Effect of Day Length on Growth and Root Morphology of Yellow Maca (*Lepidium meyenii*) Seedlings

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Abstract: *Lepidium meyenii* is a biennial herbaceous plant of the family Brassicaceae, which recently gained research attention as well as consumer interest. Its underground storage organs are used both as a food and as traditional medicine. The storage organs, called fleshy-hypocotyls, are formed by swollen hypocotyl tissues fused with a taproot. The attempts to grow maca outside of its centre of origin have increased globally, although many cropping requirements are unknown. In terms of fleshy-hypocotyl formation, the impact of day length remains unclear. In this study the effects of day length (8 h, 16 h) on early plant development and hypocotyl thickening in yellow maca were investigated in a rhizobox experiment under controlled conditions (20 °C day and 18 °C night temperature, and relative air humidity 25–30%). Results of a 13-week cultivation period showed that number of leaves and leaf length significantly increased in plants grown under long-day (LD, 16 h) conditions as compared to those from the short-day (SD, 8 h) treatment. Furthermore, plants developed under LD conditions had larger hypocotyl width within 67 days after sowing. At 88 days after sowing, the width was almost two-fold higher. Moreover, the total root length of maca plants from LD treatment was significantly longer and had more fine roots (diameter < 0.4 mm) than in plants cultivated in SD treatment. The obtained results suggest that in early stages of plant development LD can stimulate root development and hypocotyl thickening in yellow maca.

Keywords: maca; hypocotyl; rhizobox experiment; day length; photoperiod

1. Introduction

*Maca* (*Lepidium meyenii*) is a biennial crop belonging to the family Brassicaceae. It is mainly grown in the Peruvian Andes at an elevation of 3500 to 4450 m a.s.l. Maca has been cultivated by the local population for over 1300 to 2000 years [1] for its below ground storage organs (fleshy-hypocotyls). It is known as a traditional herbal medicine, mainly as a fertility enhancer for both humans and cattle [2]. During the last two decades, this crop has attracted worldwide attention. Maca has become a popular nutraceutical thanks to numerous medical studies reporting the nutritional and health benefits of dried maca hypocotyls including male and female fertility enhancement [3,4], activity against cancer cells [5], and other beneficial health effects [6].

Due to the small area of maca cultivation in Peru [7] and the drastically increased global demand, attempts to cultivate maca outside its natural habitat have gained popularity [8,9]. However, such cultivation is often problematic since specific physiological features of maca, and mechanisms of its adaptations for growth in harsh climate conditions, are not yet fully understood. A closer look to the morphological features of maca plants reveals its adaptations to growth conditions. The morphological structure of a young maca plant at 60 days after sowing (DAS) indicating leaves, hypocotyl, and root system is presented in Figure 1a,b. Reduced height growth (usually not more than 20 cm) [10] and rosette leaves laying on the soil surface are adaptations to the strong winds typical of maca cultivation areas [11,12]. Maca has a typical dicotyledonous taproot system with a main downward-growing taproot and secondary roots, which in turn branch to form tertiary roots [13]. It is
the only species among the genus *Lepidium* which develops below ground storage organs for deposition of carbohydrates, proteins, and other compounds [14]. Anatomically, these storage organs represent swollen hypocotyl tissues fused with a taproot [15]. Generally, the term “hypocotyl” refers to a part of a seedling found between the cotyledons and the radicle (embryonic root). Therefore, we will call the storage organs of maca “fleshy-hypocotyls” in order to emphasize their histological origin and to maintain consistency throughout this article. From an anatomical point of view, similar storage organs can also be found in turnip (*Brassica rapa* subsp. *rapa* L.) or radish (*Raphanus sativus*), which are often referred to as “tubers”. Correspondingly, the process of the tubers’ initiation and gradual growth is known as tuberisation [16,17]. The process of tuberisation has been intensively investigated in many species. Numerous studies have demonstrated the important role of photoperiodic signals for tuber initiation and enlargement. For radish, it has been shown that long-day photoperiods promote initiation of tuberisation, as well as growth and biomass accumulation of storage organs [18–20].

![Figure 1](image.jpg)

**Figure 1.** (a) Habitus of young maca seedling at 60 DAS; (b) morphological structure of maca seedlings indicating leaves, hypocotyl and root system consisting of a taproot and secondary roots; (c) hypocotyl of maca plant (2.5× magnification) grown in rhizoboxes under controlled conditions. Dashed lines indicate diameter a and diameter b where measurements have been performed.

It can be hypothesized that a similar process of “fleshy-hypocotyl” initiation and growth might take place in maca plants. However, the exact mechanism of storage organ induction in maca is unknown. There is limited knowledge, as well as contradicting results, in the literature especially in terms of photoperiod requirements of maca hypocotyl thickening. The day length in maca’s native production area has less than thirteen hours of light throughout its growing period, suggesting that this crop is adapted to short days or is day neutral [21,22]. However, other results showed similar plant development at both short- and long-day photoperiods, concluding that maca hypocotyl thickening was day length neutral [8]. Observations under long day length conditions in higher latitudes suggested that maca is a short day plant, perhaps with strong interaction between critical day length and temperatures.
Several studies described attempts of maca cultivation in field conditions outside the centre of origin; however, as to our knowledge none of them could achieve similar average sizes of maca fleshy-hypocotyl (60 mm) as in the cultivated areas in Peru [8]. Maca was cultivated under long day length conditions in Davis, California (latitude = 38° N), from September to May [8]. Maca hypocotyls had reached a maximum enlargement of 30 mm (in diameter) by the end of April. Maca cultivated in Gatersleben, Germany (near Berlin, latitude = 52° N) from April to November, produced only very small hypocotyls (10–15 mm) [23]. Furthermore, maca plants cultivated in Prague, Czech Republic (latitude = 50° N) from February to October had a much smaller size compared to those from Peru [9]. Considerably better results were obtained in China, mainly in Yunnan Province, where several maca cultivation sites have been established in highland areas [24–26]. Cultivation of maca at an altitude of 4200 m a.s.l. in southwestern China was achieved [12]; however, the size of yielded hypocotyls was not reported. Additionally, maca hypocotyls were successfully cultivated in the Lijiang region, Yunnan Province at an altitude of 3180 m a.s.l [27]; however, the shape of yielded hypocotyls was deformed and differed from those cultivated in Peru.

The aim of the present study was to investigate the effects of different photoperiods on (i) hypocotyl thickening during the early stages of plant development as well as on (ii) shoot growth and (iii) root system development in yellow maca seedlings. This information is essential for the development of a cultivation system for maca outside its centre of origin, and especially relevant for the adjustment and selection of appropriate sowing dates.

2. Materials and Methods

2.1. Seeds

A rhizobox experiment was carried out with yellow maca seeds. Seeds were purchased from Rühlemann’s Kräuter & Duftpflanzen (Horstedt, Germany), stored in closed paper bags in darkness at 4 °C, and kept at room temperature (20 °C) for 24 h before sowing.

2.2. Rhizobox Experiment

A rhizobox experiment was performed in order to investigate the effects of photoperiod on thickening of maca hypocotyls, development of root system, and shoot growth. For this, maca seedlings were pre-germinated in plastic trays for 36 days under greenhouse conditions receiving natural sunlight. Temperature was maintained at 18–28 °C and relative air humidity was kept between 20–70%. At 36 days after sowing (DAS), maca seedlings reached the 4th-leaf stage. Two seedlings were transplanted into each rhizobox (30 × 20 × 2 cm³) equipped with a root observation window [28], each filled with 460 g of a commercial growing substrate with pH 5.6 (MANNA® FLOR Blumenerde, Wilhelm Haug GmbH & Co. KG, Düsseldorf, Germany), which was also used for the seedlings’ pre-germination. During the experiment, soil moisture was adjusted gravimetrically to 20% (w/w) by supplying deionised (DI) water via holes on the backside of the rhizobox in order to ensure even moisture distribution. Plants were cultivated under controlled conditions in growth chambers with a day/night temperature of 20/18 °C and relative humidity of about 25%. In order to create different photoperiod treatments, three growth chambers were each divided into two compartments with a light-tight black film, where photoperiods were adjusted to 8 h (short-day, SD) or 16 h (long-day, LD). In each compartment, two rhizoboxes were placed above a table and top-lighting (350 μmol PAR m⁻² s⁻¹) was provided with three high-pressure sodium lamps (HPS) of the type SON-T Agro HPS 400 W (Philips) mounted at a height of 80 cm above the plants. Each of the three climate chambers were considered as a replicate, resulting in a total of 6 rhizoboxes per treatment.

At 88 DAS, maca plants were harvested and divided into above-ground (leaves) and below-ground (roots with hypocotyls) parts. For the above-ground part, number of leaves, leaf length, and leaf fresh weight were recorded. Subsequently, they were dried at 60 °C for 24 h and leaf dry weight was determined. The roots, together with hypocotyls, were washed of soil particles and stored in 30% ethanol until root morphology measurements
took place. The fresh weight of the below ground plant was then recorded, followed by drying for 24 h at 60 °C and determination of the dry matter. The weight of the below ground part was determined for roots and hypocotyls together, since the precise separation of hypocotyl from taproot was not possible without corresponding microscopic cross-section analysis [15]. However, in the early developmental stages of maca, the hypocotyl zone has a length of a few millimeters; therefore, the weight of the hypocotyl can be considered negligible as it might not affect the total root weight.

2.3. Regular Plant Measurements

During the experiment, measurements of leaf number and leaf length were performed on a weekly basis at 53, 60, 67, 81, and 88 DAS. In addition, five intermediate non-destructive measurements of root length were performed at 46, 53, 60, 67, and 81 DAS. For this, the observation windows of the rhizoboxes were opened and roots were sprayed with DI water in order to avoid drying. A transparent film was then placed on top of the roots, and the roots (including taproot and all lateral roots) were drawn on the film with a permanent marker. Following this, the drawings were scanned using an Epson Expression 10000XL scanner (Epson America Inc., California, USA) and analysed with WinRhizo Pro V. 2009c (Regent Instruments Inc., Ville de Québec, QC, Canada).

2.4. Hypocotyl Diameter Measurements

Photos of the hypocotyl zone of maca seedlings were made 67 and 88 DAS using a binocular microscope (Stemi 200-C, Carl Zeiss Microscopy GmbH, Oberkochen, Germany), equipped with a digital camera (DXC-390P, Sony Group Corporation, Tokyo, Japan). The obtained photos (at 0.65×, 1.25× and 2.5× magnification) were used for hypocotyl diameter measurements with Axiovision 3.1 software (Carl Zeiss Microscopy GmbH, Oberkochen, Germany). During that developmental stage, hypocotyls of maca plants had an inverted conical shape with a wide top gradually tapering down and eventually fusing with the taproot (Figure 1b). Two diameters of the hypocotyl were measured (Figure 1c), one in the widest part directly under the leaf base (diameter a) and other one 1 mm lower than a (diameter b).

2.5. Root Morphology Measurements

After harvest (at 88 DAS), roots were washed and stored in 30% ethanol. The roots were then placed on a transparent Perspex tray filled with DI water and were carefully spread out. Subsequently, the roots were scanned using an Epson Expression 10000XL scanner (Epson America Inc., Los Alamitos, CA, USA). Eventually, the root image for each replicate was analyzed using WinRhizo software (Regent Instrument Inc., Ville de Québec, QC, Canada) in order to obtain the total root length and its distribution in root diameter classes.

2.6. Statistical Analysis

The experiment was arranged as a randomized complete block design with three replicates. Collected data was analyzed using SAS®9.4 statistical software (SAS Institute Inc., Cary, NC, USA). Data was analyzed using a mixed model approach as seen in Equation (1). The model can be described as:

$$y_{ijkl} = \mu + b_j + s_{jk} + \tau_k + r_{ijk} + e_{ijkl}$$

(1)

where $b_j$ is the fixed effect of block $j$, $s_{jk}$ is the random effect of the $k$th sub-chamber in block $j$, and $\tau_k$ is the fixed effect of the $k$th treatment. Additionally, $r_{ijk}$ is the effect of the $ijk$th rhizobox, and $e_{ijkl}$ is the error of $y_{ijkl}$. After finding significant treatment differences via global F test, a multiple t-test (Fisher’s LSD test with $\alpha = 0.05$) was performed and differences were presented using a letter display [29].
3. Results

Development of parts of maca seedlings, including leaves, hypocotyl, and roots, was significantly influenced by day length treatments. The results of weekly plant measurements showed that maca plants grown via LD treatment developed significantly more leaves as compared to those in SD treatment during the whole experiment, except for the last measurement at harvest (88 DAS) (Table 1). Starting from the second plant measurement (60 DAS), average leaf length was significantly higher in LD treatment (Table 1). At harvest (88 DAS), the fresh and dry weight of leaves in LD treatment were higher compared to SD treatment. However, this difference was only significant for the weight of fresh leaves, which in LD treatment was four-times greater than in SD treatment (1196.64 and 289.86 mg plant \(^{-1}\), respectively) (Table 2). For fresh and dry root biomass at harvest, the difference between treatments was statistically significant (Table 2). The fresh weight of roots in LD treatment was four-times greater than in SD treatment (74.13 and 15.89 mg plant \(^{-1}\), respectively), and the root dry weight in LD treatment was seven-times greater (13.78 and 1.85 mg plant \(^{-1}\), respectively) than in SD treatment.

| Treatment | 53 DAS | 60 DAS | 67 DAS | 81 DAS | 88 DAS |
|-----------|--------|--------|--------|--------|--------|
| Long-day  | 3.9 ± 0.3 \(^a\) | 4.8 ± 0.3 \(^a\) | 5.1 ± 0.3 \(^a\) | 6.2 ± 0.4 \(^a\) | 5.3 ± 0.4 \(^ns\) |
| Short-day | 2.7 ± 0.3 \(^b\) | 3.4 ± 0.3 \(^b\) | 3.5 ± 0.3 \(^b\) | 4.7 ± 0.4 \(^b\) | 4.2 ± 0.4 \(^ns\) |

Table 1. Average number of leaves and average leaf length of yellow maca plants grown in rhizoboxes under controlled conditions at long (16 h) or short (8 h) day length. The measurements were performed at 53, 60, 67, 81, and 88 DAS. Results represent mean values ± SEM of three independent replicates.

| Treatment | Leaf Fresh Weight, mg Plant \(^{-1}\) | Leaf Dry Weight, mg Plant \(^{-1}\) | Root Fresh Weight, mg Plant \(^{-1}\) | Root Dry Weight, mg Plant \(^{-1}\) |
|-----------|---------------------------------|-------------------------------------|-------------------------------------|-------------------------------------|
| Long-day  | 1196.64 ± 102.28 \(^a\) | 133.00 ± 31.15 \(^ns\) | 74.13 ± 7.12 \(^a\) | 13.78 ± 3.01 \(^a\) |
| Short-day | 289.86 ± 102.28 \(^b\) | 38.67 ± 31.15 \(^ns\) | 15.89 ± 7.12 \(^b\) | 1.85 ± 3.01 \(^b\) |

Table 2. Fresh and dry weight of leaves and roots of yellow maca plants grown in rhizoboxes under controlled conditions at long (16 h) or short (8 h) day length. The measurements were performed after harvest (88 DAS). Results represent mean values ± SEM of three independent replicates.

The root growth characteristics of maca plants grown via LD treatment were significantly different to SD treatment. Thus, at four intermediate measurements namely 53, 60, 67, and 81 DAS, the total root length of maca plants in the LD treatment was significantly longer than those in the SD treatment (Figure 2), although at the beginning of the experiment (46 DAS) the root length of the seedlings was not significantly different. The total root length in the LD treatment measured after harvest (88 DAS) was 2.7-fold higher compared to the SD treatment (236.3 and 88.9 cm plant \(^{-1}\), respectively, Figure 3) and it was represented mainly by fine roots. Thus, in the LD treatment compared to the SD treatment, a 2.4- and a 4-fold increase in the length of fine roots, with diameters between 0-0.2 mm and 0.2-0.4 mm, respectively, were determined; and the length of thicker roots (>0.6 mm in diameter) in the LD treatment exceeded three times those in the SD treatment (Figure 3).
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Figure 2. Intermediate root length measurement of yellow maca plants grown in rhizoboxes under controlled conditions at long (16 h) or short (8 h) day length. The measurements were performed at 46, 53, 60, 67, and 81 DAS. Results represent mean values ± SEM of three independent replicates. Different letters indicate significant differences between treatments ($p \leq 0.05$), ns = not significant.

Figure 3. (A) The total root length; (B) distribution of the root length into different diameter classes (0–0.2 mm, 0.2–0.4 mm, 0.4–0.6 mm, and >0.6 mm) of yellow maca plants grown in rhizoboxes under controlled conditions at long (16 h) or short (8 h) day length. The measurements were performed at 88 DAS. Results represent mean values ± SEM of three independent replicates. Different letters indicate significant differences between treatments ($p \leq 0.05$), ns = not significant.

Microscopic analyses of the hypocotyl zone of maca seedlings have also shown significant differences between the treatments (Figure 4). Thus, at 67 DAS, the hypocotyl diameter in the LD treatment was significantly greater than that in the SD treatment. The same
results provided diameter measurements at 88 DAS, which have shown that the hypocotyl diameter in the LD photoperiod was two times larger than in SD conditions.

Figure 4. Images of the hypocotyl and hypocotyl diameter (mm) of yellow maca plants grown in rhizoboxes under controlled conditions at long-day (16 h) (A,C) or short-day (8 h) (B,D) conditions (2.5 × magnification). The measurements were performed in two positions: diameter a and diameter b (A), at 67 DAS and after harvest (88 DAS). Results represent mean values ± SEM of three independent replicates. Different letters indicate significant differences between treatments (p ≤ 0.05).

4. Discussion

The rhizobox experiment was performed in order to investigate the effects of day length on the early development of maca plants, and in particular on their hypocotyl thickening and roots and shoots growth. At the end of the experiment (88 DAS), plants grown under LD photoperiod had bigger leaves, longer and denser rooting systems, as well as thicker hypocotyls (Figure 5).
The first evidence of photoperiod effect on maca plant development was detected at two weeks after transplanting the seedlings into rhizoboxes (53 DAS). Despite the fact that [8] reported that maca produces the same number of leaves during the first 13 weeks via LD and SD, in our experiments leaf number in the LD treatment was significantly higher. Furthermore, maca leaves in the LD treatment were longer at 60 DAS and in all further measurements until harvest (88 DAS). Such variations in the shoot development can be explained by a more pronounced hour difference between LD and SD treatments in the present study, which was 8 h (16 h and 8 h, respectively), while in the study [8] it was only 2 h (14 and 12 h, respectively).

A very strong effect of day length treatments was observed on the root system. Five intermediate non-destructive measurements showed a clearly longer rooting system of maca plants in the LD treatment (Figure 2). The fact that root length was not different between the treatments at the first measurement (46 DAS) confirms that maca seedlings were in the same developmental stage at the beginning of the experiment, and suggests that determined differences were caused presumably by the applied photoperiod treatments. By the end of the experiment, total root length in LD treatment was 2.5-fold longer compared to plants from the SD treatment. Interestingly, the major effect was noted for the fine roots fraction (<0.4 mm in diameter). It is well known that fine roots play an important role in water and nutrient acquisition [30], and can therefore influence plant growth and biomass accumulation. In our experiments, the fresh and the dry root biomass of plants from the LD treatment was also significantly higher than in the SD treatment. This is in good agreement with previous studies, as an increase of dry biomass accumulation under LD conditions was also reported for other crops, such as sugar beet (Beta vulgaris) [31], tomato (Solanum lycopersicum) [32], and numerous grass species [33].

In Figure 5, the difference between the density of root system and especially the length of the taproot between the treatments was clearly visible. The taproot allows wider root architecture and enables...
better occupation of the soil volume and thus, nutrient acquisition leading to more vigorous plant development.

Formation of the vegetative storage organ or fleshy-hypocotyl in maca is a result of fusion of the thickened hypocotyl with the upper part of its taproot. For large-scale production of maca, revealing the factors favouring initiation of hypocotyl thickening is crucial. In our experiment, the microscopic analysis of the hypocotyl zones of young maca plants revealed significantly wider hypocotyls in the LD treatment. These measurements showed that the hypocotyl diameter in the LD treatment compared to the SD treatment at 67 DAS was 1.5-fold thicker, and at the day of harvest almost 2-fold thicker (Figure 4). These findings suggest that photoperiod and particularly LD conditions (16 h) might play an important role in induction of tuberisation in maca plants. Tello et al. [22] indicated that maca root developed from secondary parenchymatic growth of the hypocotyl tissue, while the upper part of the taproot was very similar to the ones in radish (Raphanus spp.). In radish (Raphanus sativus L. cv. Cherry Belle), LD treatment (16 h) has also initiated storage organ formation, while SD (8 h) delayed the beginning of hypocotyl enlargement [18]. Interestingly, once the initiation of the storage organ occurred, the growth rates were similar under all photoperiods.

However, our results are in contrast to previous research, which concluded that maca does not have a strict requirement for the photoperiod, and belongs rather to day neutral plants [8]. The experiment of Quiros et al. [8] was criticized by Hermann and Bernet [34] as the authors failed to recognize that this experiment was unsuitable to determine the day length sensitivity of maca. Their observation would also be consistent with maca behaving as a short-day plant with a critical day length > 14 h under the highly artificial conditions of the experiment.

In the literature, there is also evidence of the stimulating effects of LD treatment on the growth of storage organs developed from hypocotyls. For example, Zha and Liu [19] have demonstrated that under LD treatment (16 h), radish produced bigger storage organs; however, light quality and intensity also played a very important role. In the study of Guo et al. [20], cherry radishes cultivated under the long photoperiod regime (16 h/8 h) also produced the largest biomass. Furthermore, Craker et al. [18] showed that LD treatment (16 h) increased the percentage of plant assimilates transferred to the storage root. It is generally known that longer day length prolongs photosynthesis and thus accumulation of the dry weight of the plant [33,35]. The same results were demonstrated in our experiment, where the dry mass of above and below ground plant parts was higher in the LD treatment. Furthermore, the increased number of leaves and stronger developed root system might increase assimilate flow to the maca fleshy-hypocotyls. However, further investigation is needed in this regard.

Apart from photoperiod, there are also other factors, such as temperature or a combination of factors (for example of temperature and photoperiod), which can affect growth of below ground storage organs. In radish (Raphanus sativus L. var Faraon), low temperatures (4 °C) in combination with short photoperiods stimulated biomass accumulation of storage organs as compared to those in the treatment with high temperature and LD (18/14 °C) [36]. Furthermore, Nieuwhof [37] also reported that the cultivation of radish (Raphanus sativus L. var. radicula Pers.) in winter (November-December in the northern hemisphere) under low temperatures (10 °C and 14 °C) resulted in better root growth as compared to higher temperature conditions (26 °C) where almost no root thickening was observed. The focus of the present study was set on the investigation of photoperiod on maca hypocotyl thickening, while temperature was kept constant in all treatments. However, in further investigations, the effect of temperature in combination with photoperiod should also be tested.

5. Conclusions

In summary, the present study suggests that early development of maca plants, and particularly hypocotyl thickening, is promoted under LD treatment (16 h). For the development of a cropping system and the adjustment of agronomic measures for maca cultivation
under the given climatic and day length conditions of Central Europe, it is recommended
to take temperature and day length into account. For a successful hypocotyl formation
and maximized yields, maca should be either sown or young seedlings cultivated for
a certain period under long or at least at decreasing day length conditions. However, for the
determination of the most suitable sowing date for maca plants, monitoring of plant growth
and investigation of the hypocotyl development under field conditions are necessary.

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