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Sweet Potato [*Ipomoea batatas* (L.) Lam.] Cultivated as Tuber or Leafy Vegetable Supplier As Affected by Elevated Tropospheric Ozone

NORBERT KEUTGEN,*,† ANNA J. KEUTGEN,§ AND MARC J. J. JANSSENS†

Institute of Crop Science and Resource Conservation (INRES), Unit Tropical Crops, University of Bonn, Auf dem Hügel 6, D-53121 Bonn, Germany, and Department of Crop Sciences, Division Quality of Plant Products, University of Göttingen, Carl-Sprengel Weg 1, 37075 Göttingen, Germany

Sweet potato cultivars respond differently to elevated tropospheric ozone concentrations of ca. 130 μg m^{-3}, 8 h a day for 4 weeks, which affects their selection for cultivation. In the first cultivar presented here, an adequate leafy vegetable supplier, the ozone load resulted in a shift of biomass to maintain the canopy at the expense of tuber development. Starch content of leaves was reduced, indicating an impairment of quality, but carotenoid content remained stable. The second cultivar may be grown for tuber production. Although the ratio tuber/plant remained stable under ozone, tuber yield and its starch content were significantly reduced. The lower starch content indicated a worse quality for certain industrial processing, but it is desirable for chip production. Elevated tropospheric ozone concentrations also influenced free amino acids and macronutrient contents of tubers, but these modifications were of minor significance for tuber quality in the second cultivar.

KEYWORDS: ***Ipomoea batatas*; ozone; product quality; growth behavior**

INTRODUCTION

Although ozone is considered an air pollutant of regional distribution, it represents one of the important threats to vegetation and crop production (*1*). In industrial countries its concentration varies between 60 and 130 μg m^{-3}, with peak episodes from 200 to 400 μg m^{-3} (*2*). However, little research has been conducted on the influence of ambient ozone concentrations on sweet potato [*Ipomoea batatas* (L.) Lam; Convolvulaceae)], possibly because it is regarded as a less ozone-sensitive species (*3, 4*). Nevertheless, sweet potato is a unique plant, because not only can the tuber be used as a source of food, feed, and processed products, but also the leaves, including the petioles, can be used as a leafy vegetable (*5*). Sweet potato is widely grown in tropical, subtropical, and warm temperate regions in 111 countries, 90% of which are classified as "developing countries". It ranks as the seventh most important food crop after wheat, rice, maize, potatoes, barley, and cassava and, in comparison with potato, is considered to be nutritionally more valuable because of its higher levels of carbohydrates, dietary fiber, and antioxidants (*6–8*).

Elevated tropospheric concentrations of ozone can affect plants in two different ways: The oxidative gaseous pollutant can impair leaf photosynthesis, for example, by reducing chlorophyll content, and it may induce accelerated leaf aging due to an enhanced production of the phytohormone ethylene (*9*). An indirect effect of ozone is its limitation of carbohydrate supply to the root and tuber system, because of an impaired photosynthesis and investment of carbohydrates in the antioxidative defense system and in leaf growth to compensate for the primary ozone damage (*10*). Different strategies of sweet potato cultivars to compensate for elevated ozone stress levels may thus result in different effects on the harvested compounds, either the leaves or the tubers, depending on the investment of carbohydrates primarily in leaf growth to compensate for ozone damage or in tuber growth to resist unfavorable conditions in the soil.

The present study, which was conducted in 2005, represents a continuation of a previous investigation (*9*) in which the response of the photosynthetic system of two unnamed cultivars with either green or red leaves and yellow-white or purple-red tubers were compared. This earlier study revealed that leaves of the green cultivar were more susceptible to a 4 week ozone application with a medium concentration of 130 μg m^{-3} ozone applied over 8 h during the light period for 5 days a week. Whereas the green-leaf cultivar responded to the ozone stress with leaf chloroses accompanied by ethylene production, and a reduction of chlorophyll content, and net photosynthesis rate, the red-leaf cultivar showed only a slightly narrower stomatal aperture so that less ozone entered the plant. The present study intended to test the hypothesis that the differences of both cultivars investigated in the previous study to cope with the ozone load are also reflected in the quantity and quality changes of the main harvesting products.

* Corresponding author [e-mail (preferable) Keutgen_N@yahoo.com; telephone +49-228-735143or +49-2236-379815; fax +49-228/735764].
† University of Bonn.
§ University of Göttingen.

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Table 1. Modifications in Whole Plant Fresh Weight, Leaf Weight, Shoot Weight, Root Weight, and Root/Shoot Ratio Due to a 4-Week Ozone Exposure in Cvs. SP1 and SP2 (C1, Charcoal-Filtered Air; C2, Unfiltered Air; O_3, Ozone-Enriched Air)[a]

	whole plant (g)	leaves (g)	shoot (g)	root (g)	root/shoot ratio
SP1 C1	812 ± 19 c	65 ± 5 b	231 ± 4 b	581 ± 20 a	2.52 ± 0.11 a
SP1 C2	783 ± 27 c	64 ± 2 b	234 ± 4 b	559 ± 28 a	2.50 ± 0.14 a
SP1 O_3	672 ± 85 d	50 ± 8 c	191 ± 52 b	481 ± 39 b	2.61 ± 0.56 a
SP2 C1	1146 ± 54 a	189 ± 8 a	713 ± 42 a	433 ± 12 bc	0.61 ± 0.02 b
SP2 C2	1054 ± 77 a	179 ± 7 a	668 ± 42 a	386 ± 57 c	0.58 ± 0.08 b
SP2 O_3	952 ± 24 b	185 ± 7 a	702 ± 33 a	249 ± 54 d	0.36 ± 0.09 b

[a] Within columns, different letters indicate significant differences at the 5% level.

Table 2. Modifications in Tuber Fresh Weight, Fine Root Weight, Tuber/Plant Ratio, and Fine Root/Shoot Ratio Due to a 4-Week Ozone Exposure in Cvs. SP1 and SP2 (C1, Charcoal-Filtered Air; C2, Unfiltered Air; O_3, Ozone-Enriched Air)[a]

	tuber (g)	fine roots (g)	tuber/plant ratio	fine root/shoot ratio
SP1 C1	500 ± 12 a	82 ± 19 c	0.62 ± 0.02 a	0.35 ± 0.08 a
SP1 C2	487 ± 16 a	72 ± 16 c	0.62 ± 0.02 a	0.32 ± 0.07 a
SP1 O_3	431 ± 28 b	50 ± 37 c	0.64 ± 0.06 a	0.28 ± 0.24 a
SP2 C1	115 ± 23 c	318 ± 11 a	0.10 ± 0.02 b	0.45 ± 0.04 a
SP2 C2	93 ± 39 c	293 ± 26 a	0.09 ± 0.03 b	0.44 ± 0.05 a
SP2 O_3	21 ± 7 d	239 ± 48 b	0.02 ± 0.01 c	0.33 ± 0.08 a

[a] Within columns, different letters indicate significant differences at the 5% level.

MATERIALS AND METHODS

Plant Material and Growth Conditions. For the experiments, two unnamed sweet potato varieties, collections of the Institute of Crop Science and Resource Conservation (INRES), Unit Tropical Crops, University Bonn, were used, the first (SP1) being characterized by green leaves and yellow-white roots and tubers and the second (SP2) by purple-red leaves and petioles and purple-red roots and tubers. Thirty plantlets of each cultivar grown from tuber slices were planted in 5 L containers filled with a soil/sand mixture and grown since March in the greenhouse and since June on a field near the Institute of Crop Science and Resource Conservation in Bonn, Germany (about 51° N 7° E). They were watered every evening and received 500 mL of a modified Hoagland nutrient solution once a week (*11*). At the end of August, middle of September, and beginning of October nine plants of each cultivar were transferred into one of three plant chambers for 2 day acclimatization. In the first chamber, plants received ozone-enriched air (O_3), in the second they were grown under charcoal-filtered air (C1), and in the third the plants were under unfiltered air (C2). Sizes of plants were comparable between chambers, and plant density was up to 5/m^2.

Many experiments on ozone loads were conducted in controlled-environment chambers, which fail to simulate daily changes in the natural environment. The present experiment was conducted in plant chambers made of Teflon film (Norton, Pampus GmbH, Willich, Germany), which were placed in a glasshouse and exposed to the daily cycles of natural sunlight energy (*12*). To mimic the open-top chamber design, the plant chambers received air from outside the glasshouse taken at about a 2 m height by a fan, purified for all but the third chamber by passing through an air purification filter, a charcoal filter, and a particle filter. For the fumigation experiment, plants in the first chamber received 130 ± 30 μg m^{-3} ozone for 8 h during the light period, 5 days a week for 4 weeks. A mercury lamp (series 78-2046-2; Seefelder Messtechnik) was used to generate the ozone, and the ozone analyzer MLU400 (MLU, Essen, Germany) was used to measure its concentration. In the second chamber, plants were grown under charcoal-filtered air and in the third under unfiltered air with <20 μg m^{-3} ozone (*12*). To avoid position effects, the positions of plants within chambers were changed randomly twice a week. Light intensity within the plant chambers varied according to the natural sunlight intensity (about 500 μmol m^{-2} s^{-1} photosynthetically active radiation at midday), and plant chamber temperatures ranged from 10 to 25 °C during most days. Air humidity within the chambers varied between 50 and 80%, with highest values during the dark period. The CO_2 concentration was about 360 μL l^{-1}. Plants were harvested immediately after the final ozone exposure. After harvest, plants were separated into leaves, stem and petioles, tubers, and fine roots to determine fresh mass of the four fractions. Roots were separated into tubers and fine roots by a critical diameter of 2.5 cm. The fractions were freeze-dried for further analyses.

Carbohydrate Analyses, Macronutrient Analyses, and Carotenoid Contents. Starch, glucose, fructose, and sucrose contents were measured enzymatically after the extraction of freeze-dried samples with methanol (*13*). Methanol extracts were used for the identification of glucose, fructose, and sucrose, the residues for starch analyses. Chlorophyll in the methanol extracts was minimized with charcoal. The extracts were purified by centrifugation. For the sequential enzymatic degradation procedure to determine the sucrose contents, β-fructosidase and hexokinase/glucose-6-phosphatedehydrogenase were used; for the determination of glucose and fructose, hexokinase/glucose-6-phosphatedehydrogenase was applied first and then phosphoglucoseisomerase. The absorption of the carbohydrate solutions was detected at 340 nm using a UV detector before and after enzyme applications. For the starch analyses 4 mL of H_2O bidistilled was added to the residue of the methanol extraction and boiled in a water bath for 140 min. Then, 4 mL of acetate buffer and 50 μL of amyloglucosidase were added to the starch solution and kept for 20 min at 60 °C. The solutions were allowed to cool to room temperature and then were centrifuged. The supernatant was exposed to hexokinase/glucose-6-phosphatedehydrogenase, and the absorption was measured at 340 nm before and after enzyme application. The sum of the glucose, fructose, and sucrose contents was taken as soluble carbohydrate and the sum of soluble carbohydrates and starch as the total carbohydrate content.

P, K, Ca, and Mg were determined after digestion at 200 °C with H_2O_2 and HNO_3 in an MLS-1200 digestion/drying module microwave laboratory system (MLS GmbH, Leutkirch im Allgäu, Germany) (*13*). P content was measured by colorimetry with the Scalar autoanalyzer. The concentrations of K, Ca, and Mg were analyzed separately using a Perkin-Elmer-373 atomic absorption and emission spectrophotometer (Perkin-Elmer Corp., Analytical Instruments, Norwalk, CT). Nitrogen content was determined from freeze-dried samples with a C/N analyzer (CN 2000, Leco, Mönchengladbach, Germany).

Leaf carotenoid content was measured spectrophotometrically (HP8453 with Aglient ChemStation, Hewlett-Packard, Germany) according to the method of Wellburn (*14*) from leaf methanol extracts and expressed per dry weight.

Analysis of Tuber Free Amino Acids. Free amino acid derivatives were separated by reversed-phase high-performance liquid chromatography (RP-HPLC) using a precolumn LiChroCART 4-4 Purospher STAR RP-18 5 μm in combination with a separation column LiChroCART 250-3 Purospher STAR RP-18 5 μm (Merck KGaA). The HPLC separation was made using 50 mmol L^{-1} sodium acetate buffer, pH 7.0 (solvent A) and methanol (solvent B). The ratio solvent A/B was 71:29 (v/v) at the beginning followed by a linear gradient to 20:80 (v/v) over 25 min (*15*). Amino acid peaks were detected by a fluorescence detector at wavelengths of Ex 330/Em 450 nm. The separation was achieved at a flow rate of 0.65 mL min^{-1} at a temperature of 35 °C, and the injection volume was 20 μL. The detection limit ranged between 0.25 and 2.5 μmol L^{-1}. Glutamine, arginine, asparagine, proline, and tryptophan could not be identified in sweet potato using this method.

Free proline content was measured after extraction of freeze-dried material (0.4 g) with 3% of sulfosalicylic acid in water (w/w) to precipitate protein amino acids. The supernatant was exposed to ninhydrin under acid conditions, and the pink color complex was monitored at a wavelength of 546 nm and 25 °C after extraction with toluene using a Hewlett-Packard Aglient 8453 UV−vis spectrophotometer with multicell sampler. Pure toluene was used as a blank. Proline concentrations were calculated using a calibration curve from 0 to 150 μg L^{-1}. A statistical analysis of amino acid contents was impossible due to the limited number of replicates.

Data Analysis. The experimental data were analyzed with the SPSS statistical package. A 5% probability level was accepted to indicate

Table 3. Modifications in Leaf Carbohydrate and Carotenoid Content (Dry Matter Basis) Due to a 4-Week Ozone Exposure in Cvs. SP1 and SP2 (C1, Charcoal-Filtered Air; C2, Unfiltered Air; O_3, Ozone-Enriched Air)[a]

	total carbohydrates (mg g^{-1})	starch (mg g^{-1})	soluble carbohydrates (mg g^{-1})	glucose (mg g^{-1})	fructose (mg g^{-1})	sucrose (mg g^{-1})	carotenoids (mg g^{-1})
SP1 C1	93 ± 6 bc	62 ± 2 c	31 ± 8 ab	11 ± 1 bc	16 ± 4 a	3.4 ± 0.3 a	0.42 ± 0.01 a
SP1 C2	87 ± 5 c	58 ± 4 c	29 ± 1 b	10 ± 3 bc	16 ± 2 a	3.0 ± 0.3 a	0.42 ± 0.01 a
SP1 O_3	53 ± 4 d	27 ± 5 d	26 ± 3 b	9 ± 3 c	14 ± 1 a	3.6 ± 0.2 a	0.28 ± 0.04 b
SP2 C1	136 ± 4 a	105 ± 8 a	31 ± 4 ab	15 ± 1 ab	12 ± 3 a	3.8 ± 0.7 a	0.30 ± 0.02 b
SP2 C2	141 ± 6 a	104 ± 2 a	37 ± 4 a	20 ± 4 a	14 ± 2 a	3.7 ± 0.3 a	0.31 ± 0.02 b
SP2 O_3	101 ± 3 b	74 ± 5 b	27 ± 6 b	11 ± 6 bc	12 ± 2 a	3.9 ± 0.8 a	0.31 ± 0.03 b

[a] Within columns, different letters indicate significant differences at the 5% level.

Table 4. Modifications in Tuber Carbohydrate Content (Dry Matter Basis) Due to a 4-Week Ozone Exposure in Cvs. SP1 and SP2 (C1, Charcoal-Filtered Air; C2, Unfiltered Air; O_3, Ozone-Enriched Air)[a]

	total carbohydrates (mg g^{-1})	starch (mg g^{-1})	soluble carbohydrates (mg g^{-1})	glucose (mg g^{-1})	fructose (mg g^{-1})	sucrose (mg g^{-1})
SP1 C1	854 ± 53 a	712 ± 48 a	141 ± 15 a	26 ± 2 a	13 ± 1 a	102 ± 14 a
SP1 C2	834 ± 68 ab	706 ± 40 a	128 ± 35 ab	24 ± 2 a	9 ± 1 abc	94 ± 34 a
SP1 O_3	738 ± 6 c	620 ± 23 b	118 ± 28 ab	13 ± 2 b	12 ± 2 ab	93 ± 29 a
SP2 C1	832 ± 16 ab	738 ± 14 a	94 ± 15 bc	11 ± 1 b	6 ± 4 c	77 ± 17 a
SP2 C2	815 ± 30 ab	718 ± 38 a	98 ± 8 bc	10 ± 2 b	7 ± 4 bc	81 ± 13 a
SP2 O_3	762 ± 26 bc	690 ± 19 a	72 ± 15 c	5 ± 1 c	5 ± 3 c	61 ± 15 a

[a] Within columns, different letters indicate significant differences at the 5% level.

Table 5. Macronutrient Contents (Dry Matter Basis) in Tubers of Cvs. SP1 and SP2 Grown under Charcoal-Filtered Air (C1), Unfiltered Air (C2), and Ozone-Enriched Air (O_3) for 4 Weeks[a]

	K (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})	P (mg g^{-1})	N (mg g^{-1})
SP1 C1	17 ± 2 a	1.7 ± 0.1 de	1.3 ± 0.2 c	1.6 ± 0.2 ab	4.8 ± 0.6 b
SP1 C2	17 ± 3 a	1.6 ± 0.1 e	1.2 ± 0.1 c	1.5 ± 0.1 ab	4.0 ± 0.2 b
SP1 O_3	18 ± 2 a	2.2 ± 0.1 b	1.6 ± 0.1 b	1.7 ± 0.1 a	6.4 ± 0.6 a
SP2 C1	13 ± 1 b	1.9 ± 0.2 c	1.5 ± 0.1 b	1.4 ± 0.1 bc	4.2 ± 0.7 b
SP2 C2	13 ± 1 b	1.8 ± 0.1 cd	1.5 ± 0.1 b	1.5 ± 0.1 bc	4.2 ± 0.8 b
SP2 O_3	12 ± 1 b	3.3 ± 0.1 a	2.4 ± 0.1 a	1.2 ± 0.1 c	6.5 ± 1.4 a

[a] Within columns, different letters indicate significant differences at the 5% level.

significant differences. The data were tested for normal distribution and variance homogeneity and were compared by Duncan or Tamhane tests.

RESULTS

Plant Growth. At the end of the treatment the mature leaves of cv. SP1 showed visible signs of injury in the form of a few light chlorotic spots on the adaxial leaf surface, which tended to occur more frequently at the leaf tip and the leaf margin, whereas young leaves did not exhibit any visible symptoms. An elevated leaf fall as a result of ozone fumigation was not observed. Whole plant biomass, which was generally larger in cv. SP2, was significantly reduced by ozone in both cultivars (**Table 1**). The root/shoot ratio was not affected by ozone, but in cv. SP2 shoot growth was considerably more promoted than in cv. SP1. Leaf fresh weight was significantly reduced by ozone in cv. SP1; however, shoot growth was not significantly influenced in either (**Table 1**). Root growth, which was larger in cv. SP1, was significantly reduced by ozone in both sweet potato cultivars (**Table 1**), and the reduction in root fresh mass was detectable especially in tubers (**Table 2**). Remarkably, the relative amount of tuber per plant fresh mass remained stable in cv. SP1 but was significantly reduced in cv. SP2 due to ozone (**Table 2**). The fine root/shoot ratio and the root/shoot ratio were not significantly affected by the ozone fumigation.

Carbohydrate and Carotenoid Contents. Leaf total carbohydrate content was significantly larger in cv. SP2 than in cv. SP1 (**Table 3**). This cultivar difference was due to a 40% higher starch content, whereas the soluble carbohydrates glucose, fructose, and sucrose did not differ between cultivars. Ozone significantly reduced total leaf carbohydrate and starch contents in both cultivars (**Table 3**). Leaf carotenoid content was significantly reduced in cv. SP1 under ozone, but not in cv. SP2 (**Table 3**).

Table 6. Tuber Free Amino Acid Concentration (Milligrams per Gram of Dry Matter) in Tubers of Cvs. SP1 and SP2 Grown under Charcoal-Filtered Air (C1) and Ozone-Enriched Air (O_3) for 4 Weeks

	SP1 C1	SP1 O_3	SP2 C1	SP2 O_3
glutamine	0.44	0.29	0.43	nd[a]
proline	0.39	0.40	0.28	1.19
serine	0.12	0.14	0.37	0.10
glycine	0.16	0.15	0.19	0.02
cysteine	nd	nd	0.50	0.51
aspartate	0.53	0.49	1.01	0.03
lysine	0.29	0.21	0.39	nd
methionine	0.08	0.06	0.15	nd
thryrosine	0.18	0.15	0.23	0.01
isoleucine	0.15	0.12	0.18	0.01
histidine	0.03	0.03	0.04	0.03
alanine	0.12	0.17	0.15	0.02
valine	0.34	0.35	0.25	0.01
leucine	0.25	0.18	0.29	0.01
phenylalanine	0.24	0.23	0.27	0.02
tyrosine	0.19	0.16	0.21	0.07

[a] Not detected.

Tuber total carbohydrate contents were similar in both cultivars, but soluble carbohydrate content was slightly larger in cv. SP1 (**Table 4**). Ozone significantly reduced total tuber carbohydrate content in cv. SP1, but not in cv. SP2. This decrease could be attributed to significant decreases in starch and glucose contents (**Table 4**).

Tuber Macronutrient and Amino Acid Contents. Within the tubers, Ca, Mg, and N contents rose in both cultivars under ozone stress, whereas levels of K and P remained stable (**Table 5**). Tuber contents of single free amino acids remained fairly stable in cv. SP1 and were distinctly reduced in most cases in cv. SP2 (**Table 6**). In the latter cultivar grown under ozone, about half of the free amino acid content was found as proline, the concentration of which rose by 400%. Free amino acid concentrations of both cultivars were fairly similar when grown in charcoal-filtered air, with the exception of serine, cysteine, and aspartate, the concentrations of which were larger in cv. SP2; cysteine could not be identified in cv. SP1.

DISCUSSION

Sweet potato has great potential as a source of food, livestock feed, and processed products, and not only the tuber but also the leaves, including the petioles, can be used as food, the latter as a leafy vegetable (*5, 16*). The multiple-benefit potential of sweet potato implies the existence of several different cultivars with special advantages and adaptations to local climates and demands. The present study has revealed that sweet potato cultivars may invest photoassimilates preferably into either canopy development or tuber formation. This genetic variability should also result in different strategies to cope with environmental stresses such as ozone. Knowledge about these strategies will contribute significantly to decisions as to which cultivars should be selected for cultivation under these suboptimal conditions.

A chronic ozone load of ca. 130 μg m^{-3} reduced sweet potato growth by 13−16%, and this reduction was mainly in tuber development (**Tables 1** and **2**). Whereas in the purple-red cv. SP2 leaf biomass remained unaffected, it was significantly reduced by 22% in the green cv. SP1. For comparison, leaf fresh weight of ozone-exposed plants of cv. SP1 was 73% less than that of cv. SP2. According to Keutgen et al. (*9*), 4 months of ozone did not result in a significant decrease in net carbon assimilation per leaf area in either cultivar; however, the smaller leaf area of the green cv. SP1 should result in a lower total foliar photosynthetic productivity, at least during part of the growing season, even though photosynthesis per leaf area remained similar between cultivars and treatments. The reduction in leaf biomass contributed further to the decrease in plant biomass and availability of carbohydrates.

Ozone significantly reduced total leaf carbohydrate, especially starch, contents in both cultivars (**Table 3**), indicating the investment of carbohydrates into metabolic pathways to balance ozone-induced impairments. Hence, a reduction of whole plant photosynthesis due to a cumulative ozone effect on the plant canopy may potentially limit its detoxification capacity and its resistance to elevated tropospheric ozone levels (*17, 18*). In addition, several products of sweet potato leaves are derived from carbohydrates, especially from starch. They may be used to produce sugar syrups, beverages, food colorants, enzymes, and protein (*19*). In conclusion, ozone stress impairs the quality of leaves as basic raw material for chemical syntheses.

Leaves can be harvested several times per year. As a consequence, the annual yield of sweet potato leaves may be much higher than that of other green vegetables. Sweet potato greens are rich in polyphenols, vitamin C, B-vitamins, carotenoids, iron, calcium, zinc, and protein. They are more tolerant of diseases and pests, and the moisture content is higher than in many other leafy vegetables grown in the tropics (*19, 20*). The purple-red sweet potato cv. SP2 seems particularly suitable for cultivation under elevated tropospheric ozone concentrations as a leafy vegetable, because ozone did not reduce leaf and shoot growth. Leaf carotenoid content was not reduced in this cultivar, although it was reduced in cv. SP1 (**Table 3**). Sweet potato leaves are regarded as important sources of β-carotene, suitable for the human diet, but may also be used for coloring margarines and soft drinks (*19*).

For livestock feeding both roots and shoots are used in either a fresh or dried form. They are frequently fermented into silage. Roots basically represent a source of energy, and leaves are a source of protein in animal diets (*19*). The purple-red sweet potato cv. SP2 had greatly reduced tuber production under elevated ozone and, hence, may be less suitable for livestock feeding. The elevated ozone level diminished tuber yield in both sweet potato cultivars, in cv. SP1 by ca. 13% and in cv. SP2 by ca. 80%. Not only quantity but also quality of tubers was affected. In the sweet potato tubers of both cultivars, Ca, Mg, and N accumulated. Especially in the case of N, this could be interpreted as a strategy to store nutrients for regrowth during the following season. However, the shift in biomass allocation away from the tuber toward the shoot in cv. SP2 does not fit this interpretation. If one, however, considers that Ca, Mg, and N are not equally distributed within the tuber but that their concentrations are somewhat elevated close to the tuber surface as they are in potato tubers (*19, 21, 22*), then the ozone-induced reduction in tuber size (**Table 2**) can easily explain the observed change in macronutrient concentrations by an increase in the tuber surface/volume ratio.

Tuber free amino acid content decreased only in tendency in cv. SP1, but in cv. SP2 ozone induced considerable changes in the composition of the amino acid pool (**Table 6**). The observation that the contents of proline accounted for about 50% of total amino acids in the latter cv. is well in line with earlier observations that this soluble nitrogenous compound accumulates most widely in stressed plants (*23*).

The only significant impairment of tuber quality in cv. SP1 represented its lower carbohydrate level under ozone (**Table 4**), which was due to a reduction of starch and glucose. The first compound is of special importance, because the most important food products from sweet potato tubers are starch and alcohol, the latter being produced from starch and other fermentable carbohydrates (*19*). Tuber carbohydrates may also represent the basic raw material for sugar syrup and noodle production (*19*). Last, but not least, sweet potato tubers may represent the basic raw material for flour and snacks (*19*). For the production of sweet potato chips, low levels of reducing sugars are desirable as in potato chips (*22*). Because ozone reduced the ratio (glucose + fructose)/starch from 0.05 to 0.04 in cv. SP1, ozone may in this special case improve tuber quality.

In conclusion, elevated tropospheric ozone levels impair the growth and metabolism of sweet potato; however, responses of cultivars are different. In cv. SP2 tuber development was reduced, whereas leaf development remained stable. Only leaf starch content was significantly reduced, resulting in a slight reduction of leaf quality. Leaf carotenoid content remained stable, so that leaves as a source of β-carotene are not affected. Cultivars like the purple-red cv. SP2 should preferably be grown as a leafy vegetable in regions with elevated ozone levels. By contrast, the green cv. SP1 may be used for tuber production, although tuber growth was reduced under ozone stress. Remarkably, the tuber/plant ratio was not affected in this cultivar, although a preference of shoot over root growth is frequently observed under elevated tropospheric ozone. The reduction in starch content of tubers in cv. SP1 does not necessarily represent an impairment of tuber quality. A reduced ratio (glucose + fructose)/starch due to a chronic ozone load is advantageous for chip quality.

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