

Assessment of root foraging behaviour in *Aralia elata* subjected to drought stress under different light spectra

Ruifeng FAN^{1,3a}, Long TAN^{1b}, Minghao ZHENG¹, Xiaoyang HUANG¹,
Xiubo LIU^{2*}, Shenglei GUO^{1,3*}

¹Heilongjiang University of Chinese Medicine, College of Pharmacy, Harbin 150040, China; ruifeng-fan@163.com (RF);
TL1921717454@163.com (LT); 15846536683@163.com (MZ); hxiaoyang202@163.com (XH); guosbenglei@163.com (SG)

²Heilongjiang University of Chinese Medicine, College of Jiamusi, Jiamusi 154007, China; zyylxb@foxmail.com (XL)

³Heilongjiang University of Chinese Medicine, Key Laboratory of Basic and Application Research of Beiyao, Ministry of Education of the People's Republic of China, Harbin 150040, China

^{a,b}These authors contributed equally to the work

Abstract

Drought may be more frequent in foreseen decades that will threaten non-wood forest products (NWFP) in temperate forests. Plants cope with drought by increasing root foraging ability, which may be also impacted by exposure to light spectra (components of wavelengths in three colours of monochronic lights). In this study, three hybrid light spectra were provided by light-emitting diode (LED) in red (wavelength: 13.6% blue, 60.0% green, 26.4% red), green (2.9% blue, 84.6% green, 2.5% red), and blue (5.4% blue, 77.8% green, 16.9% red) lights for culturing potted *Aralia elata* seedlings in homogeneous (67.5 mg nitrogen [N] to both halves of pot) and heterogeneous (135 mg N to left half of pot) under drought and well-watered conditions. The red light spectrum was the unique illumination environment where height growth was promoted under well-watered condition and root biomass in fertilized patch was enhanced under drought. Compared to blue light spectrum, red light spectrum increased root foraging scale and precision and placement ratio. Red light spectrum also promoted aboveground biomass, but reduced root collar diameter. No interaction was detected between any pairs of factors among drought, light, and soil nutrient pattern. The heterogeneous pattern increased root to shoot biomass ratio with decreased shoot biomass and increased root foraging sensitivity and precision and fine root placement ratio. Drought enlarged the overall foraging scale with no effects on foraging sensitivity or precision. Overall, exposure to red light spectrum had the potential to promote fine root foraging behaviour under drought, but more trails deserve being tested in the future on a wider range of wavelengths.

Keywords: *Aralia elata*; non-timber forest product; Chinese pine; Cilongya; understory; water deficit

Introduction

Current forest ecosystem is subjected to a high risk of drought stress, but forecasted increase of drought frequency and severity may further reduce forest productivity (Gazol *et al.*, 2018). Drought acts as a factor that restricts development of non-wood forest products (NWFPs) derived from vegetations at the understory layer

Received: 16 Dec 2023. Received in revised form: 26 Apr 2024. Accepted: 18 Sep 2024. Published online: 23 Sep 2024.

From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

(Arosa *et al.*, 2015; Gao *et al.*, 2023; He *et al.*, 2022). It has been identified that drought can affect regeneration of hardwood forests (Arosa *et al.*, 2015) and sprouting and growth of medicinal plants (Gao *et al.*, 2023; He *et al.*, 2022). Drought is a driving factor among all meteorological dimensions that may have shaped the distributions of natural populations of NWFP plants (Duan *et al.*, 2022; Guo *et al.*, 2019). In temperate forests at the Northern Hemisphere, drought effect was characterized to be a legacy over 1-2 years post drought stress for local shrub and grass plants (Wu *et al.*, 2018). Drought sharply reduces biomass in aerial organs of shrub plants due to limits in gas exchange and photosynthesis (Arosa *et al.*, 2015; Tng *et al.*, 2022). Technically, this further results in a trend of more biomass allocated to roots which benefit foraging behaviour parameters (He *et al.*, 2022). However, dose-response results are quite less found than qualitative-dependent findings. This prohibits an effective establishment of protocol for strategies that can be generated to cope with more drought events.

Root is the sink of biomass allocation and source of water uptake. In temperate forest plants, drought can determine root system development through modifying biomass allocation (Hauer *et al.*, 2021) and mineral nutrient demand (Wang *et al.*, 2016). Plants have a nature to place fine root proliferation in soil patches with sufficient water availability for foraging water resource (Morris *et al.*, 2017). The nature of plant plasticity harbours an ability to shape fine root morphology in adaptive changes when drought is sensed (Wang *et al.*, 2020). This mechanism contributes to the acclimation of plant to drought stress by enlarging root system across the whole rhizosphere zone (Wang *et al.*, 2020) or within patch with enriched resources (Sun *et al.*, 2023). Root foraging behaviour can be characterized by parameters estimated based on fine root morphological traits, e.g., those for measuring foraging scale and precision (Zhou *et al.*, 2022). A recent study revealed that drought can increase fine root morphology but reduce nutrient utilization estimated on fine roots for juvenile temperate tree plants regardless of their species (Tan *et al.*, 2021). The effect on root foraging behaviour, however, was species specific. These together suggest a force of drought that may also stimulate fine root egress and elongation in partial rhizosphere for NWFP shrubs. However, the adaption to drought may impair aboveground organ growth and development; hence more work is needed to detect a synthesis of responses across whole-plant organs to make sure shoots were not disturbed.

Light is an essential source for plants growth and development. Light spectrum comprises of different ratios in red, blue, and green lights, the change of which can modify secondary metabolites, physiology, and mineral element cycling in NWFP plants (Guo *et al.*, 2022). These changes can further modify the allocation of dry mass to belowground (Kim *et al.*, 2019), which fuel expansion of root system (Johkan *et al.*, 2010; Kang *et al.*, 2013). Drought imposes a force to reduce biomass production and induce dry mass allocation towards underground organs (Liu *et al.*, 2011; Zhou *et al.*, 2018), which can also be impacted by the switch of light spectrum (Johkan *et al.*, 2010). Logically, one can expect that light quality can function as a modifier against negative impact of drought through regulating biomass production and allocation. The process, however, has complexity in carbohydrate production and allocation. For example, plants exposed to the red-light spectrum grew to accumulate more carbohydrate (fructose, starch, glucose, etc) and pigment (carotenoids and chlorophylls) (Shin *et al.*, 2008) compared to those cultured under blue light. Compared to the blue and green light spectra, red light limited root growth due to limited biomass allocation to roots in lettuce (Johkan *et al.*, 2010). In contrast, spectrum with high red light wavelength was also found to promote root growth in woody plants (He *et al.*, 2021; Zhao *et al.*, 2019). Rare evidence can be referred to demonstrate interactive effect of light spectrum with drought on plant root growth. New studies deserve to be conducted on some typical NWFP species to detect effect of light spectrum on plant growth and root development in plants subjected to drought.

Aralia eleta is also known as names such as Cilongya, Japanese angelica-tree, Korean angelica-tree, etc. Its newly grown bud is taken as an edible wild vegetable in many regions of Northeast Asia (Cheng *et al.*, 2021; Lin *et al.*, 2018). Its leaves, stem, and roots are all natural sources of secondary metabolites that can be used for

traditional medicine (Wei *et al.*, 2020b). Natural *A. elata* populations distribute in northeastern mountains of China (Qi *et al.*, 2018; Wei *et al.*, 2021), which are suffering over exploitations that have threatened natural reserves (Zhang *et al.*, 2021). Forests that harbour natural *A. elata* populations are subjected to climate changes with frequent drought interruptions (Lang *et al.*, 2013; Shibata *et al.*, 2014). It was found that leaf parameters of *A. elata* individuals can be modified by sunlight transmittance in forest gaps (Wei *et al.*, 2019a; Wei *et al.*, 2020b). Simulating experiment based on field environment demonstrated that secondary metabolites and physiological parameters can be adjusted by the change of light spectrum (Wei *et al.*, 2020). Hence, it is worthy to detect spectrum on root foraging behaviour in *A. elata* subjected to drought; and results can be referred to as theoretical evidence supporting the strategy to cope with drought.

In natural habitat, *A. elata* dwells in a moist and shaded environment subjected to understory atmosphere, where it has a moderate to low ability to resist drought but a high sensitivity to forage soil nutrients (Qi *et al.*, 2018). In this study, *A. elata* seedlings were raised as an objective species in a simulating experiment with drought stress and varied lighting spectra. The goals of this study were to detect root foraging behaviours in response to *A. elata* seedlings subjected to drought and spectra. We assumed that some type of spectrum can mediate balanced allocation with more robust foraging behaviours.

Materials and Methods

Plant materials and experiment layout

Seeds of *A. elata* were collected from a forest farm in a montane area at Gaoleng (45°27'–46°04' N, 129°00'–129°40' E), Fangzheng, Harbin, Northeast China. Seeds were germinated to plantlets in a local nursery where seedlings were raised to an initial size of height in 4.6±0.2 cm when root collar diameter (RCD) was 4.9±0.1 mm. Seedlings were raised to expected sizes and planted to growing pots (450 mL; top diameter, 11.5 cm; bottom diameter, 7.5 cm; height, 9.5 cm) filled with moist perlites (Tan *et al.*, 2021). The inner space of a pot was split to two halves which were divided by an obstruction of a plastic sheet. Dried perlites were placed to a height of 4 cm in both halves, on which controlled-release fertilizer (CRF) (N-P₂O₅-K₂O, 14-13-13; Scotts, Marysville, OH, USA) granules were spread at imbalanced rates between two inner spaces of pots to create the heterogeneous nutrient pattern. The left half of inner space was fertilized by CRF at a rate of 135 mg N leaving the other half unfertilized as a control (Figure 1). The homogeneous pattern was created by fertilizing both halves using CRF at rates of 67.5 mg N. A seedling was placed across the centre of the obstructed sheet leaving fine roots evenly distributed into the two halved spaces. Perlites were poured to fill up the rest of spaces in two halves with seedling fixed until all roots were covered. Distilled water was carefully sprayed to the surface of perlite to moisten substrates. Additional dried perlites were poured over the surface to replenish the top space that was reduced by lowered moist perlites. This arrangement can induce fine roots proliferating to the two halves of inner space that facilitated detecting root foraging behaviour parameters (Tan *et al.*, 2021).

Eight pots were placed in a tray (length 75 cm, width 25 cm), and four contained homogeneous fertilizer patterns leaving the other four with heterogeneous patterns. Six trays were arranged in one group subjected to different light-emitting diode (LED) light spectra (Figure 1). Three of these trays were watered every two days (well-watered treatment) and the other three were watered every six days (drought treatment) (Figure 1). Three spectra were created by varied ratios of chromatic lights in wavelengths of red, blue, and green colour lights. The red colour tinted light was created by ratios of 13.6% blue, 60.0% green, and 26.4% red lights; the green colour tinted light was created by 2.9% blue, 84.6% green, and 12.5% red lights; the blue colour tinted light was mixed by 5.4% blue, 77.8% green, and 16.9% red lights. All lights were provided at the photosynthetic photon flux density (PPFD) of approximately 70 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in an 18-h photoperiod, which is sufficient to deliver photons for plant growth (He *et al.*, 2021). These three types of LED spectra were adapted from those being simulated at natural conditions that had been identified to be available for growth of *A. elata* (Wei *et al.*,

2020b). Four potted seedlings, either in a homogeneous pattern or in heterogeneity, were arranged as a basic unit of sampling, whose data were bulked and averaged to be the mean for the unit. A total of 144 seedlings were cultured in pots subjected to a design of three lights \times two water conditions \times two fertilizer patterns \times three replicated units \times four seedlings per unit.

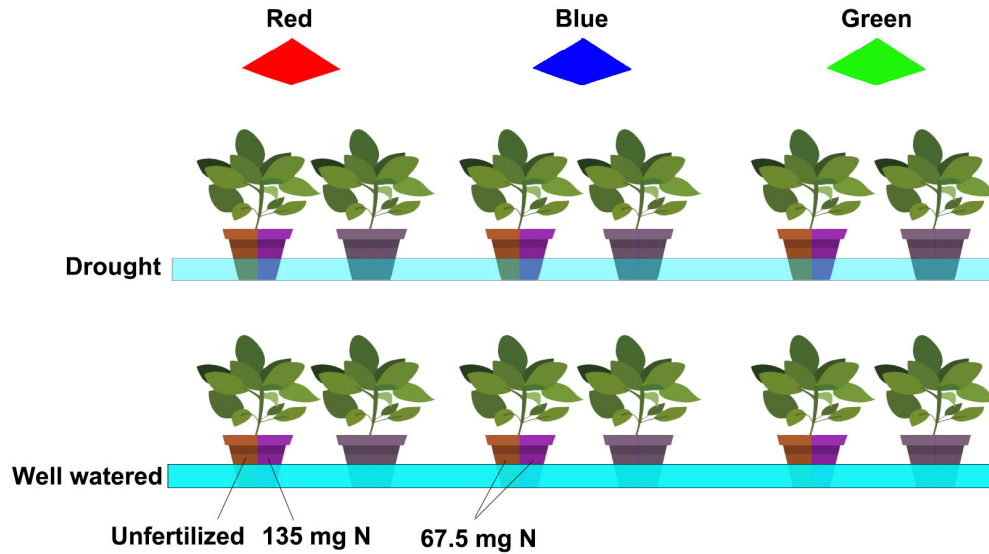


Figure 1. Layout of experiment design for potting *Arlia elata* seedlings subjected to combined treatments of lighting spectra (red, blue, and green lights), water state condition (drought control vs well-watered condition), and fertilizer distribution pattern (heterogeneous: 0 vs 135 mg N; homogeneous: 67.5 and 67.5 mg N)

Seedling treatment, sampling, and measurement

Seedlings were cultured for three months to obtain an ample time to enable a full extension of root system in *A. elata* (Wei *et al.*, 2020b). Local climate in Northeast China is changing to shape an alternatively fluctuation between drought and rainfall seasons at a pace of about every two months (Liu *et al.*, 2023). Local juvenile plants in temperate forests can generally endure an episodic drought event in a term of two-month time (Hauer *et al.*, 2021; Tan *et al.*, 2021). Therefore, drought treatment lasted for two months since the second week after transplant to pots. Seedlings were exposed to LED spectra throughout the experiment up to the time of sampling.

Roots were sampled by excising lateral roots from tap root in each half of a pot. Component organs of tap root plus aboveground parts were removed from the pot and cleaned by distilled water. Height and RCD were measured on aboveground organs. Lateral roots in each half of a pot were excavated out from perlites carefully to keep all fine roots attached. Root parts were carefully cleaned by rinsing in distilled water to remove all perlites. Therefore, belowground organs contained tap root and two groups of lateral roots distributed in two halves of pot. All seedling parts were oven-dried at 70 ± 2 °C for three days, reserved to room temperature, and weighted to measure weight of dry mass.

Parameters estimated for root foraging behaviour

Root foraging behaviour was characterized by parameters namely root foraging scale, fine root placement ratio, foraging precision, and sensitivity. Foraging scale (F_{scale}) was defined as the maximum range that a plant can proliferate fine root to, which was estimated as (Campbell *et al.*, 1991; Wei *et al.*, 2017):

$$F_{Scale} = Bio_{left} + Bio_{right} \quad (1)$$

where, Bio_{left} and Bio_{right} are fine root biomass in left side and right side of pot halves, respectively. Root foraging sensitivity (F_{sen}) was estimated as (Zhou *et al.*, 2022):

$$F_{sen} = Bio_{left} - Bio_{right} \quad (2)$$

where, in homogeneous pattern F_{sen} can be either a positive value or a negative one because fertilizers were evenly distributed to two halves of pot which drove random placements of fine roots therein; in heterogeneous pattern F_{sen} can be mostly a positive value as fine roots were more probably placed in nutrient rich patch in the left half. Root foraging precision (F_{pre}) was estimated using a hybrid equation (Zhou *et al.*, 2022) based on that in Tan *et al.* (2021) and He *et al.* (2021):

$$F_{pre} = \frac{F_{sen}}{Bio_{left} + Bio_{right}} \quad (3)$$

In homogeneous pattern, the absolute value is the difference of error in fine root placement variation between two halves; in heterogeneous pattern, this absolute value is used to assess the ability to place fine roots in patches enriched with fertilizers relative to the controlled patch without any fertilizers.

Fine root placement ratio (FR_{placeR}) was calculated as:

$$FR_{placeR} = \frac{Bio_{left}}{Bio_{left} + Bio_{right}} \quad (4)$$

In equation (4), when the fertilizer pattern was homogeneous, Bio_{left} is biomass of fine roots in one of the two evenly fertilized space halves on the left size of a pot; when the fertilizer pattern was heterogeneous, Bio_{left} is biomass of fine roots in the half of inner space enriched with fertilizers on the left size of a pot.

Data analysis and statistics

All data were analyzed using the 9.4 version of SAS software (SAS Inst., New York, NY, USA). Data were analysed under a split-block design with light spectra (degree of freedom, $df = 2$) being nested to by subplot factor of two drought levels ($df = 1$). The distinct rates of inner nutrient supplies between two pot halves were taken in a fixed factor which created contrasting variables for further comparisons. All biomass and root data succeeded to follow a normal distribution pattern; hence no transformation was necessary. All types of data were estimated for their responses to combined treatments of light spectra, drought treatment, and nutrient distribution pattern ($df = 1$) in a fully factorial design. Analysis of variance (ANOVA) was employed as to examine combined effects on biomass and root parameters, and results were compared by Tukey test (replicates, $n = 3$) at 0.05 level.

Results

Seedling morphology and biomass responses

Aboveground height showed significant responses to main effects from LED spectra (F value = 11.73; p value = 0.0003), fertilizer pattern (F value = 0.00; p value = 0.9710), drought treatment (F value = 33.70; p value < 0.0001). In addition, LED spectra and drought treatment showed combined effects on height (F value = 3.85; p value = 0.0354). According to Figure 2, seedlings exposed to the well-watered condition under the red light spectrum showed highest aboveground height across all treatments. Well-watered condition also resulted in higher aboveground height relative to the drought treatment for seedlings under green light. Well watered seedlings under blue light had higher height than those suffering drought stress in spectra from green and red lights.

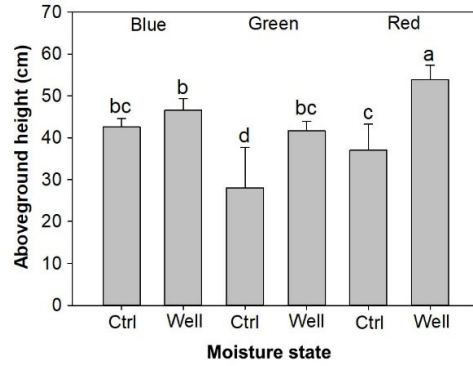


Figure 2. Aboveground height in *Aralia elata* seedlings subjected to different moisture states at well-watered condition (well) and drought stress (Ctrl) under three light emitting diode (LED) Means of are presented as columns on which error bars are presented as standard errors. Different letters above bars indicate significant differences identified by Tukey test at 0.05 level.

The red light spectrum decreased RCD compared to the blue and green light spectra (F value = 11.85; p value = 0.0003) (Figure 3A). In contrast, the spectrum of red light increased aboveground biomass compared to spectra from blue and green lights (F value = 11.69; p value = 0.0003) (Figure 3B). Nutrient distribution pattern did not affect RCD, which ranged around 0.7cm (F value = 0.01; p value = 0.9340) (Figure 3C). However, aboveground biomass was increased in the homogeneous pattern than in the heterogeneous pattern (F value = 15.97; p value = 0.0005) (Figure 3D). Compared to the drought control, well watered condition increased RCD (F value = 11.09; p value = 0.0028) (Figure 3E) and aboveground biomass (F value = 15.97; p value = 0.0005) (Figure 3F).

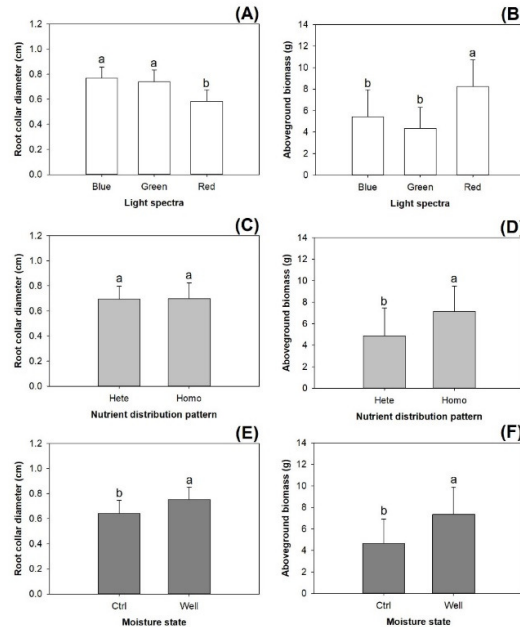


Figure 3. Root collar diameter (A, C, E) and aboveground biomass (B, D, F) in *A. elata* seedlings subjected to main effects of varied LED spectra (A, B), nutrient distribution patterns (C, D), and moisture state (E, F)

Means of are presented as columns on which error bars are presented as standard errors. Different letters above bars indicate significant differences identified by Tukey test at 0.05 level.

In red light spectrum, controlled seedlings subjected to drought showed the greatest belowground biomass in left-side roots among all combined spectra and water treatments (F value = 3.89; p value = 0.0345) (Figure 4A). Left-side root biomass was also higher in controlled drought treatment than that in well watered condition. Among all three light spectra, left-side root biomass was highest in red light spectrum (mean \pm standard error, 1.95 ± 0.81 g), followed by the blue light spectrum (0.99 ± 0.47 g), and lowest in green light (0.65 ± 0.18 g) (F value = 32.99; p value < 0.0001). Left-side of pot was fertilized when the right side was left as a control. Accordingly, left-side root biomass was higher in heterogeneous pattern (1.45 ± 0.78 g) compared to that in homogeneous pattern (0.94 ± 0.58 g) (F value = 14.22; p value = 0.0009). Left-side root biomass was greater in pots subjected to drought (1.54 ± 0.73 g) than in well watered condition (0.85 ± 0.57 g) (F value = 25.24; p value < 0.0001).

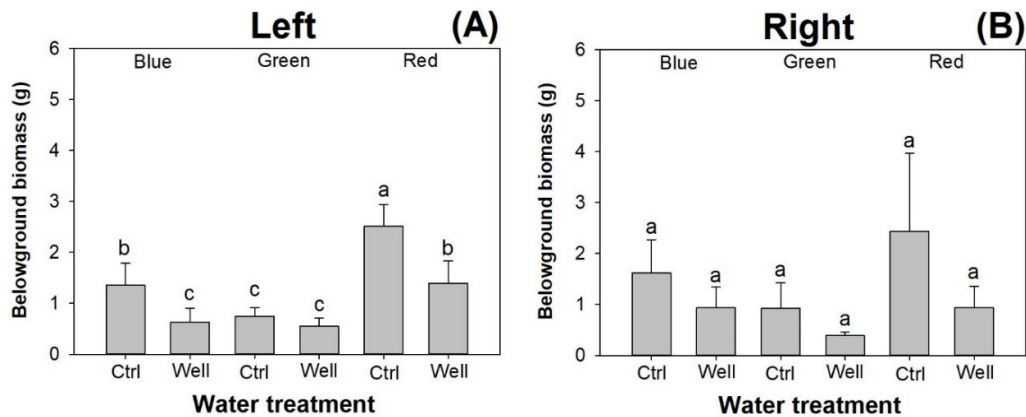


Figure 4. Belowground biomass in roots distributed in left (A) and right (B) parts of pot culturing *A. elata* seedlings subjected to combined moisture states at well-watered condition (well) and drought stress (Ctrl) under three light emitting diode (LED)

Means of are presented as columns on which error bars are presented as standard errors. Different letters above bars indicate significant differences identified by Tukey test at 0.05 level.

Although belowground biomass in right side of pot did not respond to combined treatments of light spectra and water condition, they separately had main effects on right-side root biomass (Figure 4B). Red light spectrum resulted in higher right-side root biomass (1.69 ± 1.24 g) compared to green light spectrum (0.66 ± 0.41 g), while blue light spectrum did not induce significantly different (1.27 ± 0.59 g) (F value = 4.08; p value = 0.0299). Again, like results on left side, right-side root biomass was higher in pots subjected to drought (1.66 ± 1.05 g) compared to that with well water (0.76 ± 0.38 g) (F value = 9.22; p value = 0.0057).

LED light spectra did not affect root to shoot biomass ratio (R/S) (F value = 0.15; p value = 0.8653). Instead, both nutrient distribution pattern and moisture state had main effects on R/S (pattern, F value = 4.52; p value = 0.0440; moisture, F value = 24.02; p value < 0.0001). The heterogeneous pattern resulted in a higher R/S (0.66 ± 0.50) compared to the homogeneous pattern (0.40 ± 0.24). Drought increased R/S (0.83 ± 0.42) compared to the well watered condition (0.23 ± 0.11).

Root foraging behaviour characteristics

Root foraging scale was higher in red light spectrum relative to the other two spectra (F value = 13.20; p value = 0.0001) (Figure 5A), but LED spectra did not cause significant effects on root foraging sensitivity (F value = 1.32; p value = 0.2866) (Figure 5B). Red light spectrum increased root foraging precision (F value = 3.56; p value = 0.0441) and fine root placement ratio (F value = 3.74; p value = 0.0386) relative to blue light spectrum (Figure 5C, D).

Nutrient distribution pattern did not affect root foraging scale (F value = 0.37; p value = 0.5511) (Figure 5E). The heterogeneous pattern resulted in higher root foraging sensitivity (F value = 8.64; p value = 0.0072) (Figure 5F) and precision (F value = 19.71; p value = 0.0002) (Figure 5G) and fine root placement ratio (F value = 20.04; p value = 0.0002) (Figure 5H).

The drought treatment increased root foraging scale (F value = 18.02; p value = 0.0003) compared to the well watered condition (Figure 5I), but moisture state did not affect root foraging sensitivity (F value = 0.65; p value = 0.4272) (Figure 5J) and precision (F value = 0.20; p value = 0.6596) (Figure 5K) and fine root placement ratio (F value = 0.21; p value = 0.6502) (Figure 5L).

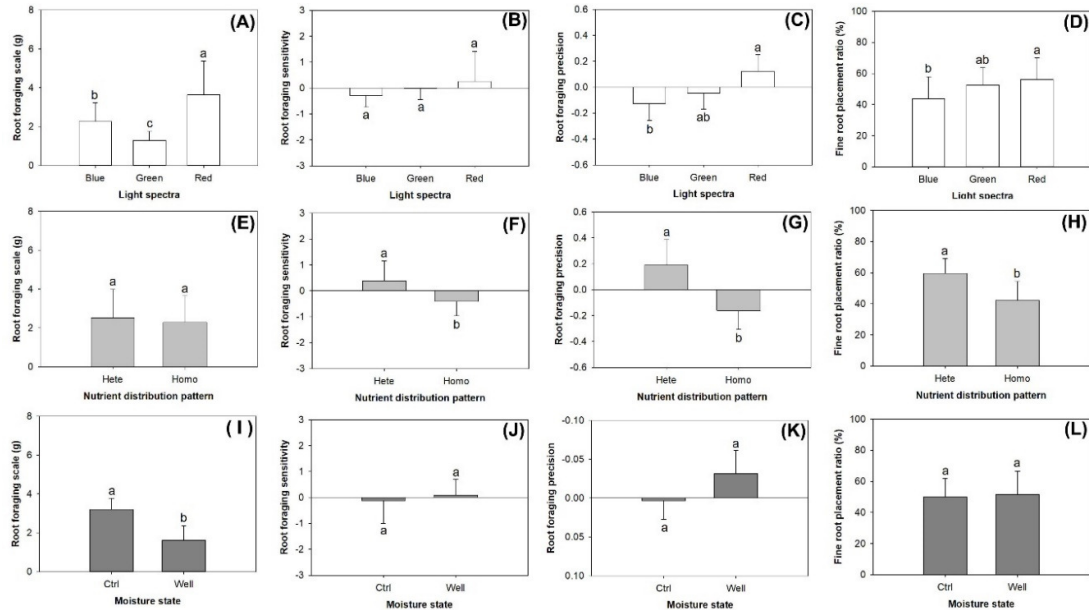


Figure 5. Root foraging scale (A, E, I), sensitivity (B, F, J), precision (C, G, K), and fine root placement ratio (D, H, L) in *A. elata* seedlings subjected to different LED spectra (blue, green, and red colours) (A, B, C, D), nutrient distribution pattern (heterogeneous, Hete; homogeneous, Homo) (E, F, G, H), and moisture state (drought, Ctrl; well watered condition, Well) (I, J, K, L)

Means of are presented as columns on which error bars are presented as standard errors. Different letters above bars indicate significant differences identified by Tukey test at 0.05 level.

Discussion

Aboveground organs' responses

Seedling height was the only shoot parameter that responded to the interaction between drought and light. Red light spectrum was found to promote height growth in *A. elata* seedlings subjected to the well watered condition. The spectrum high in red light wavelength has been proven to promote height growth in *Pinus pumila* (He *et al.*, 2021) and *Boehmeria nivea* (Rehman *et al.*, 2020). Drought is a strong force that impedes height growth of understory plants (Klein *et al.*, 2018). This negative effect can be repeated on *A. elata* seedlings subjected to spectra in red and green lights, but spectrum of blue light failed to interact with moisture state treatment on shoot height growth. According to Huang *et al.* (2020), blue light mainly functioned to improve physiological performances in leaves, such as stomatal conductance, net photosynthetic rate, and antioxidant

enzyme activities. It may be explained that blue light spectrum may have mainly modified physiological activities in response to drought with rare effect on shoot elongation in *A. elata*.

Either root collar diameter or aboveground biomass failed to respond to the interaction between drought and light. Although RCD was reduced in seedlings subjected to red light spectrum, aboveground biomass was increased at the same time. This suggests that the red light spectrum elongated shoot stem length and reduced the diameter growth, but shoot biomass was mainly accounted for by the increment of length growth which was rarely interrupted by the decrease of diameter growth. Therefore, red-light spectrum tended to shape shoots to be slender as it did on other tree species (Li *et al.*, 2018; Liu *et al.*, 2021). It was not the first time in this study to find no effect of nutrient distribution pattern on RCD, as it has also been reported on *Populus sibirica* seedlings (Park *et al.*, 2021). Instead, greater accumulation in aboveground biomass in seedlings subjected to homogeneous pattern than in heterogeneous pattern resulted from that the heterogeneous pattern increased ratio of biomass allocation to root. The promotion of R/S was also reported on major tree species in tropical forests (Yan and Ma, 2021). The proliferation of fine roots to be placed in nutrient enriched patches may be a signal that induced more biomass allocated to roots. It is not surprising that well watered seedlings showed higher RCD and greater aboveground biomass compared to those subjected to drought. Overall, neither LED light spectra nor nutrient distribution pattern generated any interactive effects with moisture state on RCD and aboveground biomass. Only height was the unique parameter that responded to interactive effects of LED spectra and moisture state. The promotion of height is not a fully expected benefit.

Root foraging behaviour

Fine roots in left side of pot showed responses of biomass to combined LED spectra and moisture state, which was not the case for roots in right side. The left side was fertilized in heterogeneous pattern hence it was the foraging behaviour that contributed to the significant response of biomass in fine roots. Drought increased fine root biomass in left side in *A. elata* seedlings subjected to blue and red lights. It is a widely confirmed phenomenon that more biomass is allocated to roots for foraging water to overcome drought stress (Zhou *et al.*, 2018). It used to reported that drought reinforced biomass allocated to fine root biomass in larch seedlings (Tan *et al.*, 2021). Our results complement this conclusion by providing more details that drought can reinforce biomass allocated to fine roots in partial distribution of a pot which was interacted with effects of LED spectra. Red and blue light spectra promoted drought effects on root biomass while green light spectrum impeded this effect. The green light is mainly reflected on leaf surface which contributes rarely to delivery of photons into photosynthetic pigments.

Again, neither LED spectra nor nutrient distribution pattern generated interactions with moisture state on parameters of root foraging behaviours. This failed to accord to root biomass findings, suggesting that strengthened biomass investment under red light in drought was not shown in any response of root morphology. Root biomass investment did not cause morphological allocation of plasticity used for foraging, suggesting drought showed a higher driving force to shape root morphology rather than needs for nutrients. Among three LED spectra, red light spectra increased root foraging precision by placing more fine roots and enlarging foraging scale. This effect of red light spectrum was also reported on *Pinus pumila* (He *et al.*, 2021), which can be explained as a result of effective energy input to plants to fuel fine root placement for foraging. The heterogeneous pattern promoted root foraging sensitivity and precision through increasing fine root placement ratio in fertilizer half of pot. However, these root foraging behaviours appeared to be species specific, and most species with high foraging sensitivity and precision mostly had higher abilities to increase fine root biomass in nutrient rich patches (Bliss *et al.*, 2002; Wijesinghe *et al.*, 2001). Drought only increased root foraging scale without any further effects on other behaviours. As reported by Tan *et al.* (2021), the drought effect on root foraging sensitivity was only significant on larch seedlings but not on birch seedlings. Therefore, we surmise that the effect of water deficit on root system is a general force that increases total biomass allocation downwards. At the same time, drought also impeded the ability of root foraging in nutrient enriched patches.

Limits of current study

This study falls in four limits that cannot be overcome by current experiment and findings. Firstly, parameters assessing root foraging behaviour were employed from previous studies, which can be updated to more precise ones according to species-specific attributes. Secondly, our study was conducted fully in an indoor environment, which should be validated by a repeat of design in outdoor field condition. Thirdly, nutrients used in this study were delivered at two rates, but more rates should be tested because root growth may be different at varied rates of nutrient supply.

Conclusions

In this study, we raised *A. elata* seedlings as a model species of UWFP and tested its response of root foraging behaviour to drought stress in homogeneous and heterogeneous nutrient distribution patterns. Varied LED spectra were employed to expect its interaction with drought that may be referred to as theoretical strategy to promote root proliferation. Among all seedling parameters, only shoot height and partial root biomass responded to combined LED spectra and drought treatments. Red light spectrum (13.6% blue, 60.0% green, 26.4% red lights) provided an illumination environment where height was promoted by well watered condition and root biomass was enhanced in fertilized half of pot. Red light spectrum also enhances root foraging sensitivity and precision by enlarging root foraging scale through more placement of fine root biomass in fertilized patches. Drought failed to generate any interactive effects on root parameters with light spectra. Although drought increased the overall root biomass, it did not cause any further effects on root placement in nutrient rich patches. The red light spectrum can fuel root biomass increment in response to drought, but it also shaped shoots to be slender and generated no effects on root foraging behaviour. More LED spectra can be considered to be tested with spectra high in red light wavelength to detect specific wavelength for benefiting root foraging behaviour.

Our study can be referred to by cultural protocol established for the culture of *A. elata* and other types of shrubs with high economic values. Given that height can be promoted by red light in a well watered condition, a spectrum being high in red light wavelength should be employed if taller plants are chased. No interactive effects on root foraging behaviour suggest an overall stronger driving force under well watered condition to promote foraging scale rather than needs for nutrients. These findings can be referred to either in a greenhouse or in field for *A. elata* culture. Light was not powerful as expected to overcome drought stress on root foraging.

Authors' Contributions

Conceptualization: SG and RF; Data curation: SG and DR; Formal analysis: SG, DR and LT; Funding acquisition: SG; Investigation: MZ, XH, DR and LT; Methodology: SG and RF; Project administration: SG; Resources: RF; Software: SG and DR; Supervision: SG; Validation: LT and RF; Visualization: DR and LT; Writing - original draft: SG; Writing - review and editing: RF. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

Acknowledgements

This work was supported by National Key Research and Development Program “Application Demonstration of Key Technology of Ginseng and Other Genuine Medicinal Materials in Rural Industry” (grant number: 2021YFD1600900), National Natural Science Foundation of China (grant number: 41971122), Natural Science Foundation of Heilongjiang Province of China (grant number: LH2021H095), Heilongjiang Province Postdoctoral Scientific Research Foundation (grant number: LBH-Q21044), and Heilongjiang Touyan Innovation Team Program (grant number: Leading Team Proclamation of Heilongjiang Touyan Program [2019] No.5).

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

References

- Arosa ML, Ceia RS, Costa SR, Freitas H (2015). Factors affecting cork oak (*Quercus suber*) regeneration: acorn sowing success and seedling survival under field conditions. *Plant Ecology & Diversity* 8(4):519-528. <https://doi.org/10.1080/17550874.2015.1051154>
- Bliss KM, Jones RH, Mitchell RJ, Mou PP (2002). Are competitive interactions influenced by spatial nutrient heterogeneity and root foraging behavior? *New Phytologist* 154(2):409-417. <https://doi.org/10.1046/j.1469-8137.2002.00389.x>
- Campbell BD, Grime JP, Mackey JML (1991). A trade-off between scale and precision in resource foraging. *Oecologia* 87(4):532-538. <https://doi.org/10.1007/BF00320417>
- Cheng Y, Liu HB, Tong XJ, Liu ZM, Zhang X, Chen YT, Wu FZ, Jiang XM, Yu XH (2021). Effects of shading on triterpene saponin accumulation and related gene expression of *Aralia elata* (Miq.) Seem. *Plant Physiology and Biochemistry* 160:166-174. <https://doi.org/10.1016/j.plaphy.2021.01.009>
- Duan YD, Guo BT, Zhang L, Li JX, Li S, Zhao WB, ... Guo P (2022). Interactive climate-soil forces shape the spatial distribution of foliar N:P stoichiometry in *Vaccinium uliginosum* planted in agroforests of Northeast China. *Frontiers in Ecology and Evolution* 10:1065680. <https://doi.org/10.3389/fevo.2022.1065680>
- Gao J, Meng P, Zhao Y, Zhang J, He C, Wang Q, Cai J (2023). Light-emitting diodes modify medicinal quality of mown *Rabdosia rubescens*, with changes in growth, physiology, and antioxidant activity, under drought stress. *Plants* 12(18):3189.
- Gazol A, Camarero JJ, Vicente-Serrano SM, Sánchez-Salguero R, Gutiérrez E, de Luis MS ... Galván JD (2018). Forest resilience to drought varies across biomes. *Global Change Biology* 24(5):2143-2158. <https://doi.org/10.1111/gcb.14082>
- Guo SL, Wang HX, Sui YW, Liu XB, Tan L (2022). Bioactive extracts and association with C and N in *Eleutherococcus senticosus* subjected to chitosan nanoparticles in contrasting light spectra. *Plos One* 17(12):e0277233. <https://doi.org/10.1371/journal.pone.0277233>
- Guo SL, Wei HX, Li JP, Fan RF, Xu MY, Chen X, Wang ZY (2019). Geographical distribution and environmental correlates of eleutherosides and isofraxidin in *Eleutherococcus senticosus* from natural populations in forests at Northeast China. *Forests* 10(10):872. <https://doi.org/10.3390/f10100872>
- Hauer RJ, Wei HX, Koeser AK, Dawson JO (2021). Gas exchange, water use efficiency, and biomass partitioning among geographic sources of *Acer saccharum* subsp. *saccharum* and subsp. *nigrum* seedlings in response to water stress. *Plants-Basel* 10(4):742. <https://doi.org/10.3390/plants10040742>
- He C, Gao J, Zhao Y, Liu J (2021). Root foraging precision of *Pinus pumila* (Pall.) Regel subjected to contrasting light spectra. *Plants* 1482. <https://doi.org/10.3390/plants10071482>

- He C, Zhao Y, Wang Y, Cai J, Gao J, Zhang J (2022). Forage quality and physiological performance of mowed alfalfa (*Medicago sativa* L.) subjected to combined light quality and drought. *Frontiers in Plant Science* 13:1047294. <https://doi.org/10.3389/fpls.2022.1047294>
- Huang L, Xiao Y, Ran J, Wei L, Li Z, Li Y, Zhang X, Liao L, Wang D, Zhao X, Xiao Q, Guo Y (2020). Drought tolerance of faba bean (*Vicia faba* L.) can be improved by specific LED light wavelengths. *Photosynthetica* 58(4):1040-1052. <https://doi.org/10.32615/ps.2020.052>
- Johkan M, Shoji K, Goto F, Hashida S, Yoshihara T (2010). Blue light-emitting diode light irradiation of seedlings improves seedling quality and growth after transplanting in red leaf lettuce. *Hortscience* 45(12):1809-1814. <https://doi.org/10.21273/hortsci.45.12.1809>
- Kang JH, KrishnaKumar S, Atulba SLS, Jeong BR, Hwang SJ (2013). Light intensity and photoperiod influence the growth and development of hydroponically grown leaf lettuce in a closed-type plant factory system. *Horticulture Environment and Biotechnology* 54(6):501-509. <https://doi.org/10.1007/s13580-013-0109-8>
- Kim HJ, Lin MY, Mitchell CA (2019). Light spectral and thermal properties govern biomass allocation in tomato through morphological and physiological changes. *Environmental and Experimental Botany* 157:228-240. <https://doi.org/10.1016/j.envexpbot.2018.10.019>
- Klein S, Fiebig A, Noga G, Hunsche M (2018). Influence of light quality on leaf physiology of sweet pepper plants grown under drought. *Theoretical and Experimental Plant Physiology* 30(4):287-296. <https://doi.org/10.1007/s40626-018-0122-5>
- Lang Y, Wang M, Zhang GC, Zhao QK (2013). Experimental and simulated light responses of photosynthesis in leaves of three tree species under different soil water conditions. *Photosynthetica* 51(3):370-378. <https://doi.org/10.1007/s11099-013-0036-z>
- Li XW, Chen QX, Lei HQ, Wang JW, Yang S, Wei HX (2018). Nutrient uptake and utilization by fragrant rosewood (*Dalbergia odorifera*) seedlings cultured with oligosaccharide addition under different lighting spectra. *Forests* 9(1):29. <https://doi.org/10.3390/f9010029>
- Lin JX, Qi MM, Peng XY, Guo N, Yan XF (2018). Effects of cooking methods on the amino acid and mineral contents in the buds of *Aralia elata*. *Cyta-Journal of Food* 16(1):1089-1094. <https://doi.org/10.1080/19476337.2018.1529710>
- Liu CC, Liu YG, Guo K, Li GQ, Zheng YR, Yu LF, Yang R (2011). Comparative ecophysiological responses to drought of two shrub and four tree species from karst habitats of southwestern China. *Trees-Structure and Function* 25(3):537-549. <https://doi.org/10.1007/s00468-010-0533-7>
- Liu P, Cao B, Wang YT, Wei ZP, Ye JF, Wei HX (2021). Spectral effect of streetlamps on urban trees: A simulated study on tissue water, nitrogen, and carbohydrate contents in maple and oak. *Plos One* 16(3):e0248463. <https://doi.org/10.1371/journal.pone.0248463>
- Liu P, He WT, Wei HX, Hu SY, Zhou YM, Wang YT (2023). Hydraulic traits in *Populus simonii* Carr. at stands of categorized ages in a semi-arid area of Western Liaoning, Northeast China. *Forests* 14(9):1759. <https://doi.org/10.3390/f14091759>
- Morris EC, Griffiths M, Golebiowska A, Mairhofer S, Burr-Hersey J, Goh T, ... Bennett MJ (2017). Shaping 3D Root System Architecture. *Current Biology* 27(17):R919-R930. <https://doi.org/10.1016/j.cub.2017.06.043>
- Park BB, Han SH, Hernandez JO, An JY, Nyam-Osor B, Jung MH, Lee PSH, Lee SI (2021). The use of deep container and heterogeneous substrate as potentially effective nursery practice to produce good quality nodal seedlings of *Populus sibirica* Tausch. *Forests* 12(4):418. <https://doi.org/10.3390/f12040418>
- Qi MM, Hua XY, Peng XY, Yan XF, Lin JX (2018). Comparison of chemical composition in the buds of *Aralia elata* from different geographical origins of China. *Royal Society Open Science* 5(8):180676. <https://doi.org/10.1098/rsos.180676>
- Rehman M, Fahad S, Saleem MH, Hafeez M, Ur Rahman MH, Liu F, Deng G (2020). Red light optimized physiological traits and enhanced the growth of ramie (*Boehmeria nivea* L.). *Photosynthetica* 58(4):922-931. <https://doi.org/10.32615/ps.2020.040>
- Shibata R, Shibata M, Tanaka H, Iida S, Masaki T, Hatta F, Kurokawa H, Nakashizuka T (2014). Interspecific variation in the size-dependent resprouting ability of temperate woody species and its adaptive significance. *Journal of Ecology* 102(1):209-220. <https://doi.org/10.1111/1365-2745.12174>

- Shin KS, Murthy HN, Heo JW, Hahn EJ, Paek KY (2008). The effect of light quality on the growth and development of *in vitro* cultured *Doritaenopsis* plants. *Acta Physiologiae Plantarum* 30(3):339-343. <https://doi.org/10.1007/s11738-007-0128-0>
- Sun TT, Ren RH, Xing MM, Duan QX, Zhao L, Yan WW, ... Zhang Y (2023a) Morphological and physiological plasticity of *Catalpa bungei* roots under partial root-zone drought as affected by nitrogen forms. *New Forests Early* <https://doi.org/10.1007/s11056-023-09983-9>
- Tan L, Fan R, Sun H, Guo S (2021). Root foraging of birch and larch in heterogeneous soil nutrient patches under water deficit. *PLoS One* 16(8):e0255848. <https://doi.org/10.1371/journal.pone.0255848>
- Tng DYP, Apgaua DMG, Paz CP, Dempsey RW, Cernusak LA, Liddell MJ, Laurance SGW (2022). Drought reduces the growth and health of tropical rainforest understory plants. *Forest Ecology and Management* 511:120128. <https://doi.org/10.1016/j.foreco.2022.120128>
- Wang GY, Liu S, Fang Y, Shangguan ZP (2020). Adaptive changes in root morphological traits of Gramineae and Leguminosae seedlings in the ecological restoration of the semiarid region of northwest China. *Land Degradation & Development* 31(16):2417-2429. <https://doi.org/10.1002/ldr.3616>
- Wang Z, Ma LY, Jia ZK, Wei HX, Duan J (2016). Interactive effects of irrigation and exponential fertilization on nutritional characteristics in *Populus x euramericana* cv. '74/76' cuttings in an open-air nursery in Beijing, China. *Journal of Forestry Research* 27(3):569-582. <https://doi.org/10.1007/s11676-015-0203-0>
- Wei HX, Chen GS, Chen X, Zhao HT (2020a). Growth and nutrient uptake in *Aralia elata* seedlings exposed to exponential fertilization under different illumination spectra. *International Journal of Agriculture and Biology* 23(3):644-652. <https://doi.org/10.17957/ijab/15.1336>
- Wei HX, Chen GS, Chen X, Zhao HT (2021). Geographical distribution of *Aralia elata* characteristics correlated with topography and forest structure in Heilongjiang and Jilin Provinces, Northeast China. *Journal of Forestry Research* 32(3):1115-1125. <https://doi.org/10.1007/s11676-020-01100-2>
- Wei HX, Chen X, Chen GS, Zhao HT (2019a). Foliar nutrient and carbohydrate in *Aralia elata* can be modified by understory light quality in forests with different structures at Northeast China. *Annals of Forest Research* 62(2):125-137. <https://doi.org/10.15287/afr.2019.1395>
- Wei HX, Guo P, Zheng HF, He XY, Wang PJ, Ren ZB, Zhai C (2017). Micro-scale heterogeneity in urban forest soils affects fine root foraging by ornamental seedlings of Buddhist pine and Northeast yew. *Urban Forestry & Urban Greening* 28:63-72. <https://doi.org/10.1016/j.ufug.2017.10.006>
- Wei HX, Zhao HT, Chen X, He XY (2020b). Secondary metabolites, carbohydrate accumulation, and nutrient uptake in *Aralia elata* (Miq.) Seem seedlings exposed to shoot cutting and different LED spectra. *Acta Physiologiae Plantarum* 42(11):162. <https://doi.org/10.1007/s11738-020-03149-2>
- Wijesinghe DK, John EA, Beurskens S, Hutchings MJ (2001). Root system size and precision in nutrient foraging: responses to spatial pattern of nutrient supply in six herbaceous species. *Journal of Ecology* 89(6):972-983. <https://doi.org/10.1046/j.0022-0477.2001.00618.x>
- Wu XC, Liu HY, Li XY, Ciais P, Babst F, Guo WC, ... Ma YJ (2018). Differentiating drought legacy effects on vegetation growth over the temperate Northern Hemisphere. *Global Change Biology* 24(1):504-516. <https://doi.org/10.1111/gcb.13920>
- Yan X-L, Ma X (2021). Responses of root morphology and seedling growth in three tree species to heterogeneous supplies of ammonium and nitrate. *Forest Ecology and Management* 479:118538. <https://doi.org/https://doi.org/10.1016/j.foreco.2020.118538>
- Zhang T, Yu LZ, Man Y, Yan QL (2021). Effects of harvest intensity on the marketable organ yield, growth and reproduction of non-timber forest products (NTFPs): implication for conservation and sustainable utilization of NTFPs. *Forest Ecosystems* 8(1):56. <https://doi.org/10.1186/s40663-021-00332-w>
- Zhao J, Chen X, Wei HX, Lv J, Chen C, Liu XY, Wen Q, Jia LM (2019). Nutrient uptake and utilization in Prince Rupprecht's larch (*Larix principis-rupprechtii* Mayr.) seedlings exposed to a combination of light-emitting diode spectra and exponential fertilization. *Soil Science and Plant Nutrition* 65(4):358-368. <https://doi.org/10.1080/00380768.2019.1631715>
- Zhou CW, Cui WJ, Yuan T, Cheng HY, Su Q, Wei HX, Guo P (2022). Root foraging behavior of two agronomical herbs subjected to heterogeneous P pattern and high Ca stress. *Agronomy-Basel* 12(3):624. <https://doi.org/10.3390/agronomy12030624>

Zhou GY, Zhou XH, Nie YY, Bai SH, Zhou LY, Shao JJ, ... Fu YL (2018). Drought-induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials. *Plant Cell and Environment* 41(11):2589-2599. <https://doi.org/10.1111/pce.13356>



The journal offers free, immediate, and unrestricted access to peer-reviewed research and scholarly work. Users are allowed to read, download, copy, distribute, print, search, or link to the full texts of the articles, or use them for any other lawful purpose, without asking prior permission from the publisher or the author.



License - Articles published in *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* are Open-Access, distributed under the terms and conditions of the Creative Commons Attribution (CC BY 4.0) License.

© Articles by the authors; Licensee UASVM and SHST, Cluj-Napoca, Romania. The journal allows the author(s) to hold the copyright/to retain publishing rights without restriction.

Notes:

- **Material disclaimer:** The authors are fully responsible for their work and they hold sole responsibility for the articles published in the journal.
- **Maps and affiliations:** The publisher stay neutral with regard to jurisdictional claims in published maps and institutional affiliations.
- **Responsibilities:** The editors, editorial board and publisher do not assume any responsibility for the article's contents and for the authors' views expressed in their contributions. The statements and opinions published represent the views of the authors or persons to whom they are credited. Publication of research information does not constitute a recommendation or endorsement of products involved.