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Research Article

Dry mass input into fruits can be predicted by fine root morphology of pepper cultivars exposed to varied lighting spectra

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Abstract

Many pepper cultivars can be raised under artificial lighting in a plant factory. An easily measured parameter is needed to fast predict fruit loading in pepper cultivars. In this study, four pepper cultivars with contrasting manners in growth and fruiting were cultured under three light-emitting diode (LED) spectra in comparison with a sunlight control. It was found that the red-light spectrum (71.7% red-, 13.7% green-, 14.6% blue-lights) increased over 40% of dry mass in fruits, while the green-light spectrum (26.2% red-, 56.4% green-, 17.4% blue-lights) induced no fruiting compared to the control. Only two cultivars responded by fine root morphology, which was characterized as smaller surface-area and fewer tip-number in the blue-light spectrum (7.8% red-, 33.7% green-, 48.5% blue-lights) than in red LED light. Tip-number showed a negative correlation with fruit dry-mass in three cultivars, while fine root diameter increased with dry mass in fruits. In conclusion, fine root tip-number can be used as a predictor of fruit dry-mass in pepper cultivars high in fruit quality or yield. The red-colour light was recommended for raising pepper cultivars in a plant factory with the purpose of greater fruit productivity.

Keywords: bioassay model; fine root plasticity; genotypes; illumination adaption; pepper

Introduction

Pepper cultivars are frequently cultured using light-emitting diode (LED) illumination in a plant factory (Kitamura *et al.*, 2008; Kokalj *et al.*, 2016). Some specific spectra in LED light irradiation can promote the quality of pepper fruits by inducing an accumulation of secondary metabolites (Alcock and Bertling, 2012; Kokalj et al., 2016). LED light can also improve contents in firmness and vitamin in pepper fruits (Liu *et al.*, 2022a). Pepper productivity of fruit biomass can also be increased by LED exposure by accelerating fruit maturation (Jokinen *et al.*, 2012; Joshi *et al.*, 2019). Given that pepper is developed in a big number of cultivars globally, it is impossible to suggest a common lighting regime that can activate fruiting for all pepper cultivars. Even for explored cultivars, were results seldomly concluded for making an explicit illumination regime with

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specific spectra (Jokinen *et al*., 2012; Joshi *et al*., 2019; Liu *et al*., 2022a). It is necessary to examine productivity of pepper cultivars in a wide range of spectra and screen the ones that benefit fruiting. This arises an economic demand to determine easily measured parameters that can precisely indicate dry mass in fruits of pepper cultivars to save the cost of measurement.

When exposed to light, physiological responses can be a precise indicator of biomass production and allocation in plants. The determination of photosynthetic production is costly and results were identified to be easily suffer a species-specific bias (Cammarisano and Korner, 2022; Wang *et al.*, 2020). Leaf morphology was suggested to be a flexible parameter that can have a solid relationship with dry mass allocation in juvenile plants (Xu *et al.*, 2019). Leaf colour was found to have a negative relationship with leaf nitrogen (N) content in pepper, which further indicated a potential relationship with dry mass allocation. However, leaves are the source of carbon (C) assimilation and roots are the sink. The determination of dry mass allocation is less driven by leaf demand than by roots. Dry mass is allocated to belowground to meet the requirement of root foraging behaviour (He *et al.*, 2021; Tan *et al.*, 2021; Wei *et al.*, 2017). Morphological traits of fine roots can be related to whole plant biomass allocation in tree seedlings exposed to varied lighting spectra (Song *et al.*, 2022). Therefore, fine root morphology has the potential to be used as a predictor of dry mass allocation for fruit production in light-exposed pepper cultivars.

Studies on horticultural plants demonstrate a trend that fine roots compete with fruits for dry mass allocation (Erel *et al.*, 2020). For example, peach tree root growth stagnated at stages of fruiting and regrowth when fruits were being harvested (Villena *et al.*, 2017). In apple trees, the portion of roots decreased in 18-31% while fruits increased in 2-49% (Lenz, 2009). For pepper cultivars, biomass was induced to allocate to roots only under rhizospheric stress at the cost of reduced whole plant biomass accumulation (Erel *et al*., 2020). Little is known about the nature of relationship between fine root morphology and dry mass in fruits of pepper cultivars if no interruption was imposed. Information is more limited about this relationship under the condition that cultivars are subjected to different light spectra.

In this study, four pepper cultivars were raised under different lighting conditions. Three LED spectra were tested for their effects from that of the natural sunlight. Fine root morphology was measured and whole-plant dry mass were weighted. Our objectives were firstly to examine effects of light spectra on fine root morphology and dry mass accumulation in organs of four pepper cultivars; and secondly to detect the allometric relationships between fine root morphology and dry mass input in every organ. We did not collect sufficient evidence to assume specific results.

Materials and Methods

Experimental condition

This study was conducted in a laboratory of Guizhou University (26°25’ N, 106°40’ E), Guiyang, China. The laboratory has an indoor space that was independent from outside environment. Air flow was controlled through a ventilation system which maintained indoor temperature around a range of 24-35 °C. Relative humidity (RH) changed between 59% and 73%, but, for peppers, was RH higher up to 91% due to the contribution of micro-environment modified by a sub-irrigation system. Sunlight was obstructed by a piece of blackout cloth for pepper plantlets except for those being subjected to the natural light spectrum. Specific illuminating conditions will be described in following text.

Plant material and cultivation

The experiment was conducted as a random block design with four spectra treatments randomly arranged in three replicated blocks. Four cultivars were tested in four independent blocks subjected to spectra. Cultivars’ distinctive pieces of information are listed in Table 1. Seeds were sown in wet sands (moisture ≥90%)

in late April of 2019, which were covered by moist towels and placed at a constant ambient temperature of 40 °C. Three weeks later were cultivars germinated to show sprouts piercing out of towels, germinant plantlets were carefully moved to growing media using a tweezer. The substrate for cultivation was made by mixing commercial peat (Zhiluntuowei A&F S&T Inc., Changchun, China) and spent mushroom residue in a volumetric proportion of 3:1 (75%:25%). This growing substance was identified to be suitable for the culture of pepper and several other species (Li *et al.*, 2021). Growing media were filled to planting cavities (each: 7cm Ø and 13cm in height) of cultivating trays. A total of 32 cavities were embedded in one tray in an even 4×8 individuals' arrangement. Five plantlets were transplanted to one cavity and finally one was left. Trays with planted pepper seedlings were placed in tank where it was maintained to a water table in about 3cm to enable sub-irrigation (water absorption kinetics in rhizosphere). Three trays of seedlings were arranged in a block as a basic unit of experiment and three blocks were arranged as three replicates.

Table 1. Biological information about four pepper cultivars used as testing materials

Cultivar name	Botanic name	Typical traits
Cultivar 1: 'Fujian King'	*Capsicum frutescens* L. var. *acuminatum* Fingh.	The aerial part can grow to 90-110 cm with slender fruits that enable continuously yields to 4.5 kg m^{-2}.
Cultivar 2: 'Proud Sun VI'	*Capsicum frutescens* L. var. *fasciculatum* (Sturt.) Bailey	Significant in fruit amount and quality as crude fat content up to 0.45 g per 100 g dry mass.
Cultivar 3: 'Perfect 215'	*Capsicum frutescens* L. var. *longum* Bailey	Big fruits as long as 23-25 cm in a diameter of 1.6-1.7 cm.
Cultivar 4: 'Zhuo Pepper VIII'	*Capsicum frutescens* L. var. *conoides* (Mill.)	Long twig in a length of about 4 cm attached to fruits in an amount over 40 and fresh weight of 13 g individually.

Seedlings were fertilized by a nutritional regime that was used for culturing juvenile plants under the hydroponic condition (Wei *et al.*, 2013; Wei and Guo, 2017). The mineral chemicals used in this regime included 4.0 mM NH_4NO_3 (ammonium nitrate), 0.5 mM K_2HPO_4 (potassium phosphate), 0.5 mM KCl (potassium chloride), 1 mM $CaCl_2$ (calcium chloride), 0.6 mM $MgSO_4$ (magnesium sulfate), 20.0 μM $FeCl_3$ (ferric chloride), 6 μM $MnCl_4$ (manganese chloride), 0.3 μM $ZnCl_2$ (zinc chloride), 0.3 μM $CuCl_2$ (cupric chloride), and 0.1 μM $NaMoO_4$ (sodium molybdate).

Illumination treatment

Four light spectra were tested in this study. Three spectra were from LED panels and one from natural sunlight as the control. Conventional culture of pepper cultivars is employed in transmitted sunlight under canopy or exposed to shading (Lanoue *et al.*, 2022; Mares-Quinones and Valiente-Banuet, 2019). The three LED light spectra were provided from panels embedded with diodes that emitted different colours of lights, namely in red, green, and blue colours. The LED spectra were mixtures of those from three basic lights. Briefly, the red-light spectrum comprised 71.7% red light, 13.7% green light, and 14.6% blue light; the green-light spectrum comprised 26.2% red light, 56.4% green light, and 17.4% blue light; the blue-light spectrum comprised 17.8% red light, 33.7% green light, and 48.5% blue light. The gross photosynthetic photon flux density (PPFD) 40 cm beneath LED panel was measured to be 95-98 μmol m^{-2} s^{-1} depending on the variation of positions. All pepper seedlings exposed to LED lights were wrapped in an ironic box with one side towards the window. This can make sure no sunlight radiation interrupted the lighting spectra that seedlings can receive.

The sunlight treatment employed seedlings trayed in a place near the window and allowed to receive sunlight at a similar PPFD with LED-exposed seedlings (Liu *et al.*, 2021). Visible light in sunlight was consisted by red, green, and blue lights in general proportions of 31.8%, 35.2%, and 33.0%. The period that sunlight transmittance through window over a PPFD of 20 μmol m^{-2} s^{-1} was from 4:00 am to 17:00 pm, when the daytime PPFD was averaged to fall in a range of 95-98 μmol m^{-2} s^{-1}. Hence, LED lights were turned on also in this period from 4:00 am to 17:00 pm to synchronize their photosynthetic periods.

Sampling and measure

Peppers were cultured in a two-month time when height growth was retarded by fruit loading. Ten individuals were randomly sampled from a tray and divided into parts of leaves, fruits, stem, and root. Roots were cleaned in distilled water carefully and attached substrates were removed. Cleaned roots were further divided into coarse root and fine root. A critical diameter of 2 mm was used to screen for fine roots (Wang *et al.*, 2017). Fine roots were scanned to be photographed in projected images, which were analyzed for fine root morphology using WinRhizo software (Regent Inc., Calgary, Canada). Fine root morphology was characterized by parameters of length, surface area, diameter, tip number, and fork number. All seedling parts were oven dried at 70 °C for 72 h. Dry mass were weighted for each seedling part. Absolute weight was further used to calculate proportional weight of each part to the total of whole plant.

Statistical analysis

Analysis of variance (ANOVA) was used to detect the effect of four light spectra on seedling parameters. When significant effect was indicated by a one-way ANOVA model, results were compared by Duncan tests ($P<0.05$). Thus, some of sampled individuals did not load fruits hence the numbers of fruit weight were uneven across treatments. The three LED light spectra were taken as objective treatments and that from sunlight as the control. The number of four cultivars was taken as four paralleled conditions hence this factor was not designed to attend the ANOVA analysis. Fine root morphological parameters were correlated with dry mass weight in every seedling part by Pearson model. Significant correlations were further detected for coefficients that can distinguish relationships.

Results

Dry mass weight and allocation

The light spectra treatment induced significant effects on dry mass weight in parts of leaves, fruit, stem, and root for all four pepper cultivars (Table 2). However, dry mass weight in stem and root of pepper cultivar 1 was not significantly affected, neither was that in stem of pepper cultivar 4. Among the four light treatments, the red light resulted in greater dry mass weight in fruits compared to that in other treatments (Figure 1). The green light did not induce fruiting and the blue light resulted in less fruit dry mass compared to the controlled sunlight. The LED light spectra did not result in greater dry mass weight in leaves and stem. Spectra from red and green lights induced greater dry mass weight in roots of pepper cultivars 2 and 3 (Figure 1B, C).

Table 2. Analysis of variance (ANOVA) of different light spectra from natural sunlight (N), red (R), blue (B), and green (G) lights on dry mass weight and weighted proportion in components of leaf, fruit, stem, and root parts of four pepper cultivars

Source of variance	Leaves		Fruit		Stem		Root	
Dry mass weight								
	F value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Cultivar 1	15.99	<0.0001	536.05	<.0001	2.62	0.0595	1.19	0.322
Cultivar 2	13.66	<0.0001	439.26	<.0001	15.14	<.0001	12.50	<.0001
Cultivar 3	4.49	0.0068	507.32	<.0001	10.75	<.0001	16.61	<.0001
Cultivar 4	5.05	0.0041	337.92	<.0001	2.61	0.0623	16.91	<.0001
Dry mass weighted proportion								
Cultivar 1	71.97	<.0001	195.02	<.0001	17.58	<.0001	11.41	<.0001
Cultivar 2	26.23	<.0001	203.46	<.0001	41.90	<.0001	24.68	<.0001
Cultivar 3	88.08	<.0001	537.38	<.0001	23.41	<.0001	33.24	<.0001
Cultivar 4	30.13	<.0001	198.52	<.0001	44.14	<.0001	31.59	<.0001

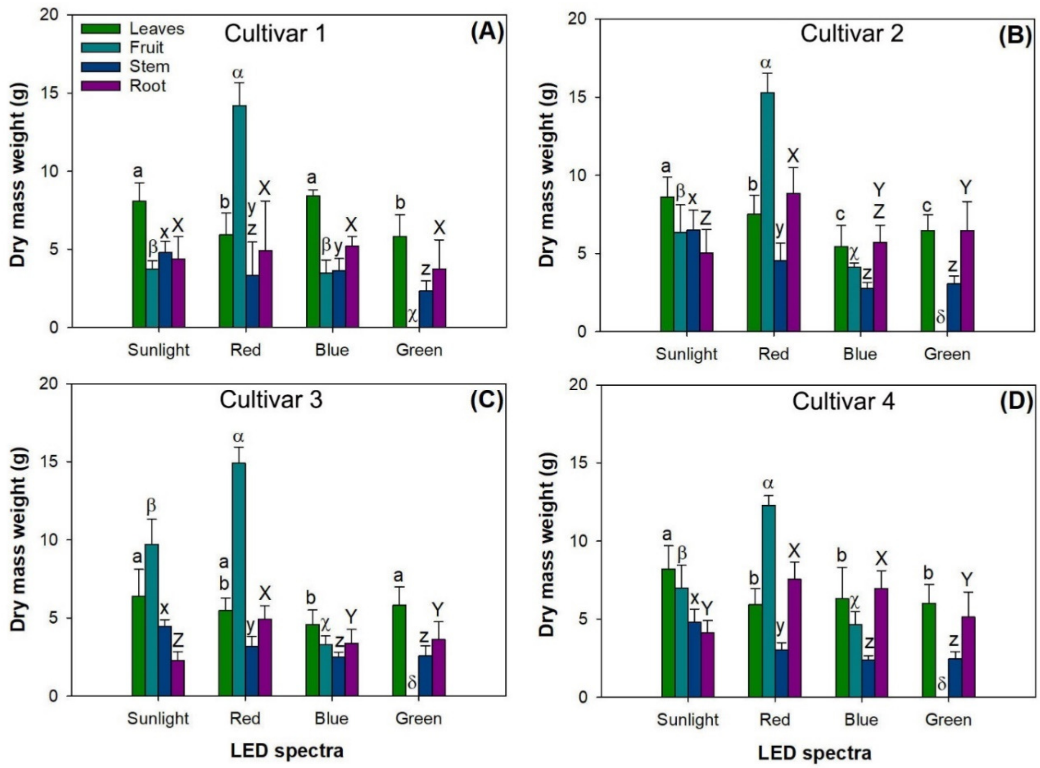

Figure 1. Dry mass weight of four pepper cultivars exposed to three light-emitting diode (LED) spectra and the controlled spectrum of sunlight; (A) Responses of cultivar 1; (B) Responses of cultivar 2; (C) Responses of cultivar 3; (D) Responses of cultivar 4. Different letters indicate significant difference evaluated by Duncan tests ($P<0.05$). Letters of a, b, c label the difference of dry mass weight in leaves; letters of α, β, χ, δ label the difference of dry mass weight in fruits; letters of x, y, z label the difference of dry mass weight in stems; letters of X, Y, Z label the difference of dry mass weight in roots

Light spectra treatment showed a significant effect on dry mass weighted proportion in organs of all four pepper cultivars (Table 2). Again, red light showed an unique spectrum that increased the weighted proportion of dry mass in fruits, which accounted for over 40% of total dry mass weight (Figure 2). Although the green light failed to induce fruits, it resulted in higher weighted proportions of dry mass in leaves and roots. The blue light did not cause any increase of dry mass weighted proportion in stem.

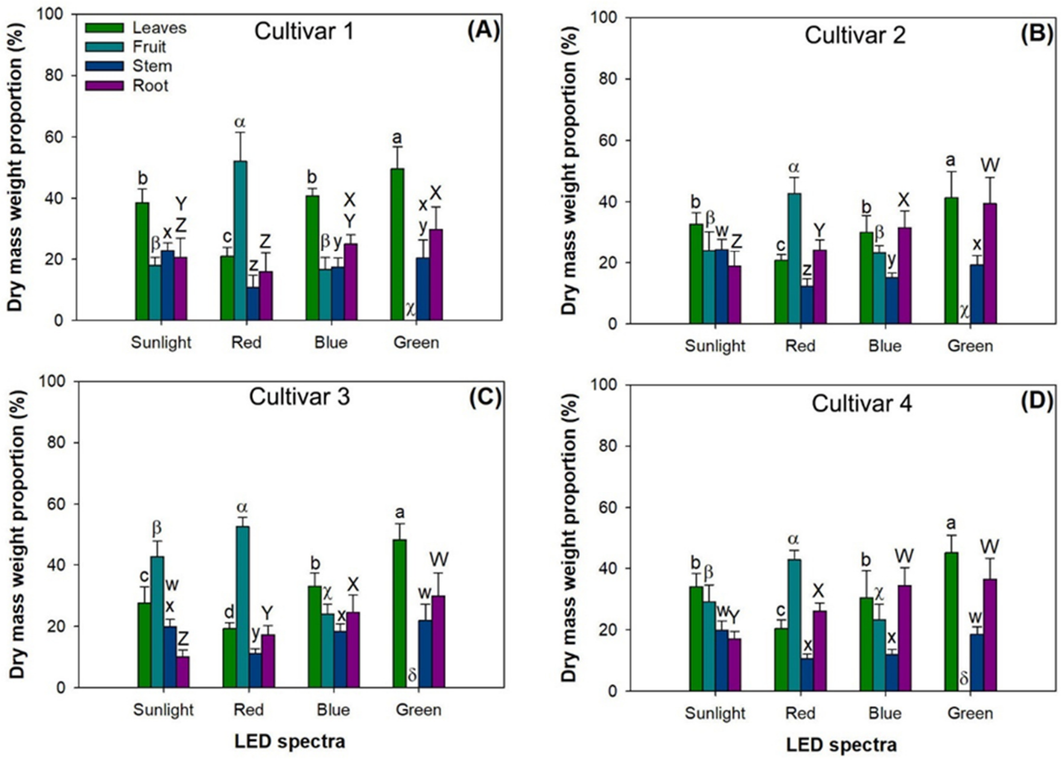

Figure 2. Dry mass weighted proportions (%) of four pepper cultivars exposed to three light-emitting diode (LED) spectra and the controlled spectrum of sunlight; (A) Responses of cultivar 1; (B) Responses of cultivar 2; (C) Responses of cultivar 3; (D) Responses of cultivar 4. Different letters indicate significant difference evaluated by Duncan tests ($P<0.05$). Letters of a, b, c label the difference of dry mass weight in leaves; letters of α, β, χ, δ label the difference of dry mass weight in fruits; letters of w, x, y, z label the difference of dry mass weight in stems; letters of W, X, Y, Z label the difference of dry mass weight in roots

Light spectra effect on fine root morphology

Light spectra did not result in any significant effect on fine root morphology in pepper cultivars 1 and 4 (Table 3). Cultivars 2 and 3 showed significant responses of fine root morphology to light spectra. All three types of LED light spectra resulted in longer fine roots compared to the control of sunlight with no further difference among LED spectra in pepper cultivars 2 and 3 (Figure 3A).

All LED light spectra also induced a larger area of fine roots in cultivars 2 and 3 (Figure 3B). In pepper cultivar 2, the blue light resulted in lower surface area of fine roots compared to spectra from red and green lights. In cultivar 3, the red light further induced a larger area of fine roots relative to the green light.

However, LED light spectra failed to induce larger fine root diameter in pepper cultivars 2 and 3 (Figure 3C). The red light did not change fine root diameter from the sunlight control in cultivar 2, while in cultivar 3, were diameter lower in the red light than in the sunlight. The blue and green light spectra induced lower fine root diameter compared to the red-light spectra in both cultivars 2 and 3.

Fine root tip-number was not statistically different between the red light and the control of sunlight in all four pepper cultivars (Figure 3D). The blue and green light spectra resulted in fewer fine root tips compared to the red light in pepper cultivars 2 and 3.

All LED spectra resulted in more fine root forks compared to the sunlight control in cultivars 2 and 3 (Figure 3E). The green light further increased fine root fork-number compared to the red and blue light spectra.

Table 3. Analysis of variance (ANOVA) of different light spectra from natural sunlight (N), red (R), blue (B), and green (G) lights on fine root morphology in components of leaf, fruit, stem, and root parts of four pepper cultivars

Source of variance	Length		Surface-area		Diameter		Tip-number		Fork-number	
	F value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Cultivar 1	1.41	0.2500	0.19	0.9027	2.6200	0.0595	1.11	0.3540	0.40	0.7535
Cultivar 2	11.80	<.0001	14.83	<.0001	15.14	<.0001	10.30	<.0001	12.76	<.0001
Cultivar 3	12.02	<.0001	8.32	0.0001	10.75	<.0001	5.03	0.0037	8.54	<.0001
Cultivar 4	2.62	0.0616	0.19	0.9058	2.61	0.0623	3.41	0.0248	1.63	0.1956

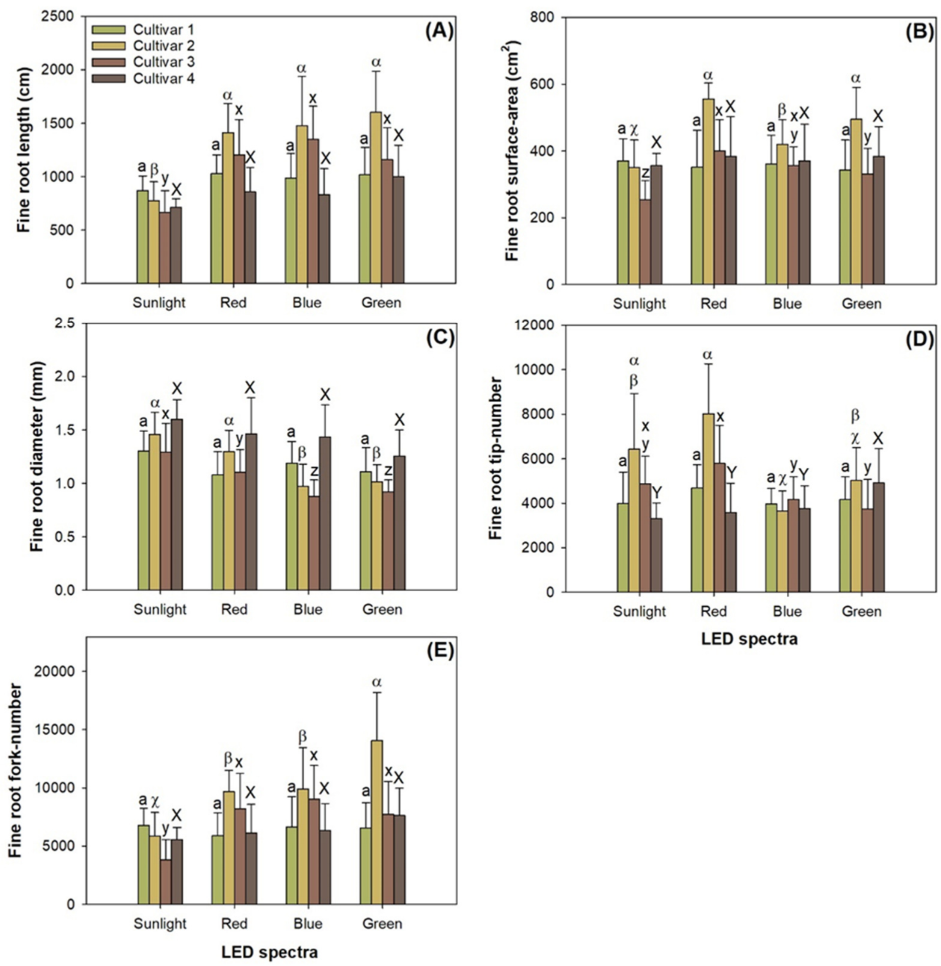

Figure 3. Fine root morphology of four pepper cultivars exposed to three light-emitting diode (LED) spectra and the controlled spectrum of sunlight; (A) Response of fine root length; (B) Response of fine root surface-area; (C) Response of fine root diameter; (D) Response of fine root tip-number; (E) Response of fine root fork-number. Different letters indicate significant difference evaluated by Duncan tests (P<0.05). The letter of a labels no difference of fine root morphology in pepper cultivar 1; letters of α, β, χ label the difference of fine root morphology in pepper cultivar 2; letters of x, y, z label the difference of fine root morphology in pepper cultivar 3; the letter of W labels no difference of fine root morphology in pepper cultivar 4

Pearson correlation analysis

Among morphological parameter, fine root length, tip-number, and fork-number revealed varied negative correlations with dry mass weight in aerial organs in pepper cultivars 2-4 (Table 4).

Table 4. Pearson correlations between parameters describing dry mass weight for plant components (leaves, stem, fruit, root) and fine root morphology (length, surface-area, diameter, tip-number, fork-number) in four pepper cultivars

Fine root morphology	Coefficient	Plant components			
		Leaves	Stem	Fruit	Root
Cultivar 1					
Length	*R*	0.15504	0.01635	0.04917	0.2528
	P	0.241	0.9022	0.7115	0.0534
Surface-area	*R*	0.37398	0.34466	-0.0359	0.59532
	P	0.0035	0.0075	0.787	<.0001
Diameter	*R*	0.28126	0.37246	-0.1566	0.40021
	P	0.0309	0.0037	0.2363	0.0017
Tip-number	*R*	0.13047	0.11973	-0.0657	0.28984
	P	0.3247	0.3664	0.6212	0.026
Fork-number	*R*	0.37844	0.29541	-0.1625	0.45122
	P	0.0031	0.0231	0.2187	0.0003
Cultivar 2					
Length	*R*	-0.4349	-0.4789	-0.1304	0.35315
	P	0.0006	0.0001	0.3294	0.0065
Surface-area	*R*	-0.0031	-0.1277	0.2673	0.66294
	P	0.9813	0.3394	0.0425	<.0001
Diameter	*R*	0.6493	0.61887	0.38966	0.06637
	P	<.0001	<.0001	0.0025	0.6206
Tip-number	*R*	-0.3963	-0.4374	-0.3748	0.23712
	P	0.0021	0.0006	0.0038	0.0731
Fork-number	*R*	-0.3099	-0.3885	-0.2996	0.30468
	P	0.0179	0.0026	0.0223	0.02
Cultivar 3					
Length	*R*	-0.3613	-0.439	-0.2021	0.31827
	P	0.0046	0.0005	0.1215	0.0132
Surface-area	*R*	-0.0978	-0.2073	0.09546	0.52159
	P	0.4571	0.112	0.4681	<.0001
Diameter	*R*	0.51648	0.50391	0.44133	-0.0072
	P	<.0001	<.0001	0.0004	0.9567
Tip-number	*R*	-0.1858	-0.1317	-0.4467	-0.1498
	P	0.1552	0.3159	0.0003	0.2532
Fork-number	*R*	-0.2588	-0.3511	-0.1622	0.38431
	P	0.0459	0.0059	0.2156	0.0024
Cultivar 4					
Length	*R*	-0.3613	-0.439	-0.2021	0.31827
	P	0.0046	0.0005	0.1215	0.0132
Surface-area	*R*	-0.0978	-0.2073	0.09546	0.52159
	P	0.4571	0.112	0.4681	<.0001
Diameter	*R*	0.51648	0.50391	0.44133	-0.0072
	P	<.0001	<.0001	0.0004	0.9567
Tip-number	*R*	-0.1858	-0.1317	-0.4467	-0.1498
	P	0.1552	0.3159	0.0003	0.2532
Fork-number	*R*	-0.2588	-0.3511	-0.1622	0.38431
	P	0.0459	0.0059	0.2156	0.0024

For example, fine root length showed a negative relationship with dry mass weight in leaves and stem in cultivars 2-4, where tip-number showed another three negative relationships with fruit dry mass weight.

However, fine root diameter had positive relationships with dry mass weight in aerial organs for all four pepper cultivars, while surface-area had positive relationships with dry mass weight in root.

Furthermore, correlations of fine root diameter with dry mass in fruit had a higher slope compared to those with dry mass in leaves and stem in pepper cultivars 2 and 3 (Figure 4J, K). In detail, the correlations between fine root diameter and fruit dry mass had slopes in a range between 7.7644 and 10.2253, which were generally higher than those in correlations with dry mass in leaves and stem in cultivar 2 (both slopes lower than 4.0) and cultivar 3 (both slopes lower than 3.0) (Table 5).

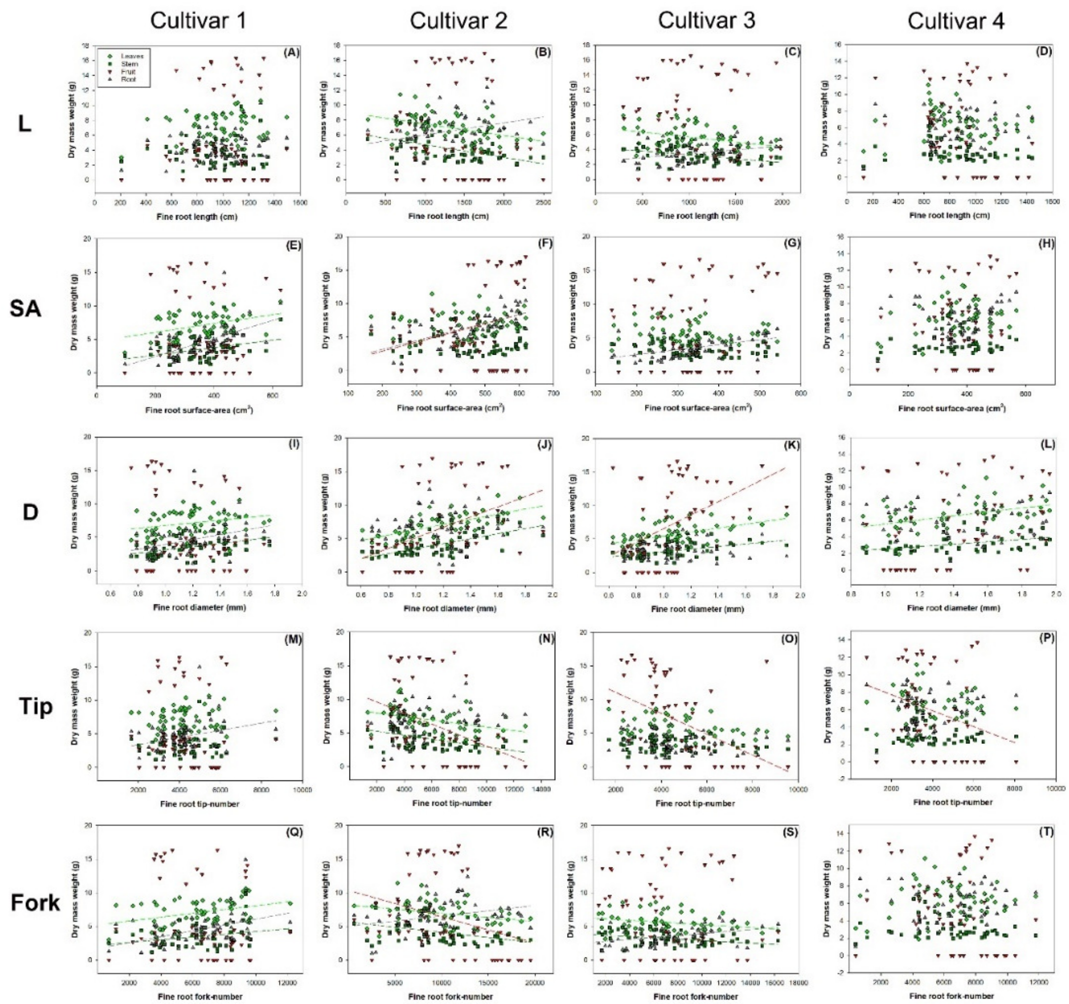

Figure 4. Curve fit of Pearson correlation for relationships between fine root morphology and dry mass weight; (A-D) Relationship of fine root length (L); (E-H) Relationship of fine root surface-area (SA); (I-L) Relationship of fine root diameter (D); (M-P) Relationship of fine root tip-number (Tip); (Q-T) Relationship of fine root fork-number (Fork). Dash lines mark curve fits for existed correlations in colours of light green, dark green, red, and dark grey for leaves, stem, fruit, and root, respectively

In addition, fine root surface-area also had correlations with higher slope for dry mass in fruit than those for dry mass in root (Figure 4F). The correlation of surface-area with fruit dry mass was 0.0136 and that with root dry mass was 0.0130 (Table 5). Correlations of numbers of fine root tips and forks with dry mass in fruit can be described by fit curves with sharper slopes than those with dry mass in leaves and stem in pepper cultivar

2 (Figure 4N, R). Slopes of fruit-fit-curves were -0.0008 and -0.0004 for correlations of tip- and fork-numbers, which were higher than those of fit curves for leaves and stem (≤-0.0003) (Table 5).

Table 5. Model descriptions of correlations between parameters describing dry mass weight for plant components (leaves, stem, fruit, root) and fine root morphology (length, surface-area, diameter, tip-number, fork-number) in four pepper cultivars

Fine root morphology	Coefficient	Plant components			
		Leaves	Stem	Fruit	Root
Cultivar 1					
Length	a [1]	n.a. [2]	n.a.	n.a.	n.a.
	R^2 [3]	n.a.	n.a.	n.a.	n.a.
Surface-area	a	0.0066	0.0056	n.a.	0.0135
	R^2	0.1399	0.1188	n.a.	0.3544
Diameter	a	1.9956	2.4174	n.a.	3.6368
	R^2	0.0791	0.1387	n.a.	0.1602
Tip-number	a	n.a.	n.a.	n.a.	0.0005
	R^2	n.a.	n.a.	n.a.	0.0840
Fork-number	a	0.0003	0.0002	n.a.	0.0004
	R^2	0.1432	0.0873	n.a.	0.2036
Cultivar 2					
Length	a	-0.0016	-0.0017	n.a.	0.0016
	R^2	0.1891	0.2293	n.a.	0.1247
Surface-area	a	n.a.	n.a.	0.0136	0.0130
	R^2	n.a.	n.a.	0.0714	0.4395
Diameter	a	3.9138	3.7155	7.7644	n.a.
	R^2	0.4216	0.3830	0.1518	n.a.
Tip-number	a	-0.0003	-0.0003	-0.0008	n.a.
	R^2	0.1570	0.1913	0.1404	n.a.
Fork-number	a	-0.0001	-0.0002	-0.0004	0.0002
	R^2	0.0960	0.1509	0.0898	0.0928
Cultivar 3					
Length	a	-0.0013	-0.0010	n.a.	0.0010
	R^2	0.1305	0.1927	n.a.	0.1013
Surface-area	a	n.a.	n.a.	n.a.	0.0073
	R^2	n.a.	n.a.	n.a.	0.2721
Diameter	a	2.9267	1.9128	10.2253	n.a.
	R^2	0.2642	0.2658	0.2074	n.a.
Tip-number	a	n.a.	n.a.	-0.0016	n.a.
	R^2	n.a.	n.a.	0.1995	n.a.
Fork-number	a	-0.0001	-0.0001	n.a.	0.0001
	R^2	0.0670	0.1233	n.a.	0.1477
Cultivar 4					
Length	a	n.a.	n.a.	n.a.	n.a.
	R^2	n.a.	n.a.	n.a.	n.a.
Surface-area	a	n.a.	n.a.	n.a.	n.a.
	R^2	n.a.	n.a.	n.a.	n.a.
Diameter	a	2.4659	1.4260	n.a.	n.a.
	R^2	0.1757	0.1607	n.a.	n.a.
Tip-number	a	n.a.	n.a.	-0.0009	n.a.
	R^2	n.a.	n.a.	0.0841	n.a.
Fork-number	a	n.a.	n.a.	n.a.	n.a.
	R^2	n.a.	n.a.	n.a.	n.a.

Note: [1] a, slope of correlation model; [2] n.a., not available to detect a correlation; [3] R^2, correlation determinative.

Discussion

Effects of LED-exposure on dry mass in pepper cultivars

When compared with the spectrum of sunlight, only that from the red LED light can result in greater dry mass allocation for fruiting. This was confirmed by either dry mass weight or weighted proportions in all four cultivars. These findings concur with previous results found in purple pepper (Liu *et al.*, 2022b) and chili pepper (Liu *et al.*, 2022a). The red light induced dry mass allocation either for an early ripeness (Liu *et al.*, 2022b) or for promoting firmness (Liu *et al.*, 2022a). Only when exposed to the red LED light will dry mass weighted proportion be higher than 40% in fruits of three cultivars. The promotion of dry mass allocated to fruits in pepper can be a trade-off that attenuated synthesizing photosynthetic pigments (Kim and Son, 2022). It is reasonable that relative higher energy output in red light does not require response to input dry mass for obtaining more photosynthesis. We can conclude here that the red light of LED panels can benefit allocating dry mass for fruiting of pepper cultivars.

None of our pepper cultivars loaded any bell fruits in the green light. The green light was also reported to be irrelevant from fruiting in chilli pepper (Darko *et al.*, 2022) and sweet pepper (Maroga *et al.*, 2019). It is a common sense that the green light has an extremely low absorptivity absorbed by photosynthetic pigments (Liu *et al.*, 2021; Wei *et al.*, 2020b). This is why transmittance at the understory layer of a forest is dominated by the component of green light in visible sunlight (An *et al.*, 2019; Wei *et al.*, 2020a). Fruiting is a process that heavily depends on energy consumption of light input (Chavan *et al.*, 2020). The high reflection of green light from the surface of pepper leaves inhibited the use of photosynthetic energy for fruiting.

The sunlight induced a nature that dry mass was mostly allocated to leaves (~40%) and least to roots (~20%). This dry mass allocation was modified by the red light which induced a greater proportion of dry mass allocated in fruits and lower in stem compared to other spectra. In contrast, the green light modified dry mass allocation to an excessive input to leaves without any in fruits. It is obvious that the blue light benefited dry mass allocated to roots which shared parts of proportion to the aerial organs. All these results can be referred to in future designs of illumination for pepper culture in plant factory. Compared to the sunlight, the red light can be more recommended for fruiting of pepper cultivars, and green and blue lights induced biomass allocation to leaves and roots, respectively.

Effects of LED-exposure on fine root morphology in pepper cultivars

Among the four cultivars, only two of them responded in fine root morphology and the other two showed no responses. This cannot be drawn to a conclusion that fine root morphology is more plastic in LED light spectra than in sunlight for pepper cultivars. Roots only accounted for about 30% of total dry mass accumulation in pepper cultivars. This allocation pattern determined the low ability of fine root plasticity regarding the general chase of intensive load of dry mass for fruiting. In cultivars 2 and 3, it was characterized in root-plastic genotypes that fine root morphology was enlarged by elongating the axis with more tips initiated that formed more forks. The LED light generated generally longer fine roots with scarce difference among the three LED-light spectra. The red spectrum was found to have a positive effect on fine root length in *Pinus pumila* (He *et al.*, 2021). These results, plus findings in this study, together suggest that fine root length is not a reliable parameter that can be plastic in different light spectra. In our study, among the three LED spectra the red light meanwhile increased surface area and tip-number of fine roots compared to the blue light. These results suggest an impact of red light that increased surface area by promoting new tips surpassing the blue light. Both of these two spectra, however, were surpassed by the green light for formatting more forks. We did not see practical meaning from these findings that can benefit pepper cultivation.

The relationship between fine root morphology and dry mass allocation

Although previous studies reported a competition of dry mass allocation between fine root and fruit in pepper and horticultural trees (Lenz, 2009; Villena *et al*., 2017; Erel *et al*., 2020), our results can only agree to these. Among all fine root parameters, only tip-number showed negative relationships with fruit dry mass in three cultivars. Along the gradient that fine root tip-number increased, fruit dry mass declined at a faster speed than dry mass in leaves and stem. Fine root fork also showed a negative relationship with fruit dry mass, but this only occurred in one cultivar. Fine root length showed no relationship with fruit dry mass, and surface-area and diameter even showed occasionally positive relationships in cultivars 2 and 3. According to these findings, the competition for dry mass with fruits resulted from the demand to newly initiate root tips instead of that to promote fine root growth. Given that cultivars 2 and 3 showed a plastic fine root growth pattern, their increases in fine root diameter and surface-area were resulted from plastic responses to the red light. This surmise can be reasonable because fine root diameter and surface-area showed positive relationships with dry mass weight in all organs. Fine root length mainly showed negative relationships with dry mass input to leaves and stem in cultivars 2 and 3, which illustrates an irrelevance from the contribution to fruit load.

Conclusions

The most surprising results in our study were that the tip-number of fine roots can be a trustable morphological parameter that indicated a competition of dry mass allocation in fruits for pepper cultivars. Fork number can be considered as a dry-mass-predictor only when cultivar 2 was the subjective material for pepper cultivation. The red-light LED spectrum (71.7% red light, 13.7% green light, and 14.6% blue light) was recommended to maximize fruit productivity in pepper. The contrasting effects between red and blue spectra together contributed to a synchronization of dry mass allocation in fruits with the increase of fine root diameter. Overall, fine root tip-number can be used as an easily measured predictor of dry mass allocation to fruits of pepper exposed to varied light spectra. The precision and accuracy of the predicting model using tip-number need to be confirmed by more cultivars in more types of lighting conditions.

Among the four cultivars, the first genotype is the only one that showed rare responses of fine root dry mass and morphology to light spectra. The cultivars 1 and 4 also had no relationship of fine root morphology with fruit biomass. These cultivars had an attributes of fast shoot growth and continuous fruiting. This determines that cultivars 1 and 4 had a natural preference to retain dry mass in above-ground organs with rare allocated downward the root. In contrast, cultivars 2 and 3 had highest numbers of relationships that were significant between fine root morphologies and fruit dry mass. These two cultivars both had attributes of big fruit productivity or abundant bioactivity in fruits. Overall, we conclude that fine root tip number can be used as a predictor of fruiting productivity with a higher precision for pepper cultivars that had significant attributes of high quality or yield in fruits.

Authors' Contributions

Conceptualization: CZ and YW; Data curation: LW; Formal analysis: LW and CZ; Funding acquisition: YW; Investigation: LW; Methodology: CZ; Project administration: YW; Resources: YW; Software: CZ; Supervision: CZ; Validation: CZ; Visualization: CZ; Writing - original draft: LW; Writing - review and editing: CZ and YW. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

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

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