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[1]Humboldt-Universität zu Berlin, Division Urban Plant Ecophysiology, Berlin, Germany
[2]Leibniz-Institute of Vegetable and Ornamental Crops Großbeeren/Erfurt e.V., Department Quality, Großbeeren, Germany

Survey of bioactive metabolites in selected cultivars and varieties of *Lactuca sativa* L. under water stress

Ines Eichholz[1], Nadja Förster[1], Christian Ulrichs[1], Monika Schreiner[2], Susanne Huyskens-Keil[1*]

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Summary

Plants respond to water stress with a variety of physiological and biochemical changes, but their response vary between species, varieties and cultivars. The present study focused on changes of bio-functional phytochemicals (phenolic compounds, chlorophyll, carotenoids, dietary fiber) in commercial cultivars and old, traditional varieties of lettuce under different water regimes (water-deficit, well-watered and water-logged).

Results revealed lettuce varieties and cultivars with a different response behavior to water stress. Biomass production under drought conditions was reduced significantly in old varieties ('Struwelpeter', 'Trianon'), but in contrast, it was only affected tendentiously in the commercial cultivars ('Wiske', 'Teodore'). Carotenoid and chlorophyll contents decreased in both water extremes, while total phenols accumulated under limited water availability, predominantly found in 'Teodore'. Dietary fiber content was not influenced by different water regimes in all lettuce cultivars and varieties. Water stress reduced biomass production and led to a change of phytochemicals in lettuce, however, old and traditional varieties did not show a different water stress adaptation compared to commercial cultivars.

Introduction

Changing climate conditions include altered rainfall patterns with increasing severity of droughts and floods (Sheffield and Wood, 2008). One of the consequences of climate change is an increase in extreme weather events worldwide, e.g. water stress (drought, waterlogging). Plants response to water stress conditions is accompanied by a variety of physiological and biochemical changes at cellular and whole-organism levels, thus making it a complex phenomenon (Shao et al., 2009). Drought stress disturbs water relation of plant and reduces leaf size, stem extension and root proliferation (Farooq et al., 2009; Shao et al., 2009). Though, the most important effects of drought stress in respect to plant growth are the impairment of cell expansion and inhibition of photosynthesis caused by increased stomatal resistance (Reddy et al., 2004). The main damage under waterlogging conditions is related to the oxygen deprivation of soils, which affects nutrient and water uptake of plants (Belford et al., 1980; Sairam et al., 2008). Plants primarily respond with hastened leaf senescence, reduced leaf area, and inhibited growth rates resulting in a decline of biomass (Promkhambut et al., 2010; Cannell et al., 2008; Zhou and Lin, 1995).

Plant compounds in lettuce (*Lactuca sativa* L.) being interesting for human diet are amongst others phenolic substances, carotenoids and dietary fiber (Schreiner and Huyskens-Keil, 2006). Water stress is known to influence biomass production as well as the composition and concentration of nutrient-providing and bio-functional plant compounds. Many studies confirmed the impact of water stress on plant compounds, as reported for carotenoids (Sabale and Kale, 2010; Loggini et al., 1999; Moran et al., 1994), phenolic compounds (Sabale and Kale, 2010; Sánchez-Rodríguez and Rubio-Wilhelmi, 2010; Alexieva et al., 2001), and dietary fibers (hemicellulose, cellulose and lignin) (Tobisa et al., 1997; Okuyama et al., 1995; Von Wilpert, 1991). While carotenoids and phenolic compounds act as protective plant compounds in plant defense mechanisms (Treutter, 2010), hemicellulose, cellulose, pectin and lignin function as essential compounds for plant cell wall metabolism thus, plant growth and textural stability. Furthermore, these cell wall polysaccharides as well as lignin are known to be the major components of dietary fibres (Waldron et al., 2003).

However, the impact of drought and waterlogging on plant metabolism is dependent on severity, time and duration of stress but also on the tolerance level of the respective plant species as well as on the cultivars or varieties (Reddy et al., 2004). Examining these genetically determined physiological differences may provide breeders with insight into how water stress tolerance of horticultural important species might be improved. Moreover, old cultivars and varieties may be a good source of breeding material and maintain the biodiversity of cultivated plants even under changing environmental conditions. An old variety is defined as a historical variety which was never before or is not any more officially licensed (Lehmann et al., 2009, Lissek-Wolf et al., 2009), whereas cultivars emerged from targeted breeding processes (Lissek-Wolf et al., 2009).

Recently, a pilot study was conducted in order to establish a collection of old *Lactuca* varieties suitable for commercial utilization in local market gardens as a tool to maintain on-farm cultivation (Lehmann et al., 2008). This study identified some attractive, old varieties for a "re-cultivation". Besides a huge range of different commercial cultivars, growers and consumers are gaining a growing interest in regional and traditional species and varieties as it is promoted by the campaign "Indigenous voice" of the international association Slow Food (Donati, 2005).

The present study focused on changes of phytochemical compounds (phenolic compounds, chlorophyll, carotenoids, and dietary fiber) of different lettuce cultivars and varieties, i.e. commercial and old origins influenced by water stress, i.e. drought stress and waterlogging conditions. Results contribute to a better understanding of the dynamics of bio-functional phytochemicals under different water stress regimes associated with climate change. Furthermore, this study may result in recommendations of appropriate cultivars and varieties for climate adaptation processes.

Material and methods

Chemicals

Gallic acid (3,4,5-Trihydroxybenzoic acid) was used as standard solution for the analysis of total phenols and was purchased from Sigma Aldrich, Germany. Folin-Ciocalteu's phenol reagent and other chemicals and reagents were obtained from Merck Chemicals Germany.

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[*] Corresponding author

Plant material

Seedlings of two commercial cultivars ('Wiske RZ', 'Teodore RZ'; seeds obtained from Ryk Zwaan, Netherlands) and three old varieties (Winter Altenburger, Struwelpeter, Trianon; seeds obtained from VERN e.V., Germany) (Tab. 1) were grown in 6 L pots filled with peat substrate ('Profisubstrat, Topfsubstrat mit Ton'; Gramoflor, Germany) for a period of 2 ½ months (sowing on 8th March 2010, harvest on 21st May 2010) under experimental greenhouse conditions. Three weeks before harvest, plants were exposed to different water regimes (water-deficit [WD], well-watered [WW], water-logged [WL]). Four replications per treatment with five plants per replication were selected randomly. During the time of treatment substrate of the water-logged treatment exhibited a soil moisture level of 61 - 70 %. Soil moisture of well-watered pots amounted up to 49 - 50 %, while water-deficit pots varied from 18 - 25 %. Used moisture levels have been selected and approved according to previous conducted experiments. The soil moisture level was measured gravimetrically for each pot at 3 days intervals and kept constant manual at the specific water regime level, respectively. Within the intervals pots of WL and WW variants were watered by drip irrigation (two times a day for WL, once a day for WW), while WD variant was watered manual. Tapwater was used for manual watering and for irrigation of the pots. No further fertilisation was conducted. Every week reference plants of each cultivar/variety were weighed in order to calculate the water supply for each water regime. Experiments were conducted as randomized block design.

Biomass

After harvest infected or damaged leaves were removed and the plant shoots were weighed in order to determine the total above-ground biomass. A total of 30 g of fresh material was dried at 105 °C for 24 h and dry matter content calculated as the ratio between leaf dry weight and fresh weight. Results were expressed in milligram per gram [mg g^{-1}].

Chemical analysis

For the determination of carotenoids samples of 40 g fresh material and for analysis of total phenols and dietary fiber samples of 200 g fresh material of each treatment and cultivar/variety were frozen immediately after harvest in liquid nitrogen and stored at -20 °C. While for carotenoid assay frozen material was thawed and used, for total phenol and dietary fiber analysis frozen samples were lyophilized for 48 h (ALPHA 1-4, Fa. Christ, Osterode am Harz, Germany), ground and stored in a vacuum desiccator.

Carotenoid and chlorophyll

Carotenoid (lutein, ß-carotene, lycopene) and chlorophyll assay was determined according to the method of GOODWIN (1980). Frozen samples were thawed, weighed and extracted in a solvent mixture of acetone and hexane (4/5; v/v). Samples were centrifuged for 10 min at 3000 rpm (Heraeus Christian Labofuge GL, Hanau, Germany). Supernatants were decanted and filtered (Macherey-Nagel, MN 260, Düren, Germany). This process was repeated twice. All lipophilic pigments in the hexane layer were collected and measured spectrophotometrically at 445 nm, 453 nm and 505 nm for lutein, ß-carotene and lycopene, respectively. Chlorophyll content was measured at a wavelength of 663 nm for chlorophyll a and 645 nm for chlorophyll b that were subsequently summarized. Results were expressed as microgram carotenoid compounds per gram dry matter [µg g^{-1} DM] and as milligram chlorophyll compounds per gram dry matter [mg g^{-1} DM].

Total phenolic content

For the determination of the Total Phenolic Content 0.5 g freeze-dried sample were extracted in 10 mL of the cooled solvent acetone/water/acetic acid (0.45/0.5/0.05; v/v/v) according to the method of EHLENFELDT and PRIOR (2001). The samples were diluted in 3 mL solvent, and centrifuged for 10 min at 3000 rpm (Heraeus Christian

Tab. 1: Description of the studied lettuce cultivars and varieties

Cultivar/Variety		**Description**
Wiske	butterhead lettuce *(Lactuca sativa var. capitata)*	Quick filling short day variety Medium-thick leaves and nice bottom High tolerance against tipburn and glassiness (RZ seed and services, Ryk Zwaan)
Teodore	butterhead lettuce *(Lactuca sativa var. capitata)*	Red winter butterhead Grow well in a cold greenhouse Larger framed lettuce with medium thick leaves (RZ seed and services, Ryk Zwaan)
Winter Altenburger*	butterhead lettuce *(Lactuca sativa var. capitata)*	Small, rather dense butterhead lettuce, blond-green colour with slightly pink-sprinkled head surface (LISSEK-WOLF et al., 2009)
Struwelpeter*	leaf lettuce *(Lactuca sativa var. crispa)*	Strong-green leaf lettuce, deep gashed and lobate leaves similar to oak leaf lettuce, large and open heads with compact leaves (LISSEK-WOLF et al., 2009)
Trianon*	romain lettuce *(Lactuca sativa var. longifolia)*	Green romain lettuce, outer leaves are slightly off and are smaller than the following, which are half-upright; funnel-shaped to upright; leaves are slightly bubbly, a few large flat bubbles, distinct and juicy midrib (LISSEK-WOLF et al., 2009)

* old, traditional varieties

Labofuge GL, Hanau, Germany). Supernatants were decanted and filtered (Macherey-Nagel, MN 260, Düren, Germany). This process was repeated twice. Extracts were filled up to a 10 mL volume and stored at -20 °C until further analysis.

Total Phenolic Content was analyzed spectrophotometrically (SP8-300, Pye Unicam, OK, USA) according to the Folin-Ciocalteu procedure (SLINKARD and SINGLETON, 1977). Absorbance was measured at a wavelength of 765 nm. Gallic acid served as a standard. Results were expressed as milligram gallic acid per dry matter [mg GAE g^{-1} DM].

Dietary Fiber

Cellulose and Lignin was analysed according to the methods of GOERING and VAN SOEST (1972) and AOAC (1999). One gram freeze-dried sample was extracted with 100 mL Acid Detergent Fibre (ADF) reagent (N-Cetyl-N, N,N-trimethyl-ammoniumbromid dissolved with 96 % H_2SO_4) using a Fibertec System (M 1020, Tecator, Sweden). Thereafter, the solution was vacuum-filtered, washed with boiled, double distilled water until removal of the acidity and again washed with 90 % acetone. The residue was dried at 105 °C for 24 h, weighed, ash-dried at 500 °C for 24 h and weighed again to calculate ADF. The dried ADF residue was used for Acid Detergent Lignin (ADL) determination. Cellulose content was calculated as the difference between ADF and ADL. The content of lignin and cellulose, respectively, were expressed as milligram compounds per gram dry matter [mg g^{-1} DM].

With the Neutral Detergent Fiber (NDL) approach (VAN SOEST and GOERING, 1963) one gram of freeze-dried material was cooked in 100 mL of NDL mixture (Titriplex III, di-sodium borate, dodecylhydrogensulfate-Na, ethylene-glycol-monoethylester) to determine the hemicellulosic cell wall fraction. Afterwards, the solution was vacuum-filtered, washed with demineralized water and with 90 % acetone. The insoluble residue was dried at 105 °C for 24 h, weighed, ash-dried at 500 °C for 24 h and weighed again to calculate NDF. The hemicellulose content was obtained as the difference between NDF and ADF and given as milligram per gram dry matter [mg g^{-1} DM]. Contents of cellulose, hemicellulose and lignin were summarized as dietary fiber. Results were expressed as milligram per gram dry matter [mg g^{-1}DM].

Statistics

The statistical evaluation was performed using SPSS 13.0 (SPSS Inc., Chicago, USA 2001). Significance of differences was conducted with Tukey-B test ($p \leq 0.05$) or in case of inhomogeneity of variances with Dunnett´s T3 test ($p \leq 0.05$).

Results and Discussion

Biomass

Struwelpeter was the variety revealing the highest biomass production in all water treatments compared to the other cultivars and varieties (Fig. 1). However, both of the two old varieties 'Struwelpeter' and 'Trianon' revealed significantly reduced biomass in the water-deficit treatment compared to well-watered and water-logged plants. Under water-deficit conditions biomass was reduced by 39 % for 'Struwelpeter' and by 30 % for 'Trianon' compared to the well-watered regime. This impact of the different water regimes was also observed in the old variety 'Winter Altenburger', however only tendentiously. Comparing water-deficit and water-logged treatments, 'Struwelpeter' and 'Trianon' revealed significant higher biomass under waterlogging conditions (+ 58 %; + 61 %, respectively), but no distinct differences were found between the well-watered and the water-logged treatment. However, most of the cultivars and varieties tended to a depletion of biomass production and thus, yield in respect to waterlogging.

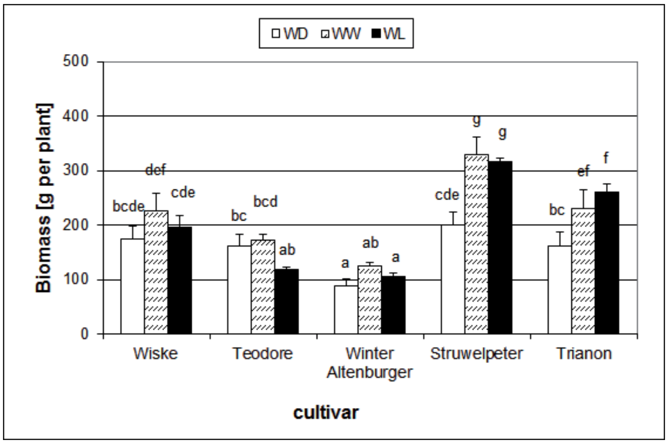

Fig. 1: Biomass [g per plant] of different cultivars and varieties of *Lactuca sativa* spp. grown under different water regimes (water-deficit = 18-25 % [WD], well-watered = 50 % [WW], water-logged = 61-70 % [WL]). Data represent n ± SD. Bars with different letters were significantly different (Tukey-B test, $p \leq 0.05$).

Ongoing drought affects the growing of roots and shoots (PASSIOURA, 1983). Here, closing of stomata inhibits the respiration and photosynthesis rate, and therefore, the formation of biomass (NAYYAR and GUPTA, 2006; ALEXIEVA et al., 2001) as also found in the two old lettuce varieties 'Struwelpeter' and 'Trianon'. Furthermore, inevitable consequence of drought is oxidative stress (MORAN et al., 1994) leading to activation of plant defense systems (LOGGINI et al., 1999). Oxidative stress causes DNA damage, membrane damage, lipid peroxidation etc. (MITTLER, 2002). In order to protect the plant from oxidative damage substantial amount of energy and substances, e.g. secondary metabolites such as carotenoids and phenolic compounds has to be procured for plant defense and are therefore in lack for biomass production under drought stress.

Many studies have proven that waterlogging has a reducing impact on crop yields, e.g. in *Triticum aestivum* (KELES and ÖNCEL, 2002), *Trifolium pratense* and *Trifolium repens* (SIMOVA-STOILOVA et al., 2011), *Vigna sinensis* and *Zea mays* (NEMAT ALLA et al., 2002) and others. Water logging also leads to an imbalance of nutrient uptake. While several minerals were depressed in their concentration e.g. nitrogen, phosphorus, potassium (BELFORD et al., 1980), others were enhanced up to toxic concentration (SHABALA, 2010). Such conditions facilitate the activation of oxygen, and therefore, oxidative stress. While most of studies examined severe water excess conditions, waterlogging (up to 70 % soil moisture) in this study we suppose that used experimental conditions did not lead to a permanent soil oxygen deprivation. This may implicate moderate stress in respect to waterlogging and did not influence biomass production of lettuce significantly.

Dry matter content of plants differed depending on lettuce variety and cultivar as well as on the water treatment (Fig. 2). The cultivar Wiske revealed the lowest dry matter content compared to the other cultivars and varieties. Furthermore, under water-deficit regime almost all cultivars and varieties exhibited the highest contents of dry matter compared to the well-watered as well as the water-logged plants. Here, except 'Wiske' all cultivars and varieties revealed higher dry mass contents, thus reduced water contents, highest for 'Teodore' (+ 44 %), followed by 'Trianon' (+ 31 %), 'Struwelpeter' (+ 28 %) and 'Winter Altenburger' (+ 22 %). No significant differences were found between well-watered and water-logged treat-

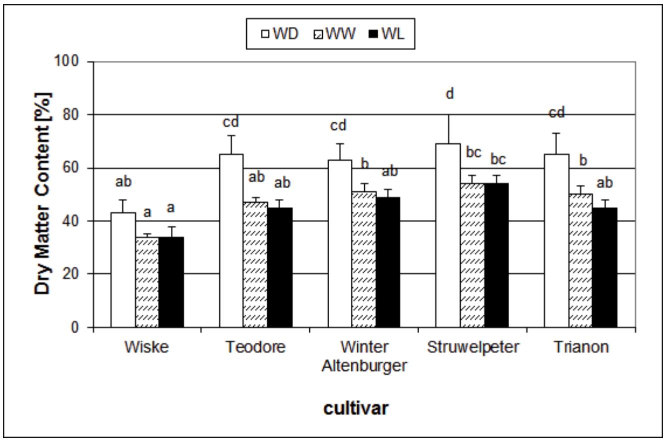

Fig. 2: Dry matter content [%] of different cultivars and varieties of *Lactuca sativa* spp. grown under different water regimes (water-deficit = 18-25 % [WD], well-watered = 50 % [WW], water-logged = 61-70 % [WL]). Data represent n ± SD. Bars with different letters were significantly different (Tukey-B test, p ≤ 0.05).

ments. Comparing water-deficit and water-logged treatments all cultivars and varieties, except ‘Wiske’, revealed lower dry matter contents and thus also a reduced water content under waterlogging conditions.

Changing sink-source relations due to drought seems to have affected the dry matter content of leaves. Increasing content of dry matter is explained by higher accumulation of assimilates (MARSCHNER, 1995) that are necessary for maintenance of plant metabolism or rather activation of stress response system (ROITSCH, 1999). In this case, leaves are not only source but also sink organs (ROITSCH, 1999). Thus, assumingly carbohydrates might have been accumulated under drought stress conditions, e.g. sucrose and sugar alcohols (SIRCELJ et al., 2005), being also osmoprotectants that protect plants from extreme oxidative stress (RONTEIN et al., 2002).

Waterlogging conditions reduce dry matter production (KUMUTHA et al., 2009) and increase fresh weight of plants (NEMAT ALLA et al., 2002). However, severe water excess leads to a reduced relative water content in leaves and subsequent wilting due to inhibition of respiration and loss of ATP synthesis in the roots (SAIRAM et al., 2008). An interference of respiratory processes and breakdown of carbohydrates are common symptoms of waterlogging stress (SUBBAIAH and SACHS, 2003; DAS et al., 2000; ZENG et al., 1999) which assumingly influenced the dry matter contents of lettuce leaves.

Carotenoid and Chlorophyll

The analysis of carotenoids revealed contents of 345 - 666 µg g^{-1} DM for ß-carotene, 370 - 686 µg g^{-1} DM for lutein and 32 - 59 µg g^{-1} DM for lycopene (Tab. 2). Chlorophyll content ranged from 4.0 - 7.6 mg g^{-1} DM (Fig. 3). Results supports findings by MOU (2005), NICOLLE et al. (2004) and THOMAS and GAUSMAN (1977).

‘Struwelpeter’ and ‘Teodore’ grown under optimum well-watered conditions revealed the highest amounts of carotenoids (lutein, ß-carotene, lycopene) and chlorophyll compared to other cultivars and varieties. However, only for ‘Teodore’ significant differences between the different water regimes were obtained. Here, the water-deficit treatment exhibited lower contents of lutein (- 41 %), ß-carotene (- 43 %), lycopene (- 38 %), and chlorophyll (- 47 %) compared to the well-watered treatment. Carotenoid and chlorophyll contents did not differ between water-deficit and water-logged plants. Nonetheless, ‘Teodore’ exhibit significant lower contents of ß-carotene under waterlogging conditions compared to the well-watered treatment (- 27 %).

Drought conditions caused a change in the biosynthesis of plant pigments especially of chlorophylls and carotenoids (FAROOQ et al., 2008; ANJUM et al., 2003). It is also known that photosynthesis of higher plants is reduced with decreasing leaf water potential (REDDY et al., 2004; ZLATEV and YORDANOV, 2004; VAN HOLSTEIJN et al., 1977) and associated with low contents of chlorophyll pigments (MAFAKHERI et al., 2010; ARUNYANARK et al., 2008). The latter finding was confirmed by results of the present study where plants of the cultivar Teodore grown under water-deficit conditions revealed significantly lower chlorophyll a and b concentrations compared to the other water regimes (data not shown). Decompensation of chlorophyll is also induced by free radicals due to oxidative stress (REDDY

Analysis	Cultivar/Variety	Water Capacity of Substrate		
		water-deficit [WD]	well-watered [WW]	water-logged [WL]
Lutein [µg g^{-1} DM]	Wiske	440,4 ± 58,9 ab	374,4 ± 4,9 a	370,2 ± 42,7 a
	Teodore	405,6 ± 4,2 a	686,2 ± 125,9 c	518,7 ± 95,6 abc
	Winter Altenburger	466,5 ± 42,6 ab	417,9 ± 73,8 a	473,2 ± 123,7 ab
	Struwelpeter	649,1 ± 58,2 bc	654,6 ± 75,2 bc	651,5 ± 153,8 bc
	Trianon	395,6 ± 26,2 a	445,8 ± 26,1 ab	400,9 ± 37,1 a
ß-Caroten [µg g^{-1} DM]	Wiske	412,7 ± 40,0 a	359,9 ± 5,2 a	344,8 ± 30,9 a
	Teodore	381,0 ± 0,9 a	665,7 ± 122,6 c	488,0 ± 100,3 ab
	Winter Altenburger	452,6 ± 34,2 ab	404,4 ± 74,0 a	388,0 ± 50,3 a
	Struwelpeter	624,2 ± 60,7 bc	625,8 ± 69,9 bc	627,5 ± 135,9 bc
	Trianon	382,5 ± 31,5 a	423,0 ± 23,3 a	382,1 ± 34,6 a
Lycopene [µg g$^{-1\,\mathrm{DM}}$]	Wiske	42,7 ± 2,2 abc	31,3 ± 1,9 a	31,6 ± 3,0 a
	Teodore	30,4 ± 2,6 a	48,9 ± 10,6 cd	38,8 ± 7,3 abc
	Winter Altenburger	34,5 ± 1,9 a	38,6 ± 2,1 abc	32,3 ± 1,5 a
	Struwelpeter	47,3 ± 2,8 bcd	59,3 ± 10,7 d	57,5 ± 3,2 d
	Trianon	33,3 ± 1,9 a	39,2 ± 1,5 abc	35,3 ± 3,5 ab

Tab. 2: Lutein, ß-carotene, lycopene [µg g^{-1} DM] of different cultivars and varieties of *Lactuca sativa* spp. grown under different water regimes (water-deficit = 18-25 % [WD], well-watered = 50 % [WW], water-logged = 61-70 % [WL]). Data represent n ± SD. Different letters in columns and rows indicate significant differences (Dunett’s T3 test, p ≤ 0.05).

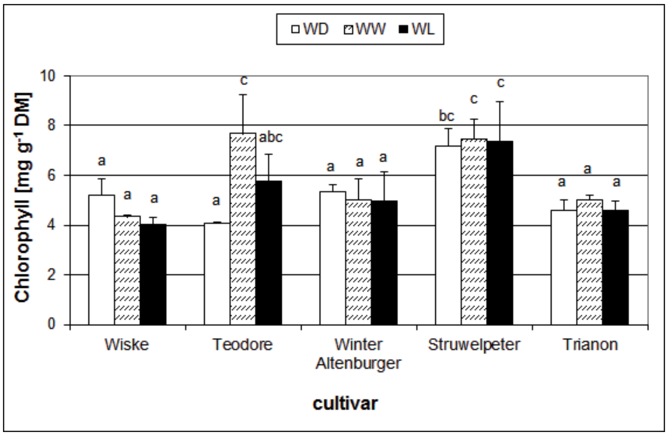

Fig. 3: Chlorophyll content [mg g^{-1} DM] of different cultivars and varieties of *Lactuca sativa* spp. grown under different water regimes (water-deficit = 18-25 % [WD], well-watered = 50 % [WW], water-logged = 61-70 % [WL]). Data represent n ± SD. Bars with different letters were significantly different (Dunett's T3 test, $p \leq 0.05$).

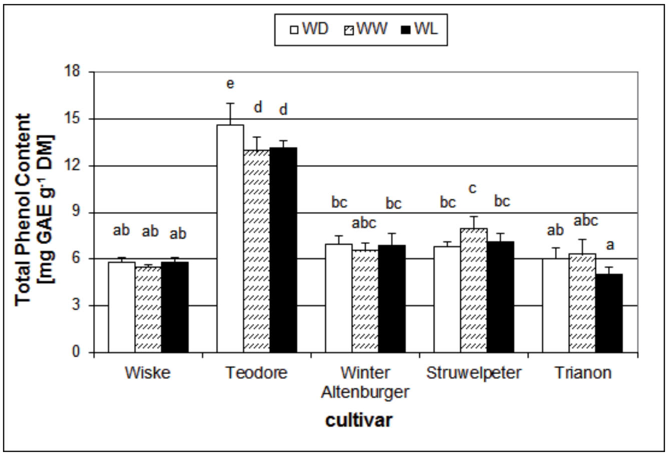

Fig. 4: Total Phenol Content [mg GAE g^{-1} DM] of different cultivars and varieties of *Lactuca sativa* spp. grown under different water regimes (water-deficit = 18-25 % [WD], well-watered = 50 % [WW], water-logged = 61-70 % [WL]). Data represent n ± SD. Bars with different letters were significantly different (Tukey-B test, $p \leq 0.05$).

et al., 2004; FU and HUANG, 2001). Although carotenoids protect chlorophyll from oxidative damage as reported by SIEFERMAN-HARMS (1987) and FOYER et al. (1994), they are highly susceptible to oxidative destruction (JALEEL et al., 2009). Drought stress leads to a degradation or re-organisation of carotenoid compounds, e.g. lutein, ß-carotene and neoxanthin (LOGGINI et al., 1999; MORAN et al., 1994), in particular, if stress is based on the production of free radicals in the thylakoids (JALEEL et al., 2009; REDDY et al., 2004). Moreover, REDDY et al. (2004) and LOGGINI et al. (1999) reported an increase in the pool of de-epoxidized xanthophyll-cycle components (i.e. zeaxanthin and antheraxanthin). A complex relationship between xanthophyll cycle-dependent energy quenching and formation of active oxygen species (AOS) exists in photosynthetic systems of plants under drought stress (REDDY et al., 2004).

Waterlogging has been reported to reduce photosynthetic rate (ZHOU and LIN, 1995; YUEHUA, 1987), chlorophyll (KUMUTHA et al., 2009; ZHOU and LIN, 1995) and also carotenoid contents in plants (PENG, 2012; SABALE and KALE, 2010; GU et al., 2009). According to DAS et al. (2000) carotenoids appeared less vulnerable to water excess than chlorophyll pigments. However, with the prolonging of waterlogging conditions their reduction also seems to be unavoidable, which is consistent with studies by GU et al. (2009). Similar to drought, oxidative stress in photosynthetic tissue might result in the decomposition of carotenoids, which was found in the present study on the commercial lettuce cultivar Teodore in the water-logged treatment.

Total phenol compounds

The content of total phenols in *Lactuca sativa* spp. ranged from 5.0 - 14.6 mg GAE g^{-1} DM (Fig. 4), which is consistent with findings by CHU et al. (2002) and VINSON et al. (1998). Cultivars and varieties and water treatments exhibited significant differences. The highest content of phenolic compounds was determined for the cultivar Teodore. Moreover, 'Teodore' grown under the different water regimes revealed contents of total phenol which almost doubled that of the other cultivars and varieties. Thus, 'Teodore' was the only cultivar with a considerable response towards the different water regimes. Plants grown under water-deficit conditions revealed higher contents of phenolic compounds (+ 11 %) than plants of the well-watered as well as of the water-logged regime. No significant differences were found between well-watered and water-logged plants.

In response to stress, plants activate the defense system, like the enzymatic and non-enzymatic antioxidants. Besides numerous enzymes (superoxid dismuthase, peroxidase etc.), phenolic compounds are strong antioxidants that help plants to survive stress conditions (MITTLER, 2002). Antioxidant compounds such as phenolic compounds are able to prevent oxidative burst of plant cells and thus protect plants from damage of proteins and lipids, DNA and RNA structures (APEL and HIRT, 2004). In the present study, the commercial cultivar Teodore revealed higher contents of total phenols under water-deficit conditions. The promotion of the synthesis of phenolic compounds due to drought was already documented in numerous studies (SÁNCHEZ-RODRÍGUEZ and RUBIO-WILHELMI, 2010; ALEXIEVA et al., 2001; ESTEBAN et al., 2001; AYAZ et al., 2000), also for lettuce (OH et al., 2010; OH et al., 2009).

Waterlogging conditions did not lead to an accelerated synthesis of phenolic compounds in the lettuce cultivars and varieties studied. This might have been related to the intensity of stress applied and/or also to the composition of phenolic substances analysed. In general, water excess is known to induce the accumulation of phenolic compounds acting as strong antioxidants (NACIF DE ABREU and MAZZAFERA, 2005; NEMAT ALLA et al., 2002). SABALE and KALE (2010) reported for *Coriandrum sativum* a decline of flavonoids being caused by water excess, while contents of anthocyanins were enhanced. One of the main phenolic compounds in lettuce is quercetin (GARCIA-MACIAS et al., 2007; DUPONT et al., 2000), which was probably not affected by waterlogging, as also reported for the medical herb *Hypericum brasiliense* by NACIF DE ABREU and MAZZAFERA (2005). As consequence of waterlogging conditions high levels of lipid oxidation and the accumulation of antioxidative enzymes, i.e. superoxide dismutase (SOD), catalase (CAT) as well as peroxidases (POD) were reported (KUMUTHA et al., 2009; ZHANG et al., 2007; ZHOU and LIN, 1995).

Dietary Fiber

Dietary fiber content of lettuce ranged between 130 and 170 mg g^{-1} DM (Fig. 5). It consisted of mainly cellulose, which constitutes the highest fraction with nearly 80 % compared to hemicellulose and lignin with 10 %, respectively. No significant differences were found for lignin. For hemicellulose tendentially higher contents were determined in drought stressed plants compared to water-logged

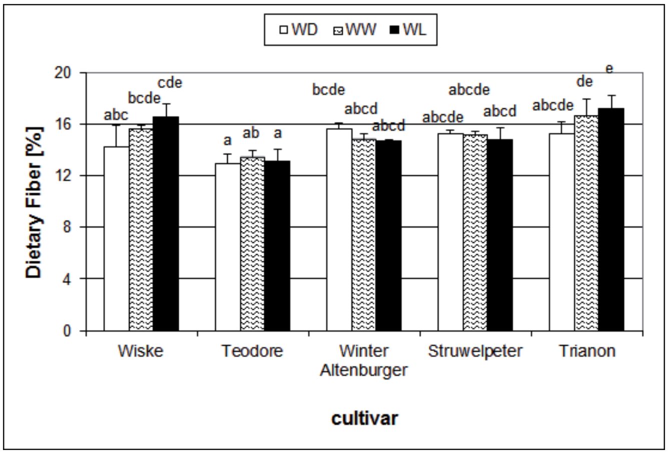

Fig. 5: Dietary Fiber [%] of different cultivars and varieties of *Lactuca sativa* spp. grown under different water regimes (water-deficit = 18-25 % [WD], well-watered = 50 % [WW], water-logged = 61-70 % [WL]). Data represent n ± SD. Bars with different letters were significantly different (Dunett's T3 test, $p \leq 0.05$).

plants in the varieties and cultivars Winter Altenburger, Struwelpeter and Trianon (Tab. 3). Cellulose exhibited contrary results. Here, plants grown under water-deficient conditions tended to lower contents than under water-logged treatment, specifically for 'Wiske' and 'Trianon'. Nevertheless, comparing the different water regimes no differences were found in the dietary fiber content (as sum of hemicellulose, cellulose, and lignin) (Fig. 5). However, cultivars/varieties differed in their content of dietary fibers. At optimal water conditions, 'Teodore' revealed the lowest dietary fiber content compared to 'Wiske' and 'Trianon'.

In general, drought stress leads to cell wall strengthening, which is accompanied by several complex processes, such as linking phenolic components to the cell wall matrix or lignification processes (Moura et al., 2010). However, lignification can differ in plant organs under drought stress conditions. While in roots, an enhanced lignin content were reported (Fan et al., 2006), the lignin content in young leaves of *Zea mays* subjected to water stress was lower than in the well-watered plants (Vincent et al., 2005). Sugar components as precursors of cell wall components are also necessary for the biomass production and the accumulation of defense compounds in plants. Under drought stress a decreased photosynthesis may inhibit the production of sugar components in sufficient quantity. However, an increase of carbohydrates (mainly mono- and disaccharides) during drought stress was reported (Sircelj et al., 2005). This accumulation is achieved for example by inhibiting the cellulose synthase, an enzyme that is involved in the synthesis of cellulose (Narciso et al., 2010; Zhu et al., 2010). Therefore, a lower proportion of cellulose under drought stress has been expected. In contrast, hemicellulose contents increased under drought stress. Due to their water-storing properties within the cell wall, hemicellulose contributes to drought tolerance in plants. Further, a change in hemicellulose content constitutes a direct control of the rate of expansion of plant cells under drought (Iraki et al., 1989).

Under waterlogging conditions, photosynthetic rate and sugar accumulation in leaves decreases. An influence on dietary fiber contents, also being a product of sugar molecules, could be expected. However, most of the studies investigated changes of lignin, hemicellulose and cellulose in the subterranean plant organ root, which is directly affected by water excess (Tobisa et al., 1997; Galamay et al., 1992). Tobisa et al. (1997) found lower contents of lignin and hemicellulose in roots of the legume *Aeschynomene americana* by waterlogging. Further, a higher content of lignin and cellulose in the plant top was determined. However, above biomass of *A. americana* consists of shoots, leaves and fruits with seed, while lettuce mostly forms only leaves until harvest. Dietary fiber content of leaves is not affected by waterlogging in contrast to the results obtained in the present study on lettuce.

Conclusion

Depending on the sensitivity to water stress of the respective variety and cultivar, drought led to reduced biomass production, which is one key factor for producers. Water stress partly affected bioactive compounds negatively, e.g. carotenoids, possibly being a decision factor for consumers. However, in the present study on different

Analysis	Cultivar/Variety	Water Capacity of Substrate		
		water-deficit [WD]	well-watered [WW]	water-logged [WL]
Hemicellulose [mg g^{-1} DM]	Wiske	13,3 ± 9,5 abc	16,6 ± 3,6 abc	11,1 ± 10,0 abc
	Teodore	10,1 ± 3,7 abc	10,7 ± 4,8 abc	2,5 ± 3,8 a
	Winter Altenburger	25,5 ± 7,2 c	24,3 ± 4,0 c	11,1 ± 9,0 abc
	Struwelpeter	17,9 ± 5,5 bc	16,2 ± 1,3 abc	15,9 ± 2,8 abc
	Trianon	16,5 ± 3,1 abc	6,2 ± 3,9 ab	10,3 ± 6,8 abc
Cellulose [mg g^{-1} DM]	Wiske	115,4 ± 20,2 ab	126,1 ± 6,4 abc	137,3 ± 13,8 bc
	Teodore	107,5 ± 2,3 a	108,3 ± 1,8 a	111,9 ± 5,2 ab
	Winter Altenburger	118,2 ± 4,8 ab	109,0 ± 7,1 a	119,3 ± 17,0 ab
	Struwelpeter	108,2 ± 2,1 a	116,0 ± 8,3 ab	117,0 ± 7,0 ab
	Trianon	124,5 ± 2,4 abc	148,0 ± 7,4 c	147,5 ± 6,1 c
Lignin [mg g^{-1} DM]	Wiske	16,5 ± 4,1 a	17,1 ± 1,8 a	17,1 ± 1,1 a
	Teodore	15,4 ± 4,0 a	15,5 ± 2,5 a	16,7 ± 1,6 a
	Winter Altenburger	12,9 ± 1,2 a	14,9 ± 2,0 a	20,4 ± 8,6 a
	Struwelpeter	16,4 ± 2,8 a	20,2 ± 6,7 a	20,0 ± 6,8 a
	Trianon	14,6 ± 1,8 a	15,2 ± 0,8 a	14,1 ± 0,2 a

Tab. 3: Hemicellulose, cellulose, lignin [mg g^{-1} DM] of different cultivars and varieties of *Lactuca sativa* spp. grown under different water regimes (water-deficit = 18-25 % [WD], well-watered = 50 % [WW], water-logged = 61-70 % [WL]). Data represent n ± SD. Column and rows with different letters were significantly different (Dunett's T3 test, $p \leq 0.05$).

lettuce cultivars and varieties drought stress increased the content of phenolic compounds, but did not influence dietary fiber contents, both are known to have biofunctional properties. At waterlogging conditions neither phenolic compounds nor dietary fiber were influenced in their contents.

Lettuce cultivars and varieties revealed different response behaviour to water stress (drought and waterlogging). In respect to biomass production, the old variety Struwelpeter exhibited the highest biomass production compared to other cultivars and varieties when growing under drought as well as waterlogging conditions, although this variety also showed the greatest loss in biomass production under drought conditions. Furthermore, 'Struwelpeter' comprised the highest carotenoid content, even under both stress conditions. On the other hand, the modern cultivar Teodore exhibited the highest content of total phenolic compounds, mainly under drought stress and here, also the least loss in biomass production, possibly indicating a valuable plant defense mechanism to water deficit conditions. The presented results lead to the conclusion that old and traditional varieties such as 'Struwelpeter' did not show a different adaptation mechanism to water stress conditions in comparison to commercial cultivars, i.e. 'Teodore'. Nevertheless, old varieties exhibit a high potential to evaluate adaptation processes in a changing climate environment, and in addition they contribute to the promotion of agrobiodiversity.

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Address of the authors:
Dr. Ines Eichholz, Dr. Nadja Förster, Prof. Dr. Dr. Christian Ulrichs, Dr. Susanne Huyskens-Keil (Corresponding author), Division Urban Plant Ecophysiology, Humboldt-Universität zu Berlin, Lentzeallee 55/57, 14195 Berlin, Germany.
E-mail: susanne.huyskens@agrar.hu-berlin.de
Prof. Dr. Monika Schreiner, Department Quality, Leibniz-Institute of Vegetable and Ornamental Crops Großbeeren/Erfurt e.V., Theodor-Echtermeyer-Weg 1, 14979 Großbeeren, Germany.