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# Productivity of the warm-climate crop sweet potato (*Ipomoea batatas* L.) in northern latitudes

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## Abstract

Sweet potato (*Ipomoea batatas* (L.) Lam.) has a potential to become a new field crop for higher latitudes. Sweet potato was cultivated for the first time in the fields of Estonia. During the study, the photosynthetic characteristics and yields of sweet potato cultivars 'Evangeline' and 'Covington' were investigated under fertilisation with two nitrogen (N) rates (0 and 100 kg ha$^{-1}$ N) and various fertilisers in 2018, 2019 and 2021. Variation in fertiliser rate and composition had no effect on $CO_2$ assimilation rate ($A$) and stomatal conductance ($g_s$). The negative relationship between photosynthetic nitrogen use efficiency (PNUE) and intrinsic water-use efficiency (iWUE) among cultivars and treatments indicated that water availability could limit nutrient availability and ultimately reduce the potential yield in northern growing regions. The highest sweet potato tuber yield (t ha$^{-1}$) was obtained from 'Evangeline' and 'Covington' at N0 in 2021. A comparison of yields of 2018 and 2021 experiments suggests that sweet potatoes can be grown in high latitudes. It can be concluded that depending on weather conditions, cultivars and soil properties, fertilisers can promote high plant productivity.

Further studies should focus on sweet potato plants traits that enable the efficient use of nutrients and water during a short and potentially dry growing season.

Keywords: nitrogen fertilising, *Ipomoea batatas*, intrinsic water-use efficiency, net photosynthesis, growth yield.

## Introduction

Meeting the projected food demand by 2050 will require a 70% increase in crop yield (Ray, Foley, 2013). Although this poses a major challenge, one strategy to achieve this is to identify new crops suitable for higher latitudes taking advantage of the potential benefits of global warming. While climate warming can cause plant stress, it has also resulted in the cultivation of new species in colder regions such as sweet potatoes (Chaudhry, Sidhu, 2021).

Sweet potato (*Ipomoea batatas* (L.) Lam.) is thought to have originated from the tropical and subtropical regions of Central and South America. The leading sweet potato growing countries are China, several African countries, South American countries, Japan, India, and Vietnam (FAOSTAT, https://www.fao.org/faostat/en/#data/QCL). In USA, intensive breeding is done to develop shorter growing and higher yielding sweet potato cultivars (Jennings et al., 2019). Determining the suitability of warm-climate plants for Nordic countries requires a detailed knowledge of plants stress response (Cui et al., 2020). However, depending on the temperature and the length of the growing season, the cultivation of this tropical tuber plant in the northern regions remains a challenge. The number of summers with warmer average temperatures has increased and is predicted to increase even more in Northern Europe (Pulatov et al., 2015). Despite the challenges such as dry springs and early autumns, late spring night frosts and a longer growing period compared to a long-term (54 year) average (Saue, 2020), sweet potato cultivation in Estonia has a great potential, although the growing season may be extended to 4–5 months at high temperatures.

Abiotic factors such as temperature fluctuation, heat waves and drought reduce the stomatal conductance ($g_s$), which reduces the net assimilation rate ($A$) and intercellular $CO_2$ ($C_i$) concentration in plants (Cui et al., 2020). These abiotic factors also limit nitrogen (N) uptake, although leaf N also affects the $A$, $g_s$, and $C_i$ and varies between N-sensitive and N-tolerant crops, not to mention different plant species (Gao et al., 2018). Sweet potato is a moderately drought-tolerant crop, and similar to drought-adapted plants, the negative effects of drought on $A$ and $g_s$ could be compensated by higher N content per unit leaf area ($N_A$) (Daryanto et al., 2016; Gao et al., 2018).

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Intrinsic water-use efficiency (iWUE) is a critical factor that affects the crop yield and is also related to plant nutrient uptake – a higher iWUE and yield would require a higher $A$ per given $g_s$ (Hatfield, Dold, 2019). However, further research is needed to understand sweet potato yield factors during dry growing seasons in Northern Europe.

Until now, sweet potatoes in Estonia have been grown under domestic conditions, in greenhouses and seedbeds as well in windless garden beds. In this study, sweet potatoes were grown for the first time in Estonian field conditions in 2018, during a particularly warm summer. The aim of this study was to show that this crop can be cultivated in Northern Europe. To our knowledge, this is the first study to investigate the suitability of two promising sweet potato cultivars at higher latitudes with simultaneous climatic, physiological and yield analyses.

This study aims to: 1) reveal the physiological mechanisms determining sweet potato yield and optimal growth conditions, 2) establish correlations between the N rates and sweet potato yields in order to determine optimal conditions for high-yield crop growth in Nordic conditions, 3) determine the influence of soil properties and various fertilisers on sweet potato productivity, and 4) reveal the efficiency of N uptake and assimilation during a short growing season.

The main goal of the field experiment was to investigate the possibility of growing sweet potatoes in an open field in Estonia under different agronomic conditions.

## Material and methods

*Cultivation site.* The experiment was conducted in the Eerika field of the Rõhu Experimental Station (58°37′ N, 26°67′ E) of the Estonian University of Life Sciences, Tartu County, Estonia. The field experiment sites were slightly different in 2018 (58°36′59.18″ N, 26°66′56.83″ E), 2019 (58°36′63.57″ N, 26°66′40.67″ E) and 2021 (58°36′47.55″ N, 26°66′76.04″ E), and pre-crops also differed. The pre-crops of the 2018 field experiment included potato (*Solanum tuberosum* L.) grown in 2016 and spring barley (*Hordeum vulgare* L.) grown in 2017. In 2019, the pre-crops were spring wheat (*Triticum aestivum* L.) and spring barley (*Hordeum vulgare* L.) grown in 2017 and 2018, respectively; in 2021, the pre-crops were spring wheat (*Triticum aestivum* L.) and spring barley (*Hordeum vulgare* L.) grown in 2019 and 2020, respectively.

During the three-year study, the soil was light sandy loam classified as *Stagnic Luvisol* (WRB, 2022). The thickness of the soil ploughing layer was 27−30 cm (Reintam, Köster, 2006), and the bulk density of the soil was 1.45–1.50 g $cm^{-3}$ (Madsen et al., 2016). Four soil subsamples were collected at a depth of 20 cm immediately before sweet potato planting. The air-dried samples were sieved through a 2 mm sieve. The soil pH was determined in a 1M KCl solution (ratio 1:2.5), and the content of plant-available P, K, Ca, and Mg was determined by the A-L method. Soil organic carbon ($C_{org}$) was determined by the Tjurin method (Soil Survey Laboratory Methods…, 2004), and total nitrogen ($N_{tot}$) content in the soil was determined by the Kjeldahl method (Van Reeuwijk, 1995). The results of 2018 and 2019 soil samples were quite similar except that K and Mg content remained lower in soil samples of 2019. However, compared to the 2018 and 2019 samples, the 2021 soil samples had the highest content of pH, $C_{org}$, and $N_{tot}$ (Table).

***Table.*** Soil quality characteristics in the experimental field in 2018, 2019, and 2021

| Soil characteristics | 2018 | 2019 | 2021 | |
|---|---|---|---|---|
| $pH_{KCl}$ | 5.6275 ± 0.051 a | 6.0275 ± 0.16 ab | 6.325 ± 0.080 b | $P < 0.05$ |
| $C_{org}$ % | 1.413 ± 0.049 a | 1.2615 ± 0.048 a | 1.624 ± 0.011 b | $P < 0.05$ |
| $N_{tot}$ % | 0.100 ± 0.009 a | 0.109 ± 0.004 a | 0.151 ± 0.003 b | $P < 0.05$ |
| P mg $kg^{-1}$ | 86 ± 7 | 71.9 ± 4.1 | 89 ± 7 | ns |
| K mg $kg^{-1}$ | 149.63 ± 2.49 a | 128.12 ± 4.66 b | 143.1 ± 6.9 ab | $P < 0.05$ |
| Ca mg $kg^{-1}$ | 1022 ± 63 a | 1060 ± 26 a | 1416 ± 49 b | $P < 0.05$ |
| Mg mg $kg^{-1}$ | 154.0 ± 5.7 a | 123.55 ± 3.20 b | 157 ± 10 a | $P< 0.05$ |

*Note.* Differences according to one-way ANOVA were significant at $P < 0.05$; ns – non-significant at $P > 0.05$, lowercase letters denote the differences in soil characteristics between field experiment locations.

*Sweet potato cultivars, slips pre-growth and planting.* Two USA-breeding sweet potato cultivars ‘Evangeline’ (Louisiana Agricultural Experiment Station) and ‘Covington’ (North Carolina State University) were selected for the experiment. ‘Covington’ is a smooth skinned, orange-fleshed sweet potato cultivar developed and cultivated at North Carolina State University (Yencho et al., 2008). The tubers of the ‘Evangeline’ were imported from Egypt, and the tubers of ‘Covington’ from the USA. To obtain sweet potato slips for planting, the tubers were placed indoors in plastic plant growth boxes (width 23 cm, length 31 cm, height 10 cm) filled with Biolan black garden soil with essential nutrients: Biolan, 12-14-24 + Mg-containing limestone powder 4 kg $m^{-3}$ (pH = 6.0). The tubers were grown under the following conditions: air temperature 22/18°C, humidity 65%, and light intensity 700 µmol $m^{-2}$ $s^{-1}$ at the box level with a 12-h day. The sprouts started to emerge 28 days after planting, and the slips were ready for planting (15–20 cm length) after 40−45 days. In 2018, 2019, and 2021, slips were planted on 6, 10, and 4 June, respectively, when the risk of late frosts was minimal. In 2018, three different variants of planting were used: whole tubers, sliced tubers (each tuber was sliced in two pieces), and slips. In 2019 and 2021, only pre-grown shoots were planted.

In all years, the experiment was designed in a randomised block design with four replications. In 2018, in all treatments, the intra-row distance between the sweet potato plants in a row was 50 cm, in 2019 – 40 cm and in 2021 – 30 cm, and the distance between rows of plants was 70 cm. There were 6 tubers, 6 slips or 5 plants in each plot, and each plot size was 2.1 m$^2$. The experiment included two nitrogen (N) fertiliser rates, 0 and 100 kg ha$^{-1}$ N (N0 and N100). In 2018 and 2019, in N100 treatment, a fertiliser with nitrogen and sulphur (YaraBela Axan N27 + S4) was used: in 2018, 50 kg ha$^{-1}$ was applied on 8 June and 50 kg ha$^{-1}$ on 15 June, and in 2019, 50 kg ha$^{-1}$ was applied on 10 June and 50 kg ha$^{-1}$ on 18 July. In 2021, a complex fertiliser YaraMila NPK 21-6-21 + S(3.6) + Mg(1.7) + B was added to the soil immediately before planting. No synthetic pesticides were used, and weeds were removed mechanically twice during all three growing seasons. In 2018, the plants were watered eight times during the growing season with an interval of 7–9 days, and every time about 500 ml of water was given to each plant. In 2019 and 2021, the plants were watered twice after planting, and every time about 1000 ml of water was given to each plant.

In 2018, 2019, and 2021, tubers were harvested on 15 October, 23 September, and 27 September, respectively, therefore, the growing seasons lasted 131, 105, and 115 days, respectively, without night frosts during the growing periods of experimental years. In 2019, the tubers were harvested immediately after the early night frosts.

*Weather conditions.* Weather data were obtained from the Rõhu Weather Station of Estonian University of Life Sciences, located 0.5 km from the experimental site, and were measured monthly during the growing season of sweet potato plants. In 2018, 2019, and 2021, the average temperatures from May to October were higher compared to the long-term (50-year) average (Figure 1). In 2018, an extremely hot 30-day period lasted from the second ten-day period of July to the first ten-day period of August, when the average air temperature was 5.4°C higher than the long-term average. A similar 30-day period lasted from the end of June to the end of the second ten-day period of July in 2021. In 2018, 2019, and 2021, the growing seasons were 2.5°C, 2.0°C, and 3.2°C warmer, respectively (average ± standard deviation (SD) of 16.4 ± 4.6°C in 2018, 15.8 ± 3.5°C in 2019, and 17.0 ± 5.2°C in 2021) than the 50-year average temperature (13.8 ± 3.9°C).

In 2018 and 2019, the amount of precipitation was almost 30% lower (233 and 225 mm in total, respectively) than the 50-year average (315 mm), and in 2019, it was similar to the 50-year average (Figure 1). In 2018 and 2021, the July was drier compared to the long-term average. In 2018 and 2019, from the second ten-day period of August to the end of September, the amount of precipitation was similar to the long-term average, and in 2021, there was twice as much precipitation as in the previous 50 years during the same period. There was no precipitation in the second ten-day period of October in any year, so the conditions for tuber crop harvesting were suitable.

*Photosynthesis measurements.* In 2018 and 2019, the gas-exchange measurements were started 77 and 67 days after planting, respectively, which lasted for one to two weeks and were performed from 10:00 to 15:00 in field conditions. In 2021, photosynthesis measurements were started 81 days after planting. However, due to low temperatures at night, the experiment could not be completed, because during the day, the photosynthesis did not recover to the level the plants had before the temperature shock.

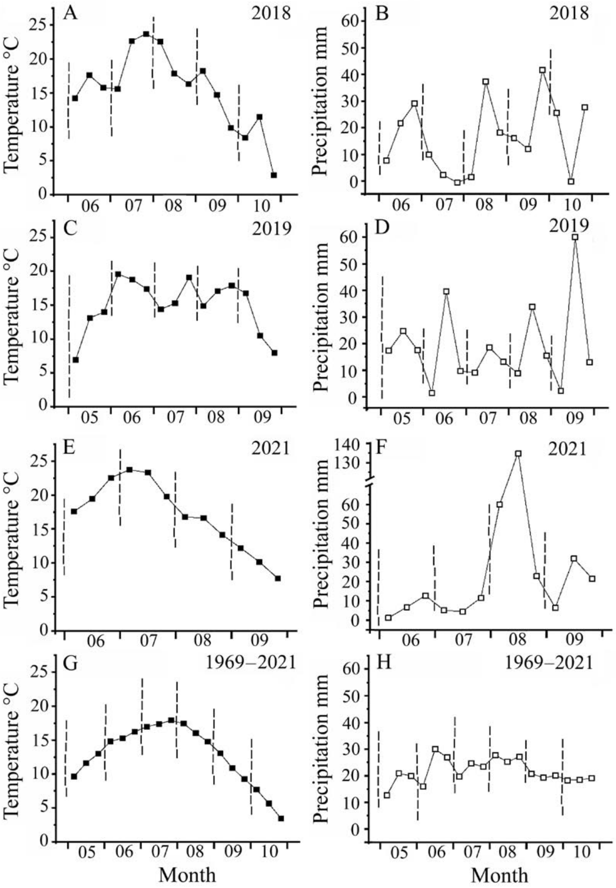


***Figure 1.*** Ten-day average temperatures (A, C, and E) and amount of precipitations (B, D, and F) in 2018, 2019, and 2021 at the Rõhu Weather Station and the long-term (1969–2021) average temperature (G) and precipitation (H) values

To record the light-saturated steady-state assimilation rate ($A$), stomatal conductance ($g_s$), and the ratio of intercellular to ambient CO$_2$ concentration ($C_i$: $C_a$), a GFS-3000 gas-exchange and fluorescence system with a standard measuring head 3010 (8 cm$^2$ window area) and LED-array/PAM-fluorometer 3056-FL (Walz GmbH, Germany) was used. Non-damaged leaves of medium age plants were selected for measurements. After placing a leaf in the clip-on type 8 cm$^2$ leaf cuvette, the leaf was stabilised for 0.5 h under standard conditions: CO$_2$ concentration of 400 µmol mol$^{-1}$, photosynthetically active quantum flux density of 1500 µmol m$^{-2}$ s$^{-1}$, cuvette block temperature of 25°C, relative air humidity of 60%, and air flow rate of 750 µmol s$^{-1}$. Photosynthesis was recorded at leaf temperatures from 25.3°C to 25.8°C. Intrinsic water-use efficiency (iWUE) was calculated as $A/g_s$ (Flexas et al., 2013), and photosynthetic nitrogen use efficiency (PNUE) as $A/N_A$, where $N_A$ is nitrogen content per leaf area. Three to four biological replicates (individual plants) of each treatment were measured in the field.

*Determination of leaf dry mass per unit area and C and N content.* In 2018, after gas-exchange measurements, the sample leaves were photographed and their area was calculated from the images with the open-source software ImageJ, version 1.52a (Wayne Rasband, National Institutes of Health, USA). The leaves were oven-dried for 48 h at 70°C (Sanyo Laboratory Convection Oven UFE 500), their dry mass was estimated and dry leaf mass per area (LMA) was calculated. Nitrogen content per leaf area ($N_A$) was also calculated as $N_M$/LMA. In 2018, 2019, and 2021, separate sets of leaves (9 to 11 replicates per treatment) were collected to determine the content of nitrogen ($N_M$) and carbon ($C_M$) per leaf dry mass by Vario MAX CNS analyzer (Elementar Analysensysteme GmbH, Germany).

*Determination of yield characteristics.* To obtain tuber yield, tuber fresh mass and tuber number per plant were determined immediately after harvesting for all sweet potato plants (5 or 6 plants per plot) in all growing periods.

*Statistical analysis.* The effect of variable nitrogen supply on leaf properties (LMA, $N_M$, $N_A$, and $C_M$), photosynthetic characteristics ($A$, $g_s$, $C_i$, $C_i$:$C_a$, iWUE ($A/g_s$), and PNUE), and yield characteristics (tuber number per plant and yield per ha) within and between cultivars were evaluated by two-way analysis of variance (ANOVA); the differences in soil characteristics during growing seasons were assessed by one-way ANOVA; the influence of cultivar, fertilisation, growth year and their combinations on yield characteristics was evaluated by three-way ANOVA. The relationship between $N_A$ and $A$ was non-linear ($y = ax^b$) and between PNUE and iWUE was linear. Statistical analysis was performed using OriginPro 2022 (OriginLab Corporation, USA), and the data were considered significant at $P < 0.05$; ns means non-significant difference at $P > 0.05$.

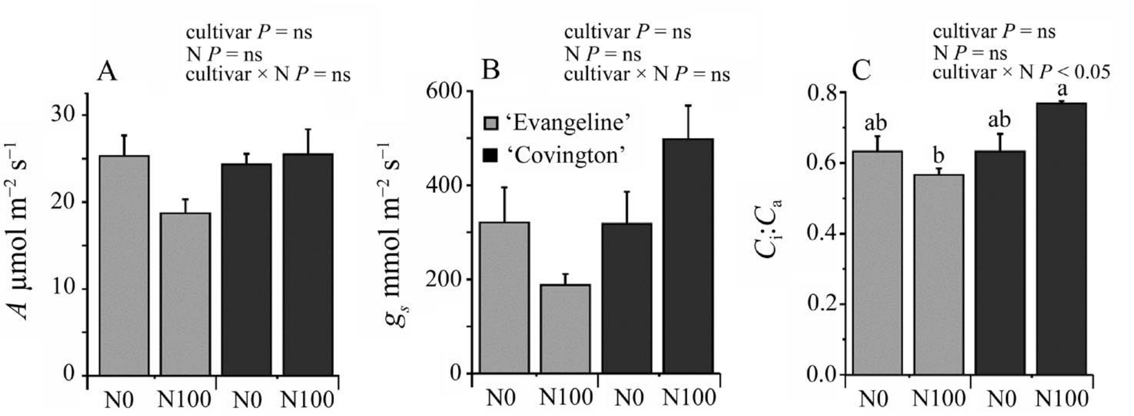
## Results

***Using of different planting methods.*** In 2018, the planting of whole and sliced tubers was mostly not successful because only 8% of 'Evangeline' and 6% of 'Covington' tubers sprouted in the field. In 2018, the growing season lasted 132 days, and both studied cultivars formed tubers in pre-grown treatments (Figure 2). Therefore, only the pre-grown sweet potato shoots were used for planting in the following years.

***Figure 2.*** Tuber yield (kg per plant fresh mass) of sweet potato cultivars 'Covington' (0.455 ± 0.068 kg) and 'Evangeline' (0.452 ± 0.055 kg) at unfertilised treatment (N0) in 2018 growing season

***Effect of fertilisation on leaf characteristics.*** In 2018, the C content per leaf dry mass ($C_M$) in 'Evangeline' and 'Covington' N0 and N100 plants was similar (on average, 42%). However, the N content per leaf dry mass ($N_M$) varied significantly ($P < 0.05$) and was the highest in 'Evangeline' N0 plants (5.37 ± 0.06%) and the lowest in 'Covington' N100 plants (4.46 ± 0.12%). The $N_M$ of 'Evangeline' N0 plants was higher than the $N_M$ of 'Covington' N0 plants (4.66 ± 0.21%), and the $N_M$ of 'Evangeline' N100 (5.02 ± 0.09%) was higher than the $N_M$ in 'Covington' N100 plants ($P < 0.05$). Nitrogen content per leaf area ($N_A$) showed a slightly different trend, as fertilisation reduced the $N_A$ from 3.35 ± 0.37 g m$^{-2}$ to 3.15 ± 0.18 g m$^{-2}$ in 'Evangeline' ($P < 0.05$), and there were no changes between cultivars. Leaf dry mass per unit area (LMA) remained stable under N treatment and between cultivars: from 63 to 73 g m$^{-2}$ in 'Evangeline' and 'Covington'.

***Effect of nitrogen fertilisation on gas-exchange characteristics and photosynthetic nitrogen use efficiency (PNUE).*** In 2018 and 2019, the measurements of photosynthesis were performed during the active growth stage of the sweet potato plants. The average mean (± SE) assimilation rate ($A$) was 23.19 ± 1.16 µmol m$^{-2}$ s$^{-1}$ in 2018 and 21.50 ± 0.87 µmol m$^{-2}$ s$^{-1}$ in 2019 with no difference between cultivars and treatments (Figure3A). In 2018, stomatal conductance ($g_s$) also remained stable between the 'Evangeline' and 'Covington' N0 and N100 plants, although its values varied between 300–500mmol m$^{-2}$ s$^{-1}$ (Figure 3B). Stable $g_s$ was similar to the plants grown in 2019, but still lower than a year ago, 227 ± 13 mmol m$^{-2}$ s$^{-1}$ in 2019 ($P < 0.05$). Almost the same variability as for



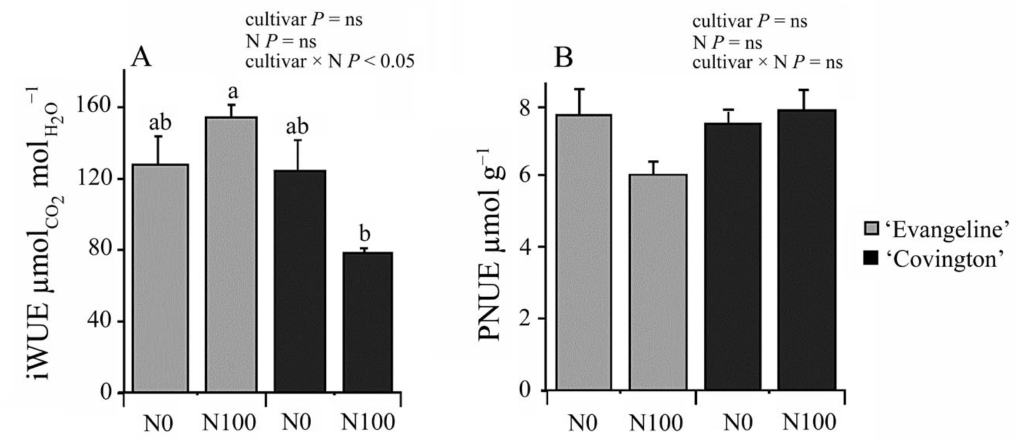
*Note.* The differences shown by lowercase letters were significant at $P < 0.05$.

***Figure 3.*** Mean (± SE) assimilation rate ($A$) (A), stomatal conductance to water vapour ($g_s$) (B), and ratio of intercellular to ambient $CO_2$ ($C_i$:$C_a$) (C) in the leaves of sweet potato cultivars 'Evangeline' and 'Covington' under N0 and N100 treatments

$g_s$ was found for the ratio of intercellular to ambient $CO_2$ ($C_i$:$C_a$) except for 'Covington', where fertilisation resulted in an increase in $C_i$:$C_a$ to level higher than in 'Evangeline' N100 plants ($P < 0.05$) (Figure 3C).

In 2019, the $C_i$:$C_a$ was not influenced by N and cultivar (0.577 ± 0.014), but the average $C_i$:$C_a$ value was significantly lower ($P < 0.05$) compared to the data of 2018. In 2018, the iWUE ($A/g_s$) was 70–150 µmol$_{CO2}$ mol$_{H2O}^{-1}$, and only the interaction of N treatment and cultivars had a significant effect on the iWUE, as the values of 'Evangeline' N100 and 'Covington' N100 plants differed ($P < 0.05$) (Figure 4A). In 2018 and 2019, due to the difference in $g_s$, the iWUE values were different and remained higher in plant leaves (150 ± 5) in 2019 ($P < 0.05$).

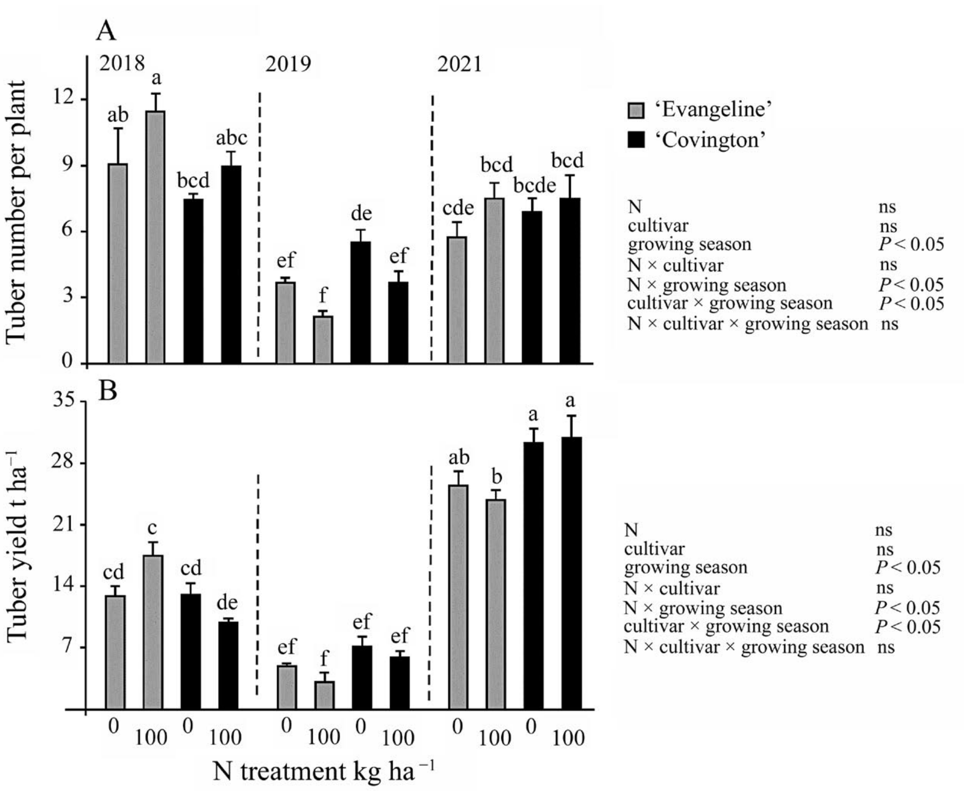
The PNUE ($A/N_A$) was evaluated only in 2018 (Figure 4B). The values show no variation within and between the cultivars of differently fertilised sweet potato plants. The data of PNUE and iWUE showed a negative linear correlation ($r = -0.66$, $P < 0.01$), and the PNUE to iWUE ratio was significantly higher in 'Covington' N100 than in 'Evangeline' N100 plants ($P < 0.05$). A positive non-linear regression was between the $N_A$ and $A$ values of the plants ($r = 0.28$, $P < 0.001$).



*Note.* The differences shown by lowercase letters were significant at $P < 0.05$.

***Figure 4.*** Mean (± SE) intrinsic water-use efficiency (iWUE, $A/g_s$) (A) and nitrogen use efficiency (PNUE) (B) in the leaves of sweet potato cultivars 'Evangeline' and 'Covington' under N0 and N100 treatments

***Effect of nitrogen fertilisation, growing season, and cultivars on sweet potato yield characteristics.*** During all three growing seasons, there was no effect of N dose and cultivar and no combined effect of these two factors on the tuber number per plant. Depending on the growing season, which involved both climate and soil properties, the tuber number per plant was the highest in 2018, followed by 2021 and 2019, which had the lowest result (Figure 5A). Nitrogen alone or in combination with cultivar and growing season had no effect on tuber yield. However, differences were found between cultivars, growing seasons, the combined effect of cultivar and growing season, and all three factors. The highest tuber yield was in 2021 for 'Covington' followed by 'Evangeline', and the lowest was in 2019 (Figure 5B).



*Note.* The differences shown by lowercase letters were significant at $P < 0.05$.

***Figure 5.*** Mean (± SE) tuber number per plant (A) and yield (B) of sweet potato cultivars 'Evangeline' and 'Covington' under combined effect of nitrogen treatment, cultivar and growing season analysed by three-way ANOVA

## Discussion

***Variability of leaf parameters of sweet potato cultivars and the effect of N fertilisation.*** During experimental years, potatoes and various cereals were used as pre-crops, and the sweet potato was cultivated by conventional farming in the area selected. Thus, pre-crops that increase soil N availability and N fixation from the atmosphere may have contributed to the higher-than-normal N content per leaf dry mass ($N_M$) in 'Evangeline' plants (Yfantopoulos et al., 2022). Previous studies have mainly investigated the effects of legumes as pre-crops on leaf area, plant height and yield of subsequent crops (Tadesse et al., 2021). According to Villordon and Clark (2018), a significant difference in $N_M$ between cultivars indicates the cultivar-specific root system architecture that may have influenced the rooting and N fixation of the plants. Unfortunately, there is no information about the cultivar 'Covington'. However, infestation of stress-tolerant 'Evangeline' with the root-knot nematode *Meloidogyne incognita* increased the growth, volume, and number of lateral roots, while there was no change in root growth in a stress-susceptible cultivar 'Beauregard' (Villordon, Clark, 2018).

Not much is known about the photosynthesis of sweet potato. The $CO_2$ assimilation rate (*A*) of different sweet potato cultivars grown under managed field conditions showed variability between 21–30 µmol $m^{-2}$ $s^{-1}$ (Velumani et al., 2017). Although 'Evangeline' and 'Covington' originate from contrasting environments, in 2018 and 2019, their *A* values in Estonian field conditions were similar and as high as reported by Velumani et al. (2017).

Nitrogen is a major component of photosynthesis, so N supply usually modulates crop photosynthesis. However, the debate on the photosynthetic response of crops to N supply continues, as it is still unclear how N supply limits crop photosynthesis and how leaf N content is related to N supply (Seufert et al., 2019). The measured stomatal conductance ($g_s$) of sweet potato cultivars varies between 400–1000 mmol $m^{-2}$ $s^{-1}$, and the ratio of intercellular to ambient $CO_2$ ($C_i$:$C_a$) is near 0.7 (He, Qin, 2020). In the present study, a higher $C_i$:$C_a$ corresponded to a significantly higher $g_s$ in 'Covington' N100, indicating a higher $CO_2$ availability for photosynthesis in the intercellular airspaces.

Crops and corresponding cultivars differ in their ability to regulate how much water is lost per unit of carbon. Cultivars with high iWUE become increasingly important in the future environments characterised by a high atmospheric vapour pressure deficiency (VPD) (Leakey et al., 2019). A higher iWUE can be achieved by reducing $g_s$ or increasing $CO_2$ assimilation rate (*A*). In sweet potato study, the iWUE-values of 'Evangeline' and 'Covington' were similar to those published for herbaceous species (Ma et al., 2021). The $CO_2$ assimilation rate (*A*) was not significantly different, as the reduced iWUE and higher water cost per assimilation was determined due to a significantly higher $g_s$ and correspondingly higher $C_i$:$C_a$ in 'Covington' N100 plants (Li et al., 2017).

***Effect of N fertilisation, soil, and climate on sweet potato yield.*** Nitrogen is of greatest importance in the formation of roots and tubers (Si et al., 2018). However, to obtain sustainable crop yields, soil properties must also be monitored and, if necessary, improved by tillage or fertilisation (Glab et al., 2016). In 2018, 2019, and 2021, after comparison of the nutritional status of the soil before planting, it was found that in 2019 the soil was low in potassium (K) and magnesium (Mg). Potassium promotes photosynthesis, flow of carbohydrates from leaves to tubers, and the formation of potato tubers (Bishwoyog, Swarnima, 2016). The positive effect of K fertiliser on sweet potato yield and nutritional value is also known (Aboyeji et al., 2019). Magnesium (Mg) content in potato roots and leaves depends on its amount in the soil (Koch et al., 2020). Magnesium is involved in chlorophyll synthesis, enzyme activation and protein synthesis and, as well as K, in the transportation of photosynthesis products (Ishfaq et al., 2022). Magnesium deficiency also reduces root growth indicating a limited phloem transport of photosynthesis products and other metabolites to the roots (Chaudhry et al., 2021). Thus, both K and Mg were able to support yield and tuber abundance in 2018 and 2021.

The increase in photosynthetic capacity of rice plants by chloroplast $CO_2$ concentration, mesophyll thickness, mesophyll cell wall thickness and chloroplast length depended on soil enrichment with ammonium ions ($NH_4^+$) or nitrate ions ($NO_3^-$) (Gao et al., 2020). To determine the relationship between the productivity of sweet potato and fertilisation, different fertilisers were tested in the present study. Since the fertiliser YaraBela Axan N27 + S4 had no effect on photosynthesis characteristics and sweet potato yield in 2018 and 2019, it was decided to change the fertiliser in 2021. The fertiliser YaraBela Axan N27 + S4 contained N in the $NH_4^+$ and $NO_3^-$ forms and sulphur (S) in the $CaSO_4$ form. Although S at different rates of N and phosphorus (P) increases sweet potato tuber yield, according to Gao et al. (2020), the positive effect of simultaneously acting $NH_4^+$ and $NO_3^-$ on leaf anatomy of sweet potato is questionable (Navarro, Padda, 1983).

Soil pH is also important, as nutrients become available to plants at a pH of 6.0–7.5. In 2018, 2019, and 2021, the soil pH and several nutrients including N varied significantly in the soil samples, so, in 2021, soil pH may have been one of the factors responsible for the high yield of sweet potato. In a study by Navarro and Paddy (1983), soil pH ranged from 7.5 to 8.2.

Further studies could be conducted with lower fertiliser rates such as at 50 kg ha$^{-1}$ to compare the yield of sweet potato cultivars with low and high fertiliser rates.

In 2018 and 2021, the tuber yield was similar to the results obtained in Malaysia (9.8–13.3 t ha$^{-1}$), Germany (16.0–34.0 t ha$^{-1}$), and Israel (15 t ha$^{-1}$) (Loebenstein, Thottappilly, 2009; Kell, Jaksch, 2014; Vosawai et al., 2015). Compared to the present study, only during the experiment carried out in the USA (Yencho et al., 2008), a higher yield of ‘Covington’ was obtained (45−48 t ha$^{-1}$). The reason why ‘Evangeline’ N100 plants produced higher tuber yield compared to ‘Covington’ N100 plants indicates a higher fertiliser requirement of ‘Evangeline’ plants. Also, ‘Evangeline’ is a cultivar from a warmer climate, while ‘Covington’ is from a cooler region.

In this study, the sweet potato tuber yield was also affected by temperature, which was significantly lower than in Africa and Asia, and the duration of the growing season, especially in 2019. Previous experiments in areas with a temperate climate and a shorter growth season showed the best yield for the cultivar ‘Beauregard’ compared to ‘Evangeline’ and ‘Covington’ (La Bonte et al., 2008; Yencho et al., 2008).

Taking into account the duration of the growing season, further studies of sweet potato should test plant growth by varying pre-cultivation conditions, planting dates and planting conditions in relation to tuber yield.

## Conclusion

1. The cultivation of sweet potato cultivars at different fertilisation rates did not affect the carbon content per leaf dry mass ($C_M$) nor photosynthetic characteristics of the plants, and nitrogen uptake and assimilation was higher in ‘Evangeline’ than in ‘Covington’.

2. The tuber number per plant and tuber yield did not increase with N fertilisation rates and different fertilisers in 2018, 2019, and 2021. Higher tuber yields in 2018 and 2021 were due to soil properties combined with a higher amount of precipitation during the tuber formation stage. In contrast to the nitrogen content per leaf dry mass ($N_M$), the tuber yield of ‘Covington’ was higher than that of ‘Evangeline’.

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