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Original article

Short- and long-term phenotypic changes of hydroponically grown tomatoes as a result of seedling production substrates

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Summary

Short- and long-term phenotypic changes of hydroponically grown tomatoes as a result of seedling production substrates were examined. As such, plants were grown for two weeks in three different seedling production substrates: horticultural growing medium on peat basis, perlite, and a 1:1 mixture of peat-perlite, before they were transplanted into a rockwool based hydroponic system.

Germination of plants in the perlite treatment resulted in significantly smaller leaves, lower stem diameter and a delayed start of harvesting compared to the other treatments, while no differences in the amount of marketable tomatoes were observed at the end of experiments. The perlite treatment yielded fewer small and blossom end rot fruits.

Applying Lichtenthaler's index and the normalized difference vegetation index showed lower chlorophyll concentrations in the leaves of the perlite treatment. The car-ratio index revealed a tighter ratio of carotenoid to chlorophyll in the perlite treatment implying some kind of stress. Due to the absent influence of smaller leaves and assumed lower chlorophyll concentration on yield, a higher photosynthetic radiation use efficiency (PRUE) was expected. Applying the photochemical reflectance index, which is correlated to the PRUE, could not support this hypothesis. Reflectance indices calculated for the optical properties of fruits did not suggest any differences in fruit pigmentation. It is therefore possible to save a portion of the finite resource peat by using perlite as seedling production substrate without worrying about loss of yield and fruit pigmentation.

Keywords

fruit pigmentation, growing media, hydroponics, optical readings, peat, perlite, tomato cultivation, tomato yield, substrates

Significance of this study

What is already known on this subject?

- Peat is widely used in horticulture, e.g., as seedling production substrate and growing media in hydroponics. Nevertheless, it is well known that peat is a finite resource and must be replaced by alternative substrates.

What are the new findings?

- The present study shows short- and long-term phenotypic changes as a result by three different seedling production substrates. As such, optical readings showed lower chlorophyll concentrations and stress responses in leaves when using perlite as seedling production substrate. Furthermore, it was found that seedling production substrates have a long-term effect on plant growth and start of harvesting, but not on total yield and fruit pigmentation.

What is the expected impact on horticulture?

- Peat or peat mixtures used as seedling production substrate can be used to shorten the start of harvesting of plants grown in hydroponics. However, all seedling production substrates, including perlite, influence the total yield and fruit pigmentation to the same extent. From this it follows that peat as seedling production substrate can be replaced by inorganic substrates.

Introduction

While in the twentieth century increased yield per area was achieved mainly by enhancing plant nutrition centered on output, nowadays the focus changes to the input regarding the input-output ratio. Where yield per area hardly can be further increased, the mentioned ratio can be raised by reducing the resource input merely. Besides improving plant performance genetically, controlled environment agriculture is introduced to meet the physiological demands of the produced crops. Developing efficient growing methods is one factor of influence to attain steady amounts of yield and lower the resource input at the same time.

The present report focused on substrates used for seedling growth of tomato plants. Established techniques involve the use of peat as a growing medium in all sectors of horticultural production. Ecological concerns expressed by politics and public and the issue of peat being a finite resource challenges research for and development of substrates suitable as a substitute for growing media based on peat. Due to public attention this issue is notably present in ornamental plant production (Jayasinghe et al., 2010) and increasingly embraces all branches in horticulture, including vegetable production (Zaller, 2007).

This effort is widely accepted and plenty literature on this topic is available. In their review, Raviv et al. (1986) outline the needs for germination, rooting and growth of plants which should be met by growing media and summarize reports dealing with peat substitutes. Growing media serve the functions of (1) physical support, (2) aeration of the root zone, (3) water supply for growth and development,

and (4) the supply of mineral nutrients (Landis et al., 1990). Besides the physical properties, the demands on chemical properties are the most important for a healthy growth of the cultivated plants. The main factor is the availability of nutrients within the medium, followed by the ability of the substrate to provide and maintain the desired pH value. Cation exchange capacity (CEC), i.e., the ability to buffer nutritional ions, is quoted as the main factor of the medium fertility (Blume et al., 2010).

Rock wool do not provide any nutrients and has a relatively low cation exchange capacity of 40 meq 100 g^{-1} (Resh, 2002). Therefore, the required nutrients and the necessary pH value have to be constantly supplied and provided by the nutrient solution. During seedling growth, juvenile tomato plants may be best prepared for rockwool-based hydroponics when an equally inert growing substrate with low CEC like perlite would be used. As such, peat could be replaced by perlite as a seedling growth medium, where a beneficial influence on plant health by minimizing the transplant shock is assumed.

Standard peat-based horticultural growing medium used for seedling production provides a relatively high amount of nutrients and a suitable pH of 6.0 for the purpose of seedling growth. Additionally sphagnum peat moss holds a relatively high CEC of 100–200 meq 100 g^{-1} available (Tripepi, 2014). In contrast, perlite includes no nutrients and provides a relatively high pH of 7.1). The CEC tends to zero (Kantiranis et al., 2007). A 1:1 peat-perlite mix involves an increased pH compared to a peat-based medium itself. Peat-based media is often enriched with perlite to balance water content and aeration in order to reduce the side effects of a lowered CEC and nutrient content compared to pure peat-based growing medium.

Other investigations in terms of effects of perlite, peat, and mixtures of perlite and peat on plants are focused on whole cultivation periods and not on long-term effects caused by a short seedling growth in different substrates. In this context, Wilson (1986) found that highest tomato yields were achieved in perlite when this substrate was compared with other organic and inorganic substrates. Ors and Anapali (2010) found a significant decrease in leaf number in strawberry plants grown in 1:1 mix of soil-perlite compared to plants grown exclusively in perlite, but no significant difference in leaf area. In our study, however, short- and long-term phenotypic changes of hydroponically grown tomatoes as a result of seedling production substrates such as peat, perlite and a 1:1 mixture of peat-perlite will be examined and possible quality differences in harvested fruits will be evaluated.

Materials and methods

Experimental set-up and crop cultivation

Experiments were conducted in a Venlo-type greenhouse at Humboldt-Universität zu Berlin, Germany (latitude 52°46'74", longitude 13°31'16") during the growing period 2015. As such, the main experiment was carried out from 5th January until 25th August 2015. On the first experimental date, 270 tomato seeds (*Solanum lycopersicum* L., cv. 'Pannovy') were sowed into three sowing shells each containing three different seedling growth substrates: perlite, peat (Klasmann-Deilmann GmbH, Geeste, Germany; N: 140 mg L^{-1}, P: 100 mg L^{-1}, K: 180 mg L^{-1}, Mg: 100 mg L^{-1}, S: 120 mg L^{-1}) and a peat-perlite mixture (50%:50%, v/v) arranged in a randomized order. During the first two weeks of germination, plants were irrigated with fresh water upon need. Thereafter, a part of these plants continued their growth under the same conditions in hydroponics. In detail, a total of 39 seedlings picked out from each seedling production substrate were transferred to rockwool cubes (Cutilene®Exact; Tilburg, The Netherlands) and transplanted into rockwool slabs used as growing substrate in a high-gully based hydroponic system when the first inflorescence was visible. The remaining seedlings served to determine the fresh and dry matter caused by different seedling production substrates as described below.

The nutrient supply in the hydroponic system was realized using a drip irrigation system, providing nutrient solution for 150 seconds mainly after a light summation of 70 klxh. The light summation was regularly adjusted to reach a drainage of 20% after each irrigation cycle. To meet the nutrient needs of plants, the nutrient solution was mixed according to the recipe of Göhler and Molitor (2002). The environmental conditions within the greenhouse were controlled using the application of proportional integral differences, including data obtained from different sensors to maintain the sought microclimatic conditions. As such, the energy screens were closed at a global radiation of less than 3 W m^{-2}, the floor level heating was set at a target temperature of 17°C for day and night, the ventilation was opened above a temperature of 23°C and the CO_2 enrichment was kept at 800 ppm during daylight hours.

Recording crop growth and yield

Measurements of phenotypic properties started after plants were planted into rockwool slabs. Stem diameter, number of trusses, and leaf area were gathered weekly from a sample of thirteen plants per treatment. Counting of leaves and trusses included all leaves with a length above 20 cm and all trusses where at least one fruit appeared, respectively. Leaf length and width of each counted leaf was measured with a folding ruler. The measurements were inserted in an exponential function developed by Dannehl et al. (2015) to estimate the leaf area (LA) of each individual leaf non-destructively. These were summed up to obtain the LA per plant expressed as m^2 $plant^{-1}$.

Furthermore, ripe tomatoes of all plants were harvested, counted and weighed weekly, where fruits were distinguished in marketable fruit (> 50 g) and further fruit sizes categories (A-class ≥ 70 g; 50 g ≤ B-class < 70 g; C-class < 50 g; blossom end rot (BER) class > 50 g). After the experiment was finished, the recorded data in terms of all quality classes were summed up to compare the fruit yield, fruit weight and the number of fruit of plants grown in different seedling growth substrates for two weeks. The fruit yield, fruit weight and the number of fruit were expressed as g $plant^{-1}$, g $fruit^{-1}$ and number $plant^{-1}$, respectively.

Optical readings

A portable, hand-held spectrophotometer device (Pigment PA/+/1101/801, CP, Control in applied Physiology GbR, Falkensee, Germany) equipped with photodiode arrays was used to measure the leaf and fruit spectra in the visible and near infrared range from 402 to 1,048 nm, providing a spectral resolution of 3.3 nm. An integrated light cup equipped with light-emitting diodes, capturing the entire wavelength range recorded, served as the light source. For calibration of this device, spectralon (20% certified, Labshere Ltd., North Sutton, USA) was used as the white reference.

To obtain the spectra of leaves, the first true leaf of each tomato plant was measured three times and recorded on August 8th, 2015. Spectra of fruits were recorded on August 16th, 2015. In this context, three replicates containing 39

tomatoes (>70 g) were randomly selected from different plants per treatment. Fruits used were selected at a ripening stage 10, which matured at the same height in the canopy. The recorded tomato raw spectra of leaves and fruits were used to calculate specific indices (*I*) for chlorophyll, carotenoids and anthocyanins. Namely Lichtenthaler's index (*I*550/*I*750, (Lichtenthaler et al., 1996)), Car-ratio index (*I*550/*I*455, (Zude and Kläring, 2009)), Chlorophyll ratio index (*I*698/*I*760, (Carter, 1994)), Photochemical reflectance (PRI = ((*I*531-*I*571)/(*I*531+*I*570), (Gamon et al., 1992)) and structure insensitive pigment index (SIPI = (*I*800-*I*445)/(*I*800-*I*680)), (Penuelas et al., 1995)) were calculated for tomato leaves. The same applies to the normalized difference vegetation index (NDVI), which was directly calculated and given by the spectrophotometer device. The Car-ratio and Chlorophyll ratio index was also used to determine the pigmentation of tomatoes. Additionally, the normalized anthocyanin index (NAI = (*I*780-*I*570)/(*I*780+*I*570), (Farneti et al., 2012)) was calculated from spectra of fruits.

Statistical methods

Effects of different treatments on the vegetative plant growth, fruit yield, fruit size, as well as on the pigmentation of leaves and fruits of tomato plants were evaluated using analysis of variance (ANOVA) with SPSS, package version 19.0. The normal distribution of the data was proved using the Kolmogorov-Smirnov test. To calculate significant differences post hoc analysis was performed using Tukey-tests at a significance level of $p < 0.05$, where different small letters describe significant differences. The mean variability was indicated using standard deviation, which was illustrated by ± in Tables or bars in Figures.

Results and discussion

Effects on phenotype

Two weeks of growth on the three different seedling growth media without additional nutrient supply resulted in a significant lower shoot fresh and dry mass in the perlite treatment compared to seedlings grown in peat or the peat-perlite mixture (Table 1). Shoot fresh and dry mass was approximately one eighth and one sixth, respectively, when seedlings were compared to the other seedling growth substrates. The limited growth caused by the perlite treatment is most likely due to a nutrient limitation in this variant. The peat containing substrates include organic material, which can be mineralized and thus provide the nutrients needed for growth, which is not feasible in the substrate perlite. However, no significant differences were found in dry matter fresh matter ratio in tomato seedlings (Table 1) ranging from 7.07% in the peat-perlite mix treatment to 7.54% in the peat treatment and 7.68% in the perlite treatment, although the values reflect the expectations of increased dry matter/fresh matter ratio in relatively stressed plants.

One week after transplanting the seedlings into rockwool slabs, measurements of stem diameter showed significantly lower values of plants initially grown in perlite towards the remaining two treatments (Figure 1A). This effect did not adjust during the following eleven weeks. The plants which were grown in perlite during the first two weeks showed half the stem diameter towards the peat treatment until the fourth week on rockwool slabs. This difference was lowered beginning with the fifth week after transplanting, but did not reach values above 90% of the remaining two treatments and thus remained significantly lower (Figure 1A). In the mix treatment lower stem diameter was measured during the first two weeks after transplanting compared to the peat treatment, but eventually leveled up with the third week after transplanting and of measurement, respectively. These data sets suggest a long-term acclimation to an initial nutrient deficiency, where there were fewer nutrients available in the perlite treatment compared to the other two treatments.

The total number of trusses reflected the hypothesis of a prolonged development in the perlite treatment, where the number of trusses attained those of the other two treatments with one week delay (Figure 1B). Furthermore, eleven weeks of homogeneous cultivation of the three different treatments did not lead to an alignment of leaf area in the perlite treatment towards the remaining treatments. No significant differences regarding leaf area were detected between the peat-perlite mix and the peat treatment (Figure 1C).

Similar to the assumed long-term acclimation regarding the stem diameter of initially relatively malnourished plants in the perlite treatment, the data sets regarding the estimated leaf area suggest a severe phenotypical long-term acclimation to an initial nutrient deficiency in the perlite treatment. Experiments by Naegle et al. (2005) with soybeans on the influence of nitrogen content and mobilization in seeds on leaf development and leaf growth during recovery after N deprivation showed inhibitions of leaf extension and leaf initiation in seedlings grown without N in the second week after germination. Depending on the time at which nitrogen was resupplied, leaf extension inhibition could be restored, although this was only possible if the leaves were at an early stage of development. This suggests that seedlings in our study should be supplied with nutrients earlier than or even during seedling growth when grown in perlite.

Long-term effects on yield quantity and quality

Though leaf area and stem diameter remained significantly smaller in the perlite treatment over the period of cultivation, no losses in total yield of marketable fruits and weekly yields of marketable fruits including fruits of A and B class were observed (Table 2). The weekly yield per plant of class C as well as blossom end rot fruits (BER) was significantly lower in the perlite treatment (Table 2). Where no differences could be found between the peat treatment with 70 g and the peat-perlite mix with 62 g regarding the amount

Table 1. Effect of different seedling growth media on shoot fresh mass (FM), shoot dry mass (DM) and DM/FM ratio.

Seedling growth media	FM (g)	DM (g)	DM/FM ratio (%)
Perlite	0.054 ± 0.022 [a]	0.005 ± 0.002 [a]	7.68 ± 3.23 [a]
Perlite/Peat	0.439 ± 0.162 [b]	0.031 ± 0.023 [b]	7.07 ± 3.47 [a]
Peat	0.398 ± 0.144 [b]	0.030 ± 0.016 [b]	7.54 ± 2.86 [a]

Data represent mean values of two-week old plants ± standard deviation. Same letters indicate no significant differences among means of treatments (Tukey's test, $p > 0.05$, $n = 15$).

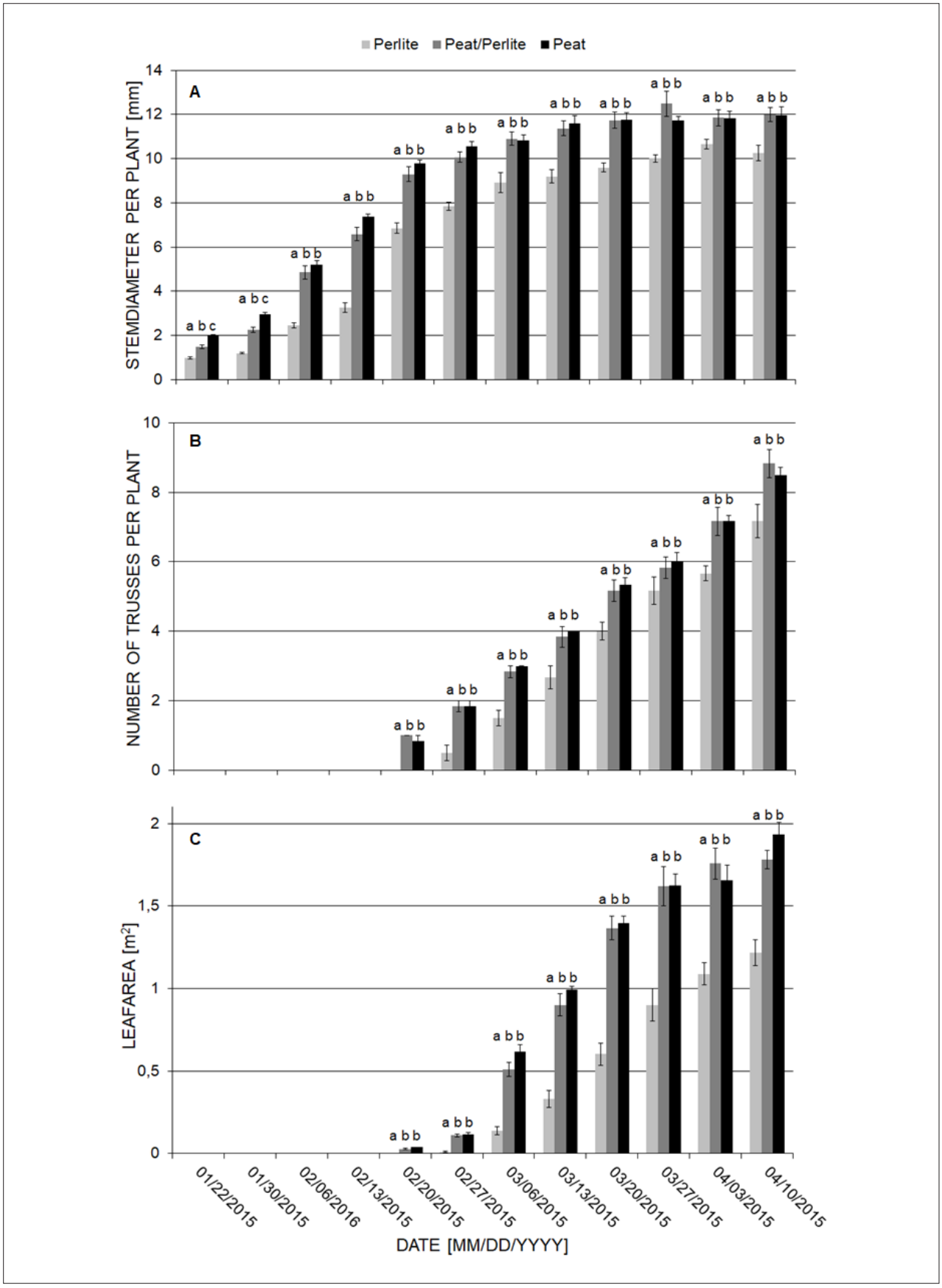


Figure 1. Changes in average stem diameter (A), total number of trusses (B) and average leaf area (C) of plants after transplanting in rock wool slaps as a result of seedling growth in different substrates (perlite = light grey, peat-perlite mix = grey, peat = black) for two weeks (mean ± standard deviation). Same letters indicate no significant differences among means of treatments (Tukey's test, $p > 0.05$, $n = 13$).

Table 2. Long-term effects of different seedling growth substrates on yield quantity and quality.

Fruit class	Treatment		
	Peat	Peat/Perlite	Perlite
	Yield per plant (g week^{-1})		
Marketable	585 ± 37 ^{a}	589 ± 40 ^{a}	586 ± 44 ^{a}
Class A	518 ± 35 ^{a}	524 ± 38 ^{a}	535 ± 41 ^{a}
Class B	67 ± 8 ^{a}	64 ± 8 ^{a}	51 ± 7 ^{a}
Class C	70 ± 8 ^{b}	62 ± 6 ^{b}	46 ± 5 ^{a}
BER	45 ± 7 ^{b}	44 ± 6 ^{b}	14 ± 3 ^{a}
	Total marketable yield per plant (g)		
	5224 ± 402 ^{a}	5252 ± 404 ^{a}	5273 ± 406 ^{a}

Same letters indicate no significant differences among means of treatments at the end of experiments (Tukey's test, $p > 0.05$, $n = 13$). ± shows the standard deviation. Fruits are categorized in marketable class (A+B), A class >70 g, 50 g ≤ B-class <70 g, C class <50 g and blossom end rot fruits (BER).

of class C fruits, the perlite treatment in this category yielded only 46 g. The difference was more pronounced within the category BER fruits per plant and week, where the peat and the peat-perlite mix treatment yielded 45 g and 44 g, respectively and perlite treatment in this category produced only 14 g per plant and week. Increased aeration through reduced leaf size may promote an improved plant health by positively affecting the microclimate in the crop and thus results in relatively lowered amount of BER fruits. On the other hand calcium deficiency in fruit tissue is responsible for the physiological disease of BER fruits (Ho et al., 1993), a lower amount of harvested diseased fruits, i.e., those infested by BER, could be attributed to the estimated smaller leaf size. This, in accordance with a similarly smaller sink for calcium, could lead to a more likely supply of calcium to the fruit tissue.

Although there were no significant differences in the average weekly harvest of marketable tomatoes, the cumulative yields at the beginning of the harvest season differed between treatments (Figure 2). In the first week, only fruits from plants pre-grown on peat or peat-perlite mix were harvested, although the differences were not significant. This changed in the second week, when significantly more tomatoes (200 g plant^{-1}) were harvested from plants influenced by the peat-perlite mix treatment. Although the pre-cultivation on peat also produced 200 g tomatoes, due to high variation (±63 g), no significant difference to the other two treatments could be distinguished. In the following two weeks, the highest cumulative harvest was achieved in the peat variant, which was significantly higher than the perlite variant. The mix treatment was in between. From the fifth harvest week onwards, the cumulative yields between the treatments could no longer be distinguished significantly. As stated before, all three treatments resulted in a similar cumulative yield, although it seems from Figure 2 that perlite pre-cultivated plants show a trend to produce lower yield. At this point, it should be pointed out once again that there might have been development delays in the perlite variant, as was already the case with truss number, as a result of which the peat and peat-perlite treatments developed marketable yield a week earlier, which could be of interest to horticultural companies. However, over time the cumulative yield recovered to similar levels in all treatments.

Deficit nutrition during seedling growth possibly improves nutrient use efficiency (NUE) of mature plants similar to the approach of improving water use efficiency by deficit irrigation as shown for maize (Kang et al., 2000), grapevine (Chaves et al., 2007) and red date (Cui et al., 2008). Generally, determination of NUE is used to quantify the ability of plants to absorb and to utilize nutrients for the production of dry matter or yield. This efficiency depends on environmen-

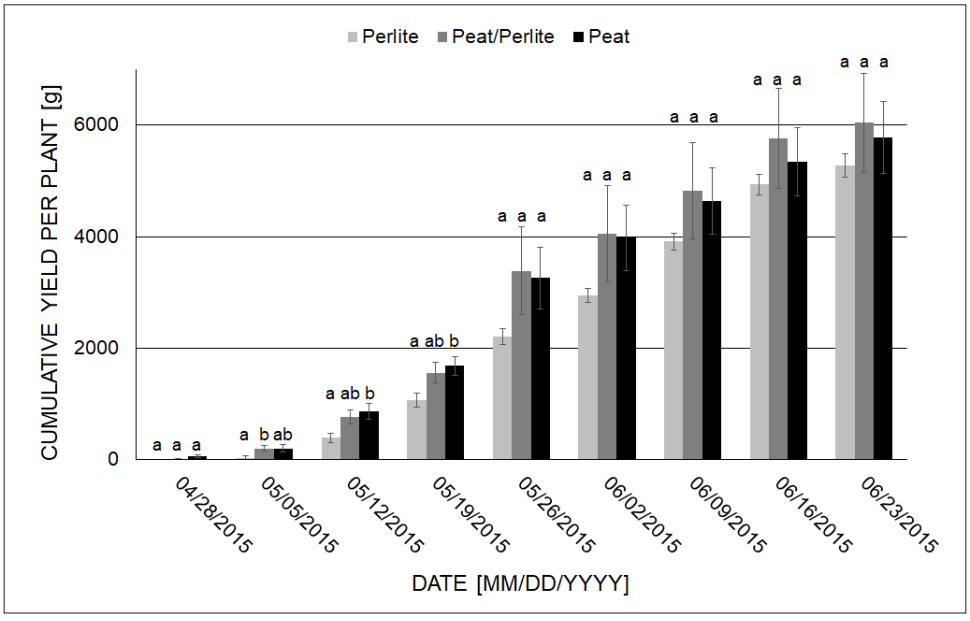


Figure 2. Cumulated marketable yield of plants as a result of seedling growth in different substrates (perlite = light grey, peat-perlite mix = grey, peat = black) for two weeks. Same letters indicate no significant differences among means of treatments (Tukey's test, $p > 0.05$, $n = 13$).

Table 3. Long-term effects of seedling growth substrates on leaf pigment concentrations and ratios.

Index	Treatment		
	Peat	Peat/Perlite	Perlite
	Reflectance indices		
NDVI	0.80 ± 0.06 [c]	0.75 ± 0.11 [b]	0.69 ± 0.10 [a]
Lichtenthaler's	2.09 ± 0.33 [b]	2.09 ± 0.63 [b]	1.75 ± 0.35 [a]
Car-ratio	0.67 ± 0.13 [a]	0.74 ± 0.13 [ab]	0.79 ± 0.11 [b]
Chlorophyll ratio	0.16 ± 0.04 [a]	0.20 ± 0.09 [a]	0.25 ± 0.08 [b]
SIPI	0.94 ± 0.02 [b]	0.92 ± 0.05 [a]	0.90 ± 0.04 [a]
PRI	0.14 ± 0.03 [b]	0.12 ± 0.03 [a]	0.11 ± 0.03 [a]

Same letters indicate no significant differences among means of treatments on the 8th of August (Tukey's test, $p > 0.05$, $n = 39$). ± standard deviation. Lichtenthaler's index (Lichtenthaler et al., 1996), Car-ratio (Zude and Kläring, 2009), chlorophyll ratio (Carter, 1994), structure insensitive pigment index (SIPI, Penuelas et al., 1995), photochemical reflectance index (PRI, Gamon et al., 1992) and normalized difference vegetation index (NDVI, Rouse et al., 1974).

tal conditions, genetic preconditions and thus physiological capability of the plant (Rakshit et al., 2015). In this context, the reallocation of nutrients should be considered, with increased NUE being achieved by reusing nutrients from older leaves to promote the growth of young leaves or harvestable organs (Chapin et al., 1990).

Among other definitions, Clark (1990) defines efficient compared to less efficient plants as producing higher yield under similar growing conditions, e.g., amount of applied nutrients. Minimizing the ratio of vegetative tissue to produced yield therefore could be one factor to reach this goal for tomato as shown in the present study. The physiological capability of tomato plants initially grown under deficit nutrition may condition the individuals to a more effective use of nutrients by a reduced growth of vegetative organs (Figure 2) related to the amount of harvested fruit (Table 2). However, this has to be proven in a distinct experiment with separated nutrient solutions for each treatment.

On the contrary, the fact of no differences in the amount of harvest depicts the redundancy of higher leaf area with higher chlorophyll concentrations and should be considered when it comes to optimal leaf area regarding tomato yield (Heuvelink et al., 2005). Decreased leaf area may result in increased light interception of the lower leaves, hence improving the plant productivity as shown for varying plant spacing in greenhouse tomatoes (Papadopoulos and Pararajasingham, 1997).

Optical properties of leaves and fruits

Comparing NDVI values of the different treatments, decreasing NDVI values with increasing content of perlite in the seedling growth substrates were found (Table 3). This means leaves of perlite grown plants contain a lower chlorophyll concentration than leaves from plants grown in the mixture. The highest concentration was found for leaves of soil-propagated plants. The NDVI has the disadvantage to do not show good correlations when plants contain medium and higher chlorophyll concentrations (Lichtenthaler et al., 1996). A more sensitive index at medium or higher chlorophyll concentrations is the index of Lichtenthaler. The decreased amplitude of Lichtenthaler's index indicates a lower chlorophyll concentration (Lichtenthaler et al., 1996) in the leaves of the plants initially grown in perlite. The chlorophyll concentration in the leaves is closely related to the nitrogen content in plants (Evans, 1983). As mentioned before, this impact of an initial malnutrition of the seedling did not align during the eleven weeks of homogeneous nutrition of the plants.

The chlorophyll ratio index responds to various stress agents, comparing stressed with relatively non-stressed leaves (Carter, 1994). In the present study, this index was increased in plants initially grown in perlite indicating slightly stressed plants in this treatment. Moran and Moran (1998) showed a relation of the mentioned index to nutrient stress in *Nepenthes rafflesiana*, whereby this possibly could be applicable to other species. This confirmed our assumption that the initial nutrient deficiency is identifiable after almost three months of homogeneous application of nutrients.

The car-ratio index was significantly lowered in the peat treatment towards the perlite treatment. The peat-perlite treatment ranked in the middle. Low oxygen in the root zone, as shown for citrus exposed to an anoxic environment in the root zone (Zude and Kläring, 2009), alters the carotenoid composition in the leaves. The xanthophyll cycle is sensitive to stress and as such stress is measurable (Penuelas et al., 1995), where the related carotenoids zeaxanthin, violaxanthin and antheraxantin change in their ratios to each other. Probably due to the results of the car-ratio index, the PRI should show similar results, since it allows a statement on the carotenoid composition as well. The PRI was designed to estimate the light use efficiency (LUE) by detecting changes in the xanthophyll cycle (Gamon and Surfus, 1999) since the composition of xanthophyll pigments rapidly change in response to environmental conditions. Surprisingly, PRI indicates a higher LUE in peat compared to other treatments. All treatments produced similar yields even though they differed in leaf area. Therefore, it was assumed that the smaller leaf area of the perlite-propagated plants increased the yield by higher LUE, but PRI did not confirm this.

Generally, the carotenoid to chlorophyll ratio increases with lower availability and thus lower uptake of nitrogen, resulting in decreased nitrogen content in the leaves. The structure insensitive pigment index (SIPI) increases with a lowered carotenoid to chlorophyll a ratio (Araus et al., 2001). The current data set indicates a decreased carotenoid to chlorophyll *a* ratio, pointing to lowered nitrogen content in the peat treatment. This is in contrast to the prior results and could be due to unsuitable chlorophyll *a* and carotenoid concentrations in the leaves, where the best fit of the carotenoid to chlorophyll *a* ratio and SIPI was found for chlorophyll at concentrations ranging from 0.06 to 54 µg cm^{-2} and for carotenoids from 1 to 16 µg cm^{-2} (Penuelas et al., 1995).

Table 4. Effects of different seedling growth substrates on pigment concentrations and ratios in fruits.

Index	Treatment		
	Peat	Peat/Perlite	Perlite
	Reflectance indices		
Car-ratio	1.01 ± 0.03 [a]	1.01 ± 0.02 [a]	0.99 ± 0.05 [a]
Chlorophyll ratio	1.06 ± 0.04 [a]	1.07 ± 0.03 [a]	1.06 ± 0.04 [a]
NAI	0.79 ± 0.01 [a]	0.79 ± 0.01 [a]	0.79 ± 0.01 [a]

Car-ratio (Zude and Kläring, 2009), chlorophyll ratio (Carter, 1994) and normalized anthocyanin index (NAI) (Farneti et al., 2012). Same letters indicate no significant differences among means of treatments on the 16th of August (Tukey's test, $p > 0.05$, $n = 39$). ± expresses standard deviation.

From these results it follows that phenotypic differences in stem diameter, leaf area and chlorophyll concentration found in the perlite treatment could not recover to the level of the other two treatments, although all plants were supplied with optimal nutrient concentrations after two weeks of seedling growth. This might be a result of a phenomenon found in literature called priming, which helps the plant to respond faster if the stress recurs. In our experiment the deficit nutrition during the first two weeks might have acted as an abiotic "stress imprint" (Bruce et al., 2007). Bruce et al. (2007) define a plant ''stress imprint'' as a genetic or biochemical modification of a plant that occurs after stress exposure, here nutrient limitation, that causes future responses to future stresses to be different.

Regarding the diffuse reflectance properties of the fruits no differences in the quality could be detected by spectral analysis (Table 4). The normalized anthocyanin index (NAI) was successfully tested as an indicator for the lycopene content by Farneti et al. (2012) and also did not reveal any differences in the lycopene concentration in between the three treatments. The distribution of assimilates between sinks is mainly controlled by the sinks themselves (Farrar, 1988; Gifford and Evans, 1981; Ho, 1988; Marcelis, 1996). Since the fruits form the largest sink in fruit crops like tomatoes, the fruits have the greatest influence on the partitioning of assimilates, i.e., biomass between fruits and vegetative plant parts (De Koning and De Ruiter, 1991; Hurd et al., 1979). During the initiation of fruit and fruit growth, all tomato plants in our experiment were subjected to an optimal nutrient supply regardless of their seedling growth substrate. Since no additional reduction of PRUE could be observed here, the influence of sink strength by the tomato fruits on photosynthesis and assimilate partitioning could be the same in all treatments, leading to similar yields and quality of fruits.

Conclusions

The present study showed that the use of peat as seedling growth substrates can lead to premature harvesting. However, it was further shown that perlite did not reduce the total yield and fruit pigmentation. The reduced stem diameter, leaf area and changed pigment composition in the leaves of the plants grown on perlite were most likely caused by the initial nutrient limitation in the seedling stage during seedling growth than by the seedling growth substrates. However, the importance of optimum nutrition seems to involve especially the seedling stage to exploit the whole genetic potential of the cultivar. Thus, the seedlings should be supplied with nutrient solution rather than tap water during seedling production.

To clarify the question if an initial deficit nutrition could lead to a tighter input output ratio regarding applied nutrients to yield, further efforts are necessary. To reveal possible differences in fruit quality, extended experiments have to be conducted.

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References

Araus, J.L., Casadesus, J., and Bort, J. (2001). Recent tools for the screening of physiological traits determining yield. In Application of Physiology in Wheat Breeding, M.P. Reynolds, J.I. Ortiz-Monasterio, and A. McNab, eds. (Mexico, D.F.: CIMMYT), p. 59–77.

Blume, H.P., Brümmer, G.W., Horn, R., Kandeler, E., Kögel-Knabner, I., Kretzschmar, R., Stahr, K., and Wilke, B.M. (2010). Scheffer/Schachtschabel: Lehrbuch der Bodenkunde (Berlin, Heidelberg: Springer-Verlag). https://doi.org/10.1007/978-3-662-49960-3.

Bruce, T.J.A., Matthes, M.C., Napier, J.A., and Pickett, J.A. (2007). Stressful "memories" of plants: Evidence and possible mechanisms. Plant Sci. *173*, 603–608. https://doi.org/10.1016/j.plantsci.2007.09.002.

Carter, G.A. (1994). Ratios of leaf reflectances in narrow wavebands as indicators of plant stress Int. J. Remote Sens. *15*, 697–703. https://doi.org/10.1080/01431169408954109.

Chapin, F.S., Schulze, E., and Mooney, H.A. (1990). The ecology and economics of storage in plants. Annu. Rev. Ecol. Evol. Syst. *21*, 423–447. https://doi.org/10.1146/annurev.es.21.110190.002231.

Chaves, M.M., Santos, T.P., Souza, C.R., Ortuño, M.F., Rodrigues, M.L., Lopes, C.M., Maroco, J.P., and Pereira, J.S. (2007). Deficit irrigation in grapevine improves water-use efficiency while controlling vigour and production quality. Ann. Appl. Biol. *150*, 237–252. https://doi.org/10.1111/j.1744-7348.2006.00123.x.

Clark, R.B. (1990). Physiology of cereals for mineral nutrient uptake, use and efficiency. In Crops as Enhancers of Nutrient Use, V.C. Baligar, and R.R. Duncan, eds. (San Diego, California: Academic Press), p. 131–209. https://doi.org/10.1016/B978-0-12-077125-7.50009-8.

Cui, N., Du, T., Kang, S., Li, F., Zhang, J., Wang, M., and Li, Z. (2008). Regulated deficit irrigation improved fruit quality and water use efficiency of pear-jujube trees. Agric. Water Manag. *95*, 489–497. https://doi.org/10.1016/j.agwat.2007.11.007.

Dannehl, D., Rocksch, T., and Schmidt, U. (2015). Modelling to estimate the specific leaf area of tomato leaves (cv. Pannovy). Acta Hortic. *1099*, 79–86. https://doi.org/10.17660/ActaHortic.2015.1099.5.

De Koning, A.N.M., and De Ruiter, H.W. (1991). Effect of temperature, plant density and fruit thinning on flower/fruit abortion and dry matter partitioning of tomato. In Annual Report 1990 (Naaldwijk, The Netherlands: Glasshouse Crops Research Station), pp. 29.

Evans, J.R. (1983). Nitrogen and photosynthesis in the flag leaf of wheat (*Triticum aestivum* L.). Plant Physiol. *72*, 297–302. https://doi.org/10.1104/pp.72.2.297.

Farneti, B., Schouten, R.E., and Woltering, E.J. (2012). Low temperature-induced lycopene degradation in red ripe tomato evaluated by remittance spectroscopy. Postharvest Biol. Technol. *73*, 22–27. https://doi.org/10.1016/j.postharvbio.2012.05.008.

Farrar, J.F. (1988). Temperature and the partitioning and translocation of carbon. Symp. Soc. Exp. Biol. *42*, 203–235.

Gamon, J.A., and Surfus, J.S. (1999). Assessing leaf pigment content and activity with a reflectometer. New Phytol. *143*, 105–117. https://doi.org/10.1046/j.1469-8137.1999.00424.x.

Gamon, J.A., Peñuelas, J., and Field, C.B. (1992). A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. Remote Sens. Environ. *41*, 35–44. https://doi.org/10.1016/0034-4257(92)90059-S.

Gifford, R.M., and Evans, L.T. (1981). Photosynthesis, carbon partitioning, and yield. Ann. Rev. Plant Physiol. *32*, 485–509. https://doi.org/10.1146/annurev.pp.32.060181.002413.

Göhler, F., and Molitor, H.D. (2002). Erdelose Kulturverfahren im Gartenbau (Stuttgart, Germany: Eugen Ulmer GmbH & Co.).

Heuvelink, E., Bakker, M.J., Elings, A., Kaarsemaker, R.C., and Marcelis, L.F.M. (2005). Effect of leaf area on tomato yield. Acta Hortic. *691*, 43–50. https://doi.org/10.17660/ActaHortic.2005.691.2.

Ho, L.C. (1988). Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. Ann. Rev. Plant Physiol. Plant Mol. Biol. *39*, 355–378. https://doi.org/10.1146/annurev.pp.39.060188.002035.

Ho, L.C., Andrews, J., Brown, M., Adams, P., and Belda, R. (1993). Uptake and transport of calcium and the possible causes of blossom-end rot in tomato. J. Exp. Bot. *44*, 509–518. https://doi.org/10.1093/jxb/44.2.509.

Hurd, R.G., Gay, A.P., and Mountifield, A.C. (1979). The effect of partial flower removal on the relation between root, shoot and fruit growth in the indeterminate tomato. Ann. Appl. Biol. *93*, 77–89. https://doi.org/10.1111/j.1744-7348.1979.tb04729.x.

Jayasinghe, G.Y., Arachchi, I.D.L., and Tokashiki, Y. (2010). Evaluation of containerized substrates developed from cattle manure compost and synthetic aggregates for ornamental plant production as a peat alternative. Resour. Conserv. Recycl. *54*, 1412–1418. https://doi.org/10.1016/j.resconrec.2010.06.002.

Kang, S., Shi, W., and Zhang, J. (2000). An improved water-use efficiency for maize grown under regulated deficit irrigation. Field Crops Res. *67*, 207–214. https://doi.org/10.1016/S0378-4290(00)00095-2.

Kantiranis, N., Filippidis, A., Vouta, S., Drakoulis, A., Koutles, T., and Tzamos, E. (2007). The cation exchange capacity of industrial minerals and rocks of Milos Island. Bull. Geol. Soc. Gr. *40*, 775–780. https://doi.org/10.12681/bgsg.16718.

Landis, T.D., Tinus, R.W., McDonald, S.E., and Barnett, J.P. (1990). Containers and growing media, Vol. 2. In Agriculture Handbook 674, The Container Tree Nursery Manual (Washington, DC: U.S. Department of Agriculture, Forest Service), p. 41–85.

Lichtenthaler, H.K., Gitelson, A., and Lang, M. (1996). Non-destructive determination of chlorophyll content of leaves of a green and an aurea mutant of tobacco by reflectance measurements. J. Plant Physiol. *148*, 483–493. https://doi.org/10.1016/S0176-1617(96)80283-5.

Marcelis, L.F.M. (1996). Sink strength as a determinant of dry matter partitioning in the whole plant. J. Exp. Bot. *47*, 1281–1291. https://doi.org/10.1093/jxb/47.Special_Issue.1281.

Moran, J.A., and Moran, A.J. (1998). Foliar reflectance and vector analysis reveal nutrient stress in prey-deprived pitcher plants (*Nepenthes rafflesiana*). Int. J. Plant Sci. *159*, 996–1001. https://doi.org/10.1086/314086.

Naegle, E.R., Burton, J.W., Carter, T.E., and Rufty, T.W. (2005). Influence of seed nitrogen content on seedling growth and recovery from nitrogen stress. Plant Soil *271*, 329–340. https://doi.org/10.1007/s11104-004-3242-4.

Ors, S., and Anapali, O. (2010). Effect of soil addition on physical properties of perlite based media and strawberry cv. Camarosa plant growth. Sci. Res. Essays *5*, 3430–3433.

Papadopoulos, A.P., and Pararajasingham, S. (1997). The influence of plant spacing on light interception and use in greenhouse tomato (*Lycopersicon esculentum* Mill.): A review. Sci. Hortic. *69*, 1–29. https://doi.org/10.1016/S0304-4238(96)00983-1.

Penuelas, J., Baret, F., and Filella, I. (1995). Semi-empirical indices to assess carotenoids/chlorophyll *a* ratio from leaf spectral reflectance. Photosynthetica *31*, 221–230.

Rakshit, A., Singh, H., and Sen, A. (2015). Nutrient Use Efficiency: from Basics to Advances (New Delhi, India: Springer India). https://doi.org/10.1007/978-81-322-2169-2.

Raviv, M., Chen, Y., and Inbar, Y. (1986). Peat and peat substitutes as growth media for container-grown plants. In The Role of Organic Matter in Modern Agriculture, Y. Chen, and Y. Avnimelech, eds. (Dordrecht: Springer Netherlands), p. 257–287. https://doi.org/10.1007/978-94-009-4426-8_11.

Resh, H.M. (2002). Hydroponic Tomatoes. For the Home Gardener (Boca Raton, USA: Taylor & Francis Group).

Tripepi, R.R. (2014). What Is Your Substrate Trying to Tell You – Part II (Moscow, USA: Plant Science Division).

Wilson, G.C.S. (1986). Tomato production in different growing media. Acta Hortic. *178*, 115–120. https://doi.org/10.17660/ActaHortic.1986.178.14.

Zaller, J.G. (2007). Vermicompost as a substitute for peat in potting media: Effects on germination, biomass allocation, yields and fruit quality of three tomato varieties. Sci. Hortic. *112*, 191–199. https://doi.org/10.1016/j.scienta.2006.12.023.

Zude, M., and Kläring, H.P. (2009). Two case studies of precision horticulture approaches in citrus production. Tree For. Sci. Biotechnol. *3*, 139–151.

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