area (Table 1). As the temperature was increased, shoot growth gradually increased with aeration. The seedlings with a RZT of 25°C showed the highest shoot fresh and dry weights and shoot area compared to those with RZTs of 20°C and 15°C . Specifically, the shoot fresh weight of the seedlings treated with RZT of 25°C was 1.5 and 2.2 times higher than the weights of the seedlings treated with RZTs of 20°C and 15°C , respectively. There were no significant differences in the root fresh and dry weights, the number of leaves, or the crown diameter between the seedlings under the RZT and aeration treatments.

In study II, the seedlings treated with AT and RZT showed some growth differences (Fig. 2 and Table 2). All measured growth parameters showed a similar pattern. The AT 25°C treatment enhanced shoot growth (fresh and dry weights,

number of leaves, and shoot area), root growth (fresh and dry weights), and the crown diameter compared to the AT 20°C treatment (Table 2). The RZT 25°C treatment led to significantly higher values of the shoot fresh weight, number of leaves, and shoot area relative to those of the RZT 20°C treatment. The seedlings under the treatment of AT 25°C with

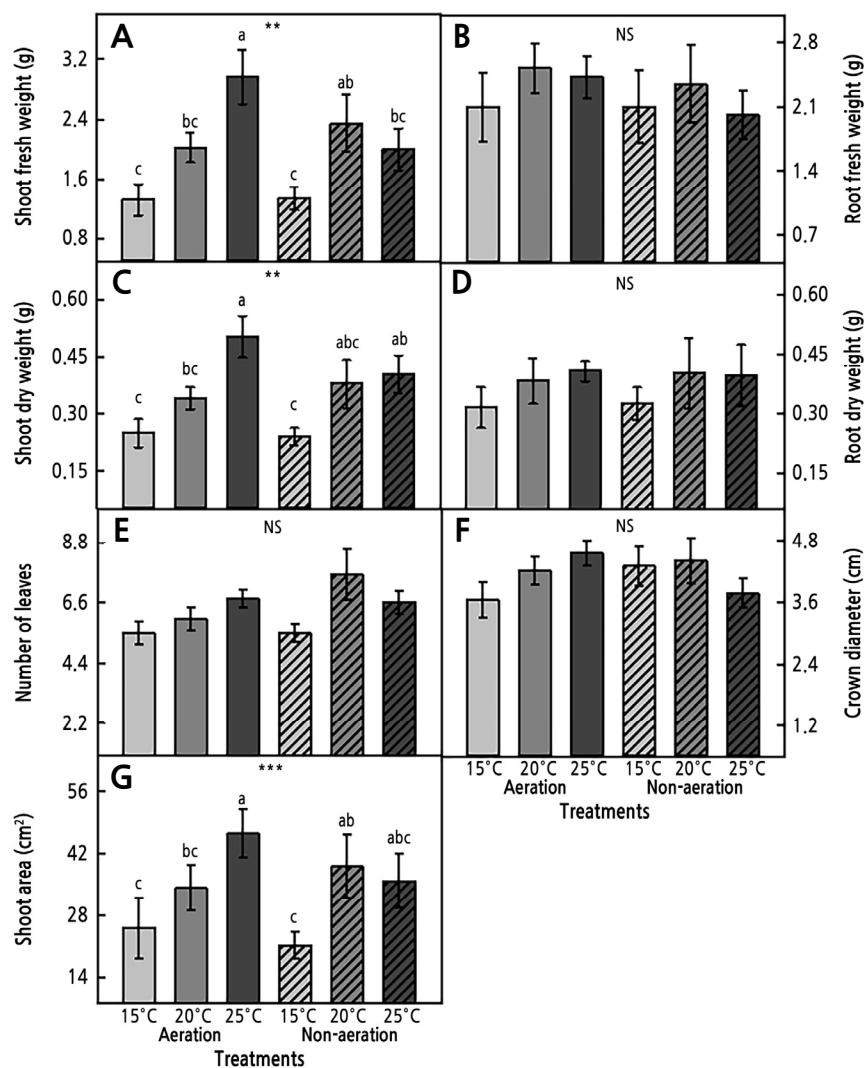


Fig. 1. Fresh and dry weights of shoots (A and C) and roots (B and D), number of leaves (E), crown diameter (F), and shoot area (G) grown under aeration, non-aeration, and RZT treatments for four weeks after transplanting, where ** and *** indicate significance, respectively, at $p < 0.01$ and 0.001 . NS denotes no significant difference ($n = 7$).

Table 1. Two-way ANOVA results of fresh weight (FW) and dry weight (DW) of shoot and root, number of leaves (No. of leaves), shoot area, and crown diameter of coastal glehnia treated with root-zone temperature (RZT) and aeration for four weeks after transplanting

	Shoot FW	Shoot DW	Root FW	Root DW	No. of leaves	Shoot area	Crown diameter
Aeration (A)	NS	NS	NS	NS	NS	NS	NS
RZT (B)	***	***	NS	NS	NS	***	NS
A × B	NS	NS	NS	NS	NS	NS	NS

*** indicates significance at $p < 0.001$. NS denotes no significant difference ($n = 7$).

RZT 25°C showed the highest growth characteristics, and in particular, all growth parameters were significantly improved compared to the seedlings grown under AT of 20°C with a RZT of 20°C. The AT 25°C treatment with a RZT of 25°C led to 2.6, 2.4, 2.2, and 2.2 times higher shoot and root fresh and dry weights, respectively, than those of the AT treatment of

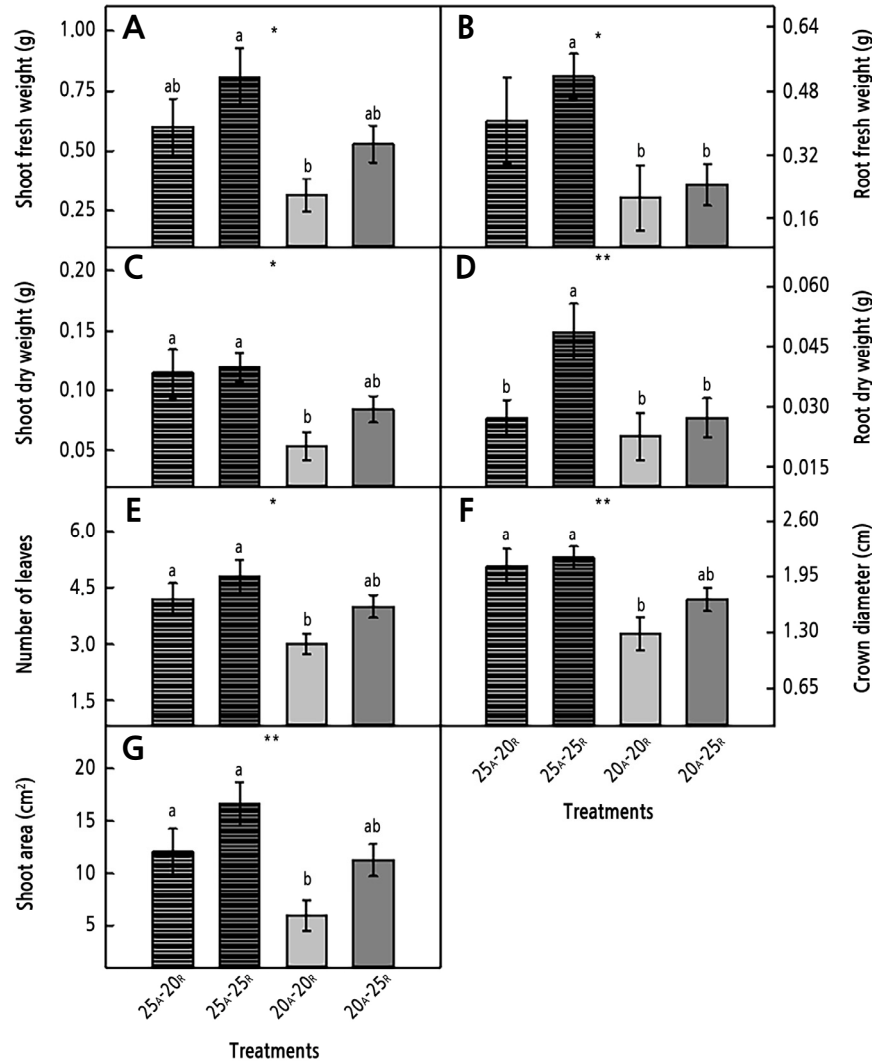


Fig. 2. Fresh and dry weights of shoots (A and C) and roots (B and D), number of leaves (E), crown diameter (F), and shoot area (G) grown under AT (subscript, A) and RZT (subscript, R) treatments for four weeks after transplanting. Here, * and ** indicate significance, respectively, at $p < 0.05$ and 0.01 . NS denotes no significant difference ($n = 10$).

Table 2. Two-way ANOVA results of measurements for shoot and root fresh weights (FW) and dry weight (DW), number of leaves (No. of leaves), shoot area, and crown diameter of coastal glehnia treated with AT and RZT for four weeks after transplanting

	Shoot FW	Shoot DW	Root FW	Root DW	No. of leaves	Shoot area	Crown diameter
AT (A)	**	**	*	*	*	**	***
RZT (B)	*	NS	NS	NS	*	*	NS
A × B	NS	NS	NS	NS	NS	NS	NS

*, **, and *** indicate significance at $p < 0.05$, 0.01 , and 0.001 , respectively. NS denotes no significant difference ($n = 10$).

20°C with a RZT of 20°C (Fig. 2A-2D). The number of leaves, the crown diameter, and the shoot area showed similar patterns (Fig. 2E-2G). No significant interaction effects between AT and RZT on the growth characteristics were observed (Table 2).

Photosynthetic and Chlorophyll Fluorescence Parameters

In study II, the photosynthetic parameters (stomatal conductance and photosynthetic rate) and chlorophyll fluorescence parameters (Fv/Fm, rETR, NPQ, and QY) were measured four weeks after transplanting (Figs. 3 and 4). The photosynthetic

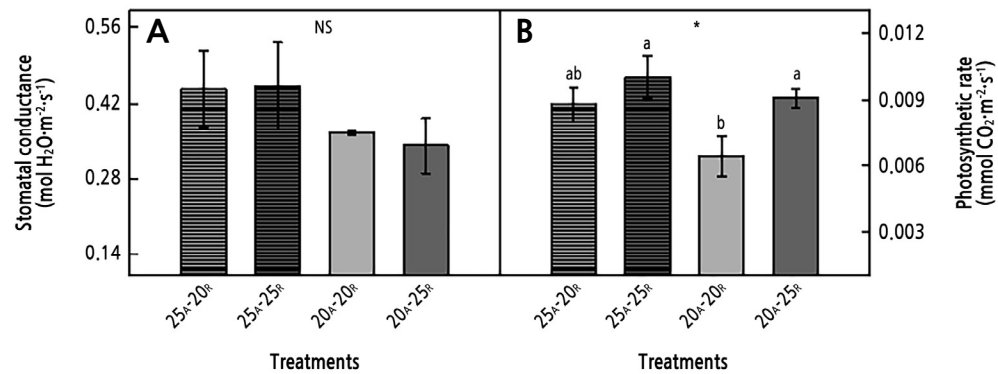


Fig. 3. Stomatal conductance (A), and photosynthetic rate (B) of coastal glehnia grown under AT (subscript, A) and RZT (subscript, R) treatments for four weeks after transplanting, where * indicates significance at $p < 0.05$ and NS denotes no significant difference ($n = 4$).

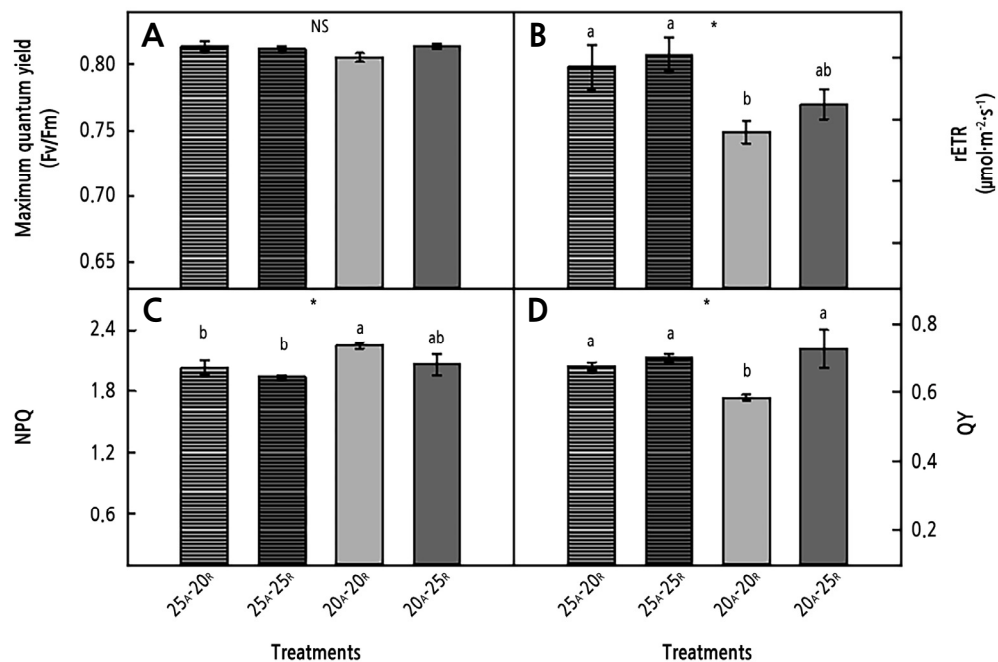


Fig. 4. Maximum quantum yield (Fv/Fm) (A), relative electron transport rate (rETR) (B), non-photochemical quenching (NPQ) (C), and quantum yield (QY) of PS II (D) of coastal glehnia grown under AT (subscript, A) and RZT (subscript, R) treatments for four weeks after transplanting. Here, * indicates significance at $p < 0.05$, and NS denotes no significant difference ($n = 4$).

rate showed a trend similar to that found in the growth results. The AT of 25°C tended to increase the rate of photosynthesis compared to the AT of 20°C, and the rate at the RZT of 25°C was significantly higher than that at the RZT of 20°C (Fig. 3B and Table 3). The photosynthetic rate at the AT of 25°C with the RZT of 25°C was 1.6 times higher than that at the AT of 20°C with the RZT of 20°C. There were no significant differences in stomatal conductance among the treatments.

The Fv/Fm ratios did not differ significantly among the AT and RZT treatments (Fig. 4A). The rETR and NPQ outcomes were significantly different between the AT 20°C and AT 25°C treatments (Fig. 4B, 4C, and Table 3). There was a significant difference in QY between the RZTs of 20°C and 25°C, similar to the photosynthetic rate results. The AT 20°C/RZT 20°C treatment showed the lowest values of rETR and QY, though this treatment also showed a high NPQ value (Fig. 4B-4D).

Mineral Content

To investigate the growth potential of coastal glehnia seedlings, the contents of several minerals (P, K, S, Mg, Ca, and Fe) were measured (Table 4). Although there were no differences in the P, K, S, Mg, and Ca contents per gram, the AT 25°C/RZT 25°C treatment showed higher contents of P, K, and S per gram than the other treatments. Likewise, the AT 25°C/RZT 25°C treatment led to the highest measured mineral contents per plant compared to the other treatments, with outcomes remarkably higher than those from the AT 20°C/RZT 20°C treatment.

Table 3. Two-way ANOVA results of measurements for photosynthetic and chlorophyll fluorescence parameters of coastal glehnia treated with AT and RZT for four weeks after transplanting

	Photosynthetic parameters		Chlorophyll fluorescence parameters			
	Stomatal conductance	Photosynthetic rate	Fv/Fm	NPQ	rETR	QY
AT (A)	NS	NS	NS	*	**	NS
RZT (B)	NS	*	NS	NS	NS	*
A × B	NS	NS	NS	NS	NS	NS

* and ** indicate significance, respectively, at $p < 0.05$, and 0.01 . NS denotes no significant difference ($n = 4$).

Table 4. Two-way ANOVA results of mineral contents of coastal glehnia treated with AT and RZT for four weeks after transplanting

Treatment		Mineral contents											
AT (°C)	RZT (°C)	mg·g ⁻¹						mg·plant ⁻¹					
		P	K	S	Mg	Ca	Fe	P	K	S	Mg	Ca	Fe
20	20	65.92	25.05	43.06	2.35	11.1	0.19a	4.82b	2.01b	3.22b	0.18b	0.9b	0.01b
	25	49.61	21.46	42.05	1.9	8.57	0.08b	5.61b	2.39b	4.64b	0.21b	1.0b	0.01b
25	20	44.42	18.94	36.78	1.66	8.21	0.07b	7.68ab	3.2ab	5.44b	0.26ab	1.26ab	0.01b
	25	67.39	25.85	53.2	2.15	10.1	0.11ab	13.1a	4.97a	10.3a	0.42a	1.99a	0.02a
AT (A)		NS	NS	NS	NS	NS	*	**	**	**	**	**	*
RZT (B)		NS	NS	NS	NS	NS	NS	NS	NS	**	*	NS	NS
A × B		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

* and ** indicate significance at $p < 0.05$ and 0.01 , respectively. NS denotes no significant difference ($n = 6$).

Discussion

Compared to non-aeration, the root zone aeration treatment led to no significant difference in the growth of coastal glehnia seedlings (Fig. 1 and Table 1). The average dissolved oxygen (DO) values in the aeration and non-aeration treatments were 9 and 6.5 mg·L⁻¹, respectively, with a difference of 2.5 mg·L⁻¹. Asao et al. (1999) used DO in a hydroponic system for 6 h (1.7–3.1 ppm) and 24 h (5.0–7.5 ppm) to treat cucumber seedlings; their difference of 3.3–4.4 mg·L⁻¹ did not affect the vegetative growth, but the length of the primary lateral branch decreased in the low DO treatment. In the present study, the difference in the DO content was likely not sufficient to induce growth differences in the coastal glehnia seedlings.

The shoot fresh and dry weights and the shoot area increased as the RZT was increased, and the seedlings under the RZT 25°C treatment showed the highest values (Fig. 1 and Table 1). RZT is a critical physical environment factor that affects seedling root development, water, and nutrient uptake, as well as the biosynthesis of metabolites (Wilcox and Pfeiffer, 1990). Stoltzfus et al. (1998) reported that the shoot fresh and dry weights were high at RZTs of 25–35°C depending on the size (large and small) of musk melon, with the mineral content and plant dry weight rapidly decreasing at RZTs above 35°C due to the limited water uptake rate and reduced mineral transport to the shoots. Compared to RZTs of 10, 20, 26, and 35°C, the RZT of 20°C was shown to improve growth and camptothecin accumulation in *Ophiorrhiza pumila*, a medicinal plant (Lee et al., 2020). Karnoutsos et al. (2021) investigated the effect of the RZT during the summer and winter seasons in a greenhouse without thermal control on the production of rocket and baby lettuce. Compared to the control and winter (AT approximately 8–24°C) seasons, in the summer season (ca. 26–43°C of AT), the cooled RZT condition (approximately 21.9°C) improved the production yields of rocket and baby lettuce by 18.9% and 31.4%, respectively. The treatment with a RZT of approximately 11–17°C, 3–4°C higher than the control treatment, increased the production yields of rocket and baby lettuce by 15.1% and 16.3%, respectively, compared to the control. This highlights the importance of RZT control in non-ideal AT environments.

Murai-Hatano et al. (2008) suggested that the root hydraulic conductivity increases when the RZT ranges from 10°C to 35°C and is manipulated by aquaporin activity. A high RZT treatment of coastal glehnia most likely stimulated water and nutrient uptake levels, increased root hydraulic conductivity and aquaporin activity, and promoted growth and development, as evidence by the photosynthetic rate and mineral contents (Fig. 3 and Table 4).

In study II, plant growth was affected by different shoot and root temperature combinations. In general, the optimum temperature of the shoot is higher than that of the root zone (Xu and Huang, 2000). Karlsen (1980) reported that the most suitable conditions for the growth of cucumber seedlings were an AT of 30°C with a RZT of 25°C among AT treatments of 15, 20, 25, and 30°C and RZTs of 15, 20, 25, 30, and 35°C. However, Carotti et al. (2021) reported that the light use efficiency of lettuce was higher at an AT of 24°C and a RZT of 28°C compared to the treatment combinations of ATs and RZTs of 20, 24, 28, and 32°C. Therefore, the optimal AT and RZT combination depends on the plant species and growth stage, and an improper temperature combination can cause a metabolic imbalance, ultimately inhibiting biomass accumulation (Thompson et al., 1998). In particular, the carbon reaction of photosynthesis using ATP and NADPH generated by the light-dependent reaction during photosynthesis is carried out through an enzyme-catalyzed reaction, therefore, the Calvin–Benson cycle operates well in plants under proper environmental conditions, including proper temperature conditions (Taiz et al., 2018). In this study, coastal glehnia seedling growth was significantly increased at the AT and RZT of 25°C compared to that when these factors were set to 20°C (Table 2 and Fig. 2). The AT of 25°C may activate the Calvin–Benson

cycle more efficiently than the AT of 20°C. The photosynthetic rate of coastal glehnia leaves increased at ATs of 15 – 25°C and decreased at an AT of 30°C, and the transpiration rate was lower than that at an AT of 25°C (data not shown). This implies that temperature conditions above 25°C result in the inhibition of photosynthesis by inducing heat stress, which can negatively affect the growth and development of coastal glehnia seedlings. In addition, the crown, located at the borderline between the shoot and root, is the growing point for new leaves of coastal glehnia and plays an important role in transporting minerals and water from the roots to the shoots. Therefore, the RZT of 25°C improved the growth and mineral contents of seedlings compared to the RZT of 20°C due to the active absorption of water and nutrients in the root zone as well as the active photosynthesis reaction by indirectly heating the crown of coastal glehnia (Figs. 2-4 and Table 4). Both root zone and crown heating have already been applied in greenhouse cultivation systems, and in the winter season, such treatments have been found to increase the absorption of nutrients by strawberries, cucumbers, and tomatoes (Choi et al., 1995; Kim et al., 2010; Sato and Kitajima, 2010; Kwon et al., 2019), resulting in improved growth.

When plants are stressed by excessive light energy or other environmental factors, the photoprotective mechanism is activated to release excess energy by the emission of light energy via photochemistry, fluorescence, and heat (NPQ). Chlorophyll fluorescence parameters are affected by the temperature due to the structure and function of the thylakoid membrane (Janssen et al., 1992). However, in the present study, a temperature treatment was not sufficient to induce stress in coastal glehnia seedlings. One of the chlorophyll fluorescence parameters, the Fv/Fm values, was similar among the treatments, but the AT and RZT of 20°C led to decreased QY and rETR outcomes with an increase in NPQ compared to the other treatments (Fig. 4). It was confirmed that the AT and RZT of 20°C led to the emission of more heat from excessive light than the AT and RZT of 25°C, and the plants' ability to use light photochemically with the former treatment was lower than that under the latter treatment.

In conclusion, AT and RZT were found to be closely related to the growth performance of coastal glehnia seedlings. The optimal combination of temperature conditions during the seedling stage promoted the growth and development of high-vigor seedlings of coastal glehnia. The combination of an AT of 25°C and a RZT of 25°C effectively enhanced the growth of coastal glehnia seedlings via improved photosynthesis and mineral uptake. These results can be used to develop cultivation strategies for coastal glehnia production in controlled-environment plant production systems, such as PFALs or greenhouses.

Literature Cited

- Aroca R, Tognoni F, Irigoyen JJ, Sánchez-Díaz M, Pardossi A (2002) Different root low temperature response of two maize genotypes differing in chilling sensitivity. *Plant Physiol Biochem* 39:1067-1073. doi:10.1016/S0981-9428(01)01335-3
- Asao T, Ohba Y, Tomita K, Ohta K, Hosoki T (1999) Effects of activated charcoal and dissolved oxygen levels in the hydroponic solution on the growth and yield of cucumber plants. *J Jpn Soc Hortic Sci* 68:1194-1196. doi:10.2503/jjshs.68.1194
- Carotti L, Graamans L, Puksic F, Butturini M, Meinen E, Heuvelink E, Stanghellini C (2021) Plant factories are heating up: hunting for the best combination of light intensity, air temperature and root-zone temperature in lettuce production. *Front Plant Sci* 11:2251. doi:10.3389/fpls.2020.592171
- Choi KJ, Chung GC, Choi WY, Han KP, Choi SK (1995) Effects of root zone environment on the mineral composition of xylem sap and the photosynthesis in cucumber. *Acta Hort* 396:161-166. doi:10.17660/ActaHortic.1995.396.18
- Criddle RS, Smith BN, Hansen LD (1997) A respiration-based description of plant growth rate responses to temperature. *Planta* 201:441-445. doi:10.1007/s004250050087
- Grossnickle SC (2005) Importance of root growth in overcoming planting stress. *New Forest* 30:273-294. doi:10.1007/s11056-004-8303-2

- Hiraoka N, Chang JI, Bohm LR, Bohm BA (2002) Furanocoumarin and polyacetylenic compound composition of wild *Glehnia littoralis* in North America. *Biochem Syst Ecol* 30:321-325. doi:10.1016/S0305-1978(01)00104-1
- Hoagland DR, Arnon DI (1950) The water-culture method for growing plants without soil. Cal Agric Exp Sta, Berkeley
- Inkham C, Hongpakdee P, Kajornrunsilp I, Thanamatee C, Ruamrungrisi S (2020) Root-zone cooling by cold energy from LNG regasification process for quality improvement of flower and bulb of *Hippeastrum*. *Hortic Environ Biotechnol* 61:643-650. doi:10.1007/s13580-020-00250-w
- Janssen LH, Wams HE, Van Hasselt PR (1992) Temperature dependence of chlorophyll fluorescence induction and photosynthesis in tomato as affected by temperature and light conditions during growth. *J Plant Physiol* 139:549-554. doi:10.1016/S0176-1617(11)80368-8
- Jeon YH, Kim EJ, Ju SH, Myung DJ, Kim KH, Lee SJ, Na HY (2022) Comparison of climate between a semi-closed and conventional greenhouse in the winter season. *Hortic Sci Technol* 40:400-409. doi:10.7235/HORT.20220036
- Karlsen P (1980) The influence of root and air temperature on young cucumber plants. *Acta Horti* 118:95-104. doi:10.17660/ActaHortic.1981.118.11
- Karnoutsos P, Karagiovanidis M, Bantis F, Chatzistathis T, Koukounaras A, Ntinis GK (2021) Controlled root-zone temperature effect on baby leaf vegetables yield and quality in a floating system under mild and extreme weather conditions. *J Sci Food Agric* 101:3933-3941. doi:10.1002/jsfa.11033
- Kim EK (2013) Halophytes of Korea. *Econature*, Seoul, Korea, pp 194-197
- Kim SE, Sim SY, Lee SD, Kim YS (2010) Appropriate root-zone temperature control in perlite bag culture of tomato during winter season. *Korean J Hort Sci Technol* 28:783-789
- Koevoets IT, Venema JH, Elzenga JT, Testerink C (2016) Roots withstanding their environment: exploiting root system architecture responses to abiotic stress to improve crop tolerance. *Front Plant Sci* 7:1335. doi:10.3389/fpls.2016.01335
- Kozai T (2018) Plant factories with Artificial Lighting (PFALs): Benefits, Problems, and Challenges. In Kozai T, ed, *Smart Plant Factory: The Next Generation Indoor Vertical Farms*. Springer, Singapore, pp 16-20. doi:10.1007/978-981-13-1065-2_2
- Kozai T, Niu G (2019) Role of the plant factory with artificial lighting (PFAL) in urban areas. In Kozai T, Niu G, Takagaki M, eds, *Plant factory: an indoor vertical farming system for efficient quality food production*. Academic Press, London, UK, pp 28-33
- Kwon JK, Kang SW, Paek Y, Moon JP, Jang JK, Oh SS (2019) Effects of local cooling and root pruning on budding and local heating on heating energy consumption in forcing cultivation of Strawberry. *J Bio-Environ Control* 28:46-54. doi:10.12791/KSBEC.2019.28.1.46
- Lee BK, Pham MD, Shin JW, Cui M, Lee HI, Myung JS, Na HY, Chun CH (2022) Photosynthetic changes and growth of paprika transplants as affected by root-zone cooling methods under high air temperature conditions after transplanting. *Hortic Sci Technol* 40:672-688. doi:10.7235/HORT.20220061
- Lee JY, Hiyama M, Hikosaka S, Goto E (2020) Effects of concentration and temperature of nutrient solution on growth and camptothecin accumulation of *Ophiorrhiza pumila*. *Plants* 9:793. doi:10.3390/plants9060793
- Leskovar DI, Stoffella PJ (1995) Vegetable seedling root systems: Morphology, development, and importance. *HortScience* 30:1153-1159. doi:10.21273/HORTSCI.30.6.1153
- Murai-Hatano M, Kuwagata T, Sakurai J, Nonami H, Ahamed A, Nagasuga K, Matsunami T, Fukushi K, Maeshima M, et al. (2008) Effect of low root temperature on hydraulic conductivity of rice plants and the possible role of aquaporins. *Plant Cell Physiol* 49:1294-1305. doi:10.1093/pcp/pcn104
- Sato K, Kitajima N (2010) Local heating temperature effects on the growth and yield of strawberries [Fragaria] in high-bench culture. *Fukuoka Agricultural Research Center Report* 29:27-32
- Stoltzfus RMB, Taber HG, Aiello AS (1998) Effect of increasing root-zone temperature on growth and nutrient uptake by 'gold star' muskmelon plants. *J Plant Nutr* 21:321-328. doi:10.1080/01904169809365406
- Taiz L, Zeiger E, Møller IM, Murphy A (2018) *Fundamentals of plant physiology*. Oxford University Press, UK, pp 181-186
- Thompson HC, Langhans RW, Both AJ, Albright LD (1998) Shoot and root temperature effects on lettuce growth in a floating hydroponic system. *J Am Soc Hort Sci* 123:361-364. doi:10.21273/JASHS.123.3.361
- Tuteja N, Gill SS (2013) Climate change and plant abiotic stress tolerance. In Hatfield JL, ed, *Climate Change: Challenges for future crop adjustments*. WILEY Blackwell, Hoboken, USA, pp 7-11. doi:10.1002/9783527675265
- Um YR, Lee JI, Lee JH, Kim HJ, Yea SS, Seo YW (2010) Chemical constituents of the halophyte *Glehnia littoralis*. *Korean Chem Soc* 54:701-706. doi:10.5012/jkcs.2010.54.6.701
- Went FW (1953) The effect of temperature on plant growth. *Annu Rev Plant Physiol* 4:347-362. doi:10.1146/annurev.pp.04.060153.002023
- Wilcox GE, Pfeiffer CL (1990) Temperature effect on seed germination, seedling root development and growth of several vegetables. *J Plant Nutr* 13:1393-1403. doi:10.1080/01904169009364161
- Xu Q, Huang B (2000) Growth and physiological responses of creeping bentgrass to changes in air and soil temperatures. *Crop Sci* 40:1363-1368. doi:10.2135/cropsci2000.4051363x
- Yeom MS, Nguyen TKL, Cho JS, Oh MM (2021) Improving germination rate of coastal *glehnia* by cold stratification and pericarp removal. *Agronomy* 11:944. doi:10.3390/agronomy11050944