

Development, growth and chemical composition of the potato crop (*Solanum tuberosum* L.). I. leaf and stem

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Summary

In this first part of a review the development of the potato leaf and stem is described, based on research data and literature. The development over time, the daily changes of fresh and dry matter, the contents of organic and inorganic components (dry matter, starch, sugars, organic acids, ascorbic acid, nitrogenous compounds, nitrate, glycoalkaloids, chlorophyll, P, K, Ca, Mg, Mn, Na, trace elements), and physiological parameters (rate of assimilation and photosynthesis, activity of enzymes) of the leaf and stem are described and discussed for every phenological growth stage of the potato crop.

Introduction

This paper presents a compendium of available information including the experiments of Deffner (1987) and Stephan (1989) about the development, growth and composition of the potato leaf, stem and tuber during the vegetative period. Therefore, experimental data, including different cultivars, years and locations, has been collected and analyzed to develop universal statements. Through graphic and tabular presentations of the individual components an overall view of the phenological growth shall be obtained.

For the preparation of graphs and tables results have been used from the following papers: Wilfarth et al. (1906), Appleman & Miller (1926), Lehmann (1926), Ahmed (1931), Dastur & Agnihotri (1934), Singh & Mathur (1937, 1938) cited by Burton (1966), Lampitt et al. (1945), Street et al. (1946), Wolf & Duggar (1946), Barker (1950), Minina (1953), Carpenter (1957), Plaisted (1957), Passeschnitschenko (1957), Thorne (1960), Buhr (1961) cited by Mengel (1971), Radley et al. (1961), Hagemann (1962, 1964), Johnston & Rowberry (1962), Müller (1962, 1964, 1975a,c), Werner (1962), Wittstock (1962), Carpenter (1963), Heyland (1963), Baerug (1964), Pätzold & Stricker (1964), Burt (1965), Lorenz (1965) cited by Smith (1977), Raeuber & Engel (1966), Moorby (1968), Vertregt (1968), Hughes & Evans (1969), Soltanpour (1969), Staikov (1969), Burton & Wilson (1970), Nakaseko et al. (1970), Umaerus (1970), Varis (1970), Doll et al. (1971), Sowokinos (1971), Sanders et al. (1972), Wünsch (1972), Gray (1973), Kopp (1973), Kunkel et al. (1973), Sowokinos (1973), Berkeley & Galliard (1974), Hunnius (1974), Necas (1974), Dambroth (1976),

Zimmermann & Rosenstock (1976), Iritani & Weller (1977), Snyder et al. (1977), Wurr (1977), Clutterbruck & Simpson (1978), Holm & Nylund (1978a,b), McCollum (1978), Scott & Wilcockson (1978), Shekhar et al. (1978), Soltanpour & Cole (1978), Ahmed & Müller (1979), Reust (1979), Shekhar & Iritani (1979), Allen & Scott (1980), Haeseler (1980), Moll (1980), Randeni (1980), Aeppli et al. (1981), Caesar et al. (1981), Heerkloss (1981), Iritani (1981), Kleinkopf et al. (1981), Putz (1981), Forster & Beringer (1983), Ifenkwe & Allen (1983), Kapoor & Li (1983), Mazza (1983), Weaver & Timm (1983), Olteanu (1984), Greenwood et al. (1985), MacKerron & Davies (1986), Millard & Marshall (1986), Rhue et al. (1986), Davies et al. (1987, 1988), Deffner (1987), Green (1987), Zgorska (1987), Jefferies & MacKerron (1989), Stephan (1989), Röhricht (1990), Vander Zaag et al. (1990), Haverkort et al. (1991), Nitsch & Varis (1991), Harris (1992), Moll (1992), Domek et al. (1995).

In the first part the development of the biomass and the chemical composition of the potato leaf and stem are described. In the second part (Kolbe & Stephan-Beckmann, 1997) the development of tubers and of the whole plant is presented from emergence until maturity.

Phenological growth stages of the potato crop

The growth and development of potato plants can be divided into several genetically and environmentally controlled growth stages. Knowledge of these stages is required for scientists as well as for farmers. Previous research has described schemes which make it possible to assess the stages quantitatively (Müller, 1975b; Bätz et al., 1980; Griess & Moll, 1985; Griess et al., 1987).

The two-digit scale of Hack et al. (1993) includes 10 stages of growth and development in relative scales from 00 (dormant seed tuber) to 99 (harvested tuber). In Fig. 1 these growth stages are shown. For reasons of exact comparison between these growth stages and the following representations, the days after emergence (d.a.e.) are given as well.

The leaves

Fig. 2 shows the vegetative course of the total leaf dry matter and of the photosynthetically inactive yellow leaf portion (hatched). After a steep initial increase, during which the leaf dry matter mounts nearly 3-fold in about 15 days, a decrease of about 60% of the maximal values follows because of leaf fall and remobilization of minerals at the end of the vegetation period.

The production of leaf dry matter as well as the leaf area index, the concentration of chlorophyll and the water consumption of the plant (Schröder, 1976) are characterized by similar time courses, while the rate of assimilation shows the highest values in meristematic young leaves (Moll, 1982). During the time of exponential increase of dry matter, the rate of nett assimilation decreases rapidly to a level of 7–8 g dry matter per m² leaf area and day. The rate of nett assimilation strongly depends

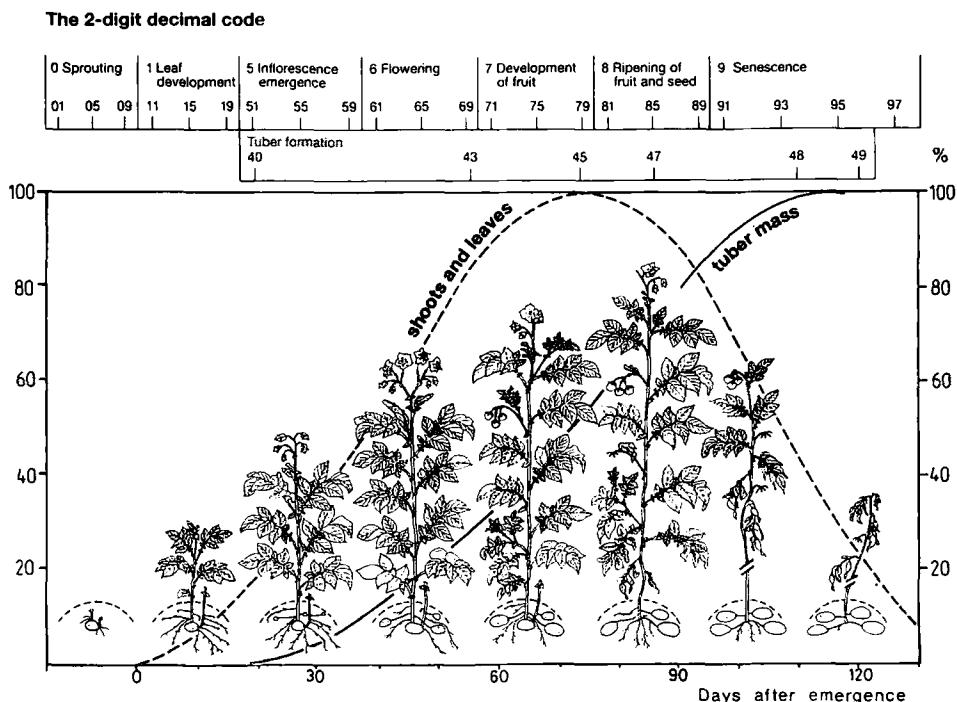


Fig. 1. Phenological growth stages of the potato crop (after Hack et al., 1993).

on cultivar, photoperiod and other environmental conditions (Frier, 1977; Moll, 1982) so that the relative rate of photosynthesis can differ from the presented course (see Fig. 2). After the beginning of the reduction of the photosynthetically active biomass these parameters decrease again. In addition, the course of nutrient uptake per root unit is similar to that of the rate of assimilation or photosynthesis (de Willigen & van Noordwijk, 1988).

The dry matter concentration of very young leaves is relatively high (Fig. 2). Thereafter, it declines to an intermediate level (about 10% dry matter) which is relatively constant (cf. Hagemann, 1964). During leaf senescence the dry matter concentration increases markedly.

The concentration of starch in the leaves can vary greatly at the same developmental phase. In some experiments levels of more than 20% were measured; in others only 1% starch in DM were found. Moreover, a diurnal rhythm can be observed. Depending on the rate of photosynthesis and translocation of assimilates during the day, an increase of the starch content located in chloroplasts (up to 5–7% of the leaf DM) takes place. During the night, translocation of assimilates into growing tubers occurs, so that shortly before the onset of light exposure the starch

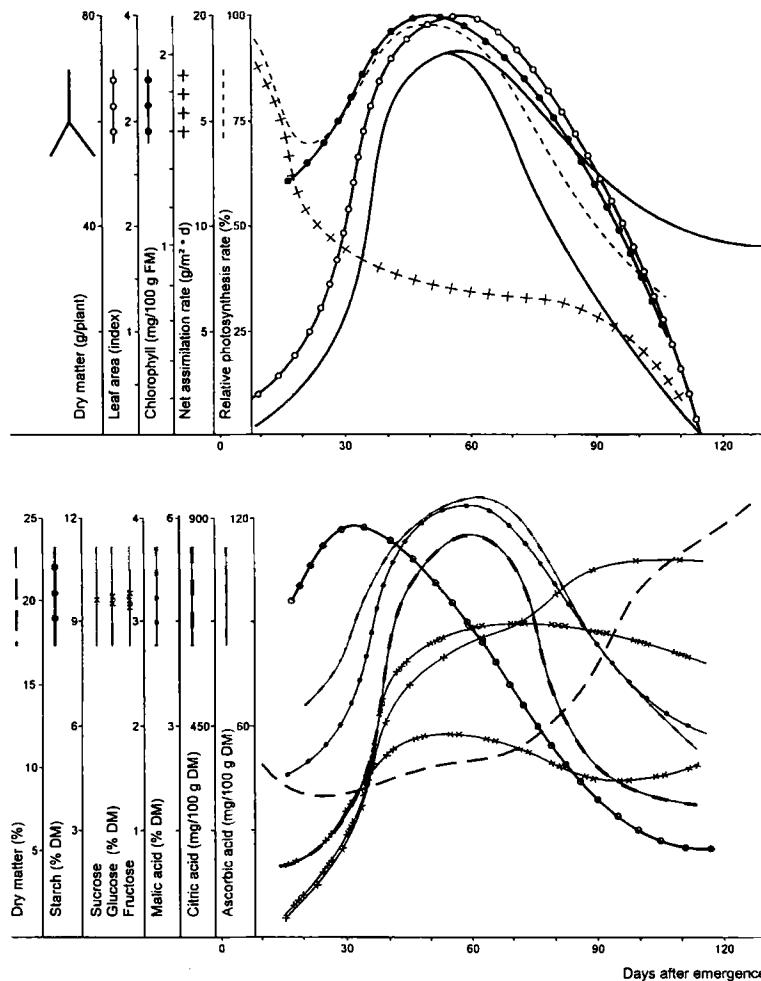


Fig. 2. Development over time of dry matter, leaf area, rate of assimilation and contents of organic and inorganic compounds of leaves.

content may be only about 1% (Müller, 1964). Generally, the concentration of starch increases in the young plant and then subsequently, starting at the time of tuberization, decreases continuously (Fig. 2). However, during periods of high temperatures, tuber starch synthesis is inhibited and starch content of the leaves may remain stable or even increase during the later vegetative growth (Müller, 1962; Randeni, 1980).

Parallel to the marked increase in leaf dry matter of young plants, an increase of the sugar content can be seen (sucrose, glucose, fructose). Old leaves which are no longer

assimilating have the highest concentrations of sucrose, while the reducing sugar content (glucose, fructose) decreases again at the end of the vegetative period. Tsovyan & Kotikyan (1974) also observed a decrease in sucrose content during the late season. The weather conditions can influence the carbohydrate concentrations in stems and leaves. High contents of sucrose and starch always occur when high temperatures lead to low starch deposition into the growing tubers.

The leaf contents of sucrose and reducing sugars show a strict daily rhythm. Sugars and starch decrease during the night and lowest values occur a short time before sunrise (about 04.00 h) in potato stems and leaves. The highest reducing sugar content is usually obtained between 14.00 h and 16.00 h; of starch at 16.00 h and of sucrose between 16.00 h and 18.00 h. Maximal rates of CO_2 uptake (apparent assimilation) occur between 10.00 h and 16.00 h (Meinl, 1963). The light condition in the canopy also influence sugar levels. In the lower canopy maximum sugar contents are reached at 12.00 h but in the upper parts of the canopy not before 20.00 h. Usually, there is more than 100% difference between day and night in the contents of sucrose and reducing sugars. Younger leaves (15 days) contain about 20% lower levels of sucrose and older leaves (about 30 days) have 20% higher values respectively. The diurnal course of reducing sugar concentrations do not change with leaf age (Meinl, 1963).

The changes of ascorbic, malic and citric acid during the vegetative period are similar to those described for the sugars (Fig. 2). Citric acid shows the largest oscillation. Minina (1953) found a diurnal cycle for these acids. In contrast to the sugars, leaves have the highest values for acids at the end of the darkness and the lowest values at 18.00 h.

The leaves of young plants show maximal contents of glycoalkaloids (β -solanine, β -chaconine) (Fig. 3). Varying environmental conditions can affect the contents of these alkaloids too. The courses of several nitrogen compounds in potato leaves are also shown in Fig. 3. The highest concentrations of crude protein, pure protein, nonprotein nitrogen (including free amino acids and amides) and of nitrate are found in very young plants. After the beginning of exponential dry matter growth, the concentrations of crude and pure protein decrease down to a level of 3.5–4.0% DM at maturity. Later, in senescing leaves a marked decrease of protein containing components can be seen as the result of nutrient remobilization (Millard & Marshall, 1986).

The activity of the enzyme nitrate reductase, which is mostly localized in leaves, takes a close reciprocal course in relation to the protein content of the leaves, while the relation between the nitrate reductase activity and the nitrate content of leaves or in the sap of stems is different (Kapoor & Li, 1983; Davies et al., 1987). Dependent upon the light conditions, the highest nitrate reductase activity is observed during the time of maximal dry matter growth of the potato crop (Davies et al., 1987; von Meltzer, 1987; cf. Table 1). According to results of Murti & Balasimha (1983) the activity of this enzyme shows an initial maximum in very young plants. During tuber initiation the enzyme activity is very low; thereafter, the activity rises very markedly with a course similar to the relative rate of photosynthesis (cf. Fig. 2).

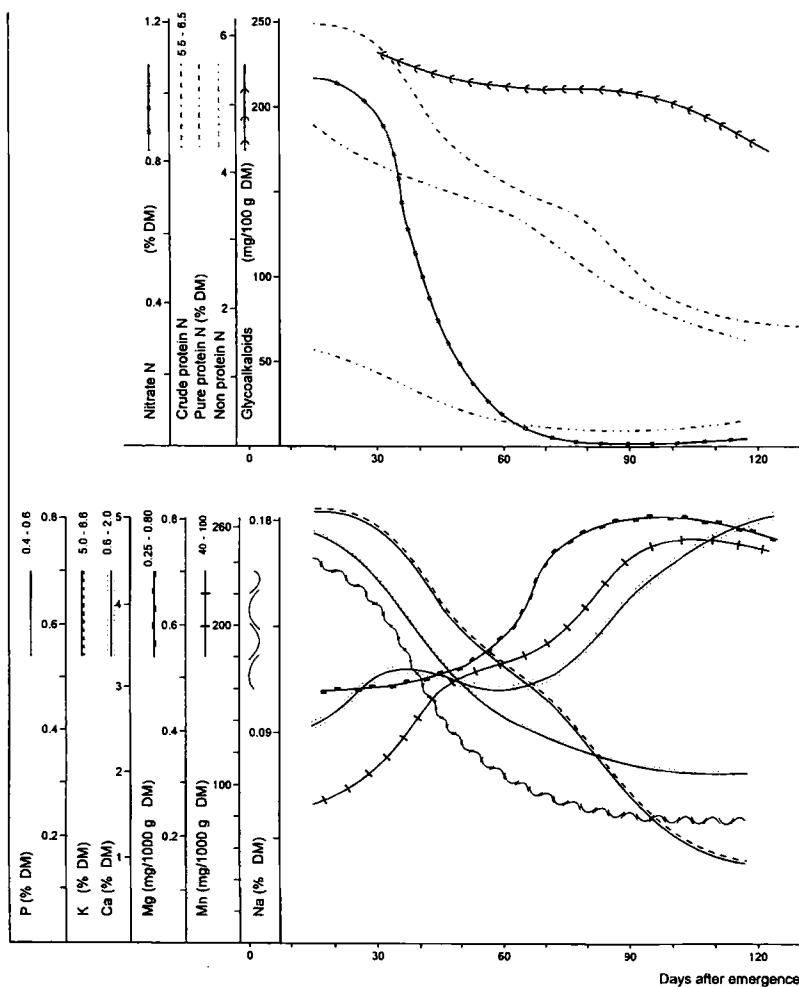


Fig. 3. Development over time of the concentrations of nitrogen compounds, glycoalkaloids and minerals in leaves of the potato crop (contents of sufficient nutrient supply are given after Bergmann, 1993).

The nonprotein nitrogen and nitrate concentrations of leaves are continuously decreasing during the whole plant development (Fig. 3). Notably the nitrate and other nutrient levels vary over different nutritional and climatic conditions (Lorenz, 1965, cited by Smith, 1977; MacKerron & Davies, 1986; Nitsch, 1987; Müller, 1988). In contrast to most of the nutrients, the contents of free amino acids and amides often increase, to some extent, at the end of the season because catabolized, but not translocated, protein-N is accumulated in the leaves.

The courses of the mineral concentrations (phosphorus, potassium, sodium) are similar to that of nitrate and, therefore, they are characterized by a very strong decrease during the vegetation period (Fig. 3). A more or less pronounced intermediate level between fruit development and fruit ripening (cf. Fig. 1) can be described for the high polymeric nitrogen compounds and for several minerals, especially potassium. In contrast, the concentrations of calcium, magnesium and manganese in senescing leaves show characteristically large increases. Remobilization and translocation of these minerals are low or does not take place.

Table 1 provides information about the time courses for potato leaf components. Maximal values of leaf biomass, organic and inorganic compounds are reached between 45 and 50 d.a.e. The development of leaf fresh matter is more rapid than that of the dry matter. During the time of highest growth rates between 30 and 45 d.a.e., daily values of $28.3 \text{ g plant}^{-1}$ and 1.13 t ha^{-1} of leaf fresh matter or 3.0 g plant^{-1} and 0.12 t ha^{-1} dry matter at 40,000 plants per hectare can be expected.

Maximal values of nitrate and nonprotein nitrogen for early in the season, about 30 d.a.e., are also shown in Table 1. The crude protein and pure protein are synthesized in lower rates. For example, in comparison to the maximal contents at 45 days, only 37% of pure protein is found 30 d.a.e.

Table 1. Development over time of fresh and dry matter and of the amounts of organic and inorganic components of potato leaves.

| content/plant | Days after emergence | | | | | | | |
|--------------------------|----------------------|-------|-------|-------|------|------|------|--------|
| | 15 | 30 | 45 | 60 | 75 | 90 | 105 | 120 |
| Fresh matter (g) | 57 | 277 | 702 | 697 | 520 | 310 | 190 | 152 |
| Dry matter (g) | 5.2 | 23.2 | 68.4 | 73.2 | 62.4 | 50.0 | 41.6 | 36.8 |
| Chlorophyll (mg/100g FM) | 0.75 | 4.73 | 15.15 | 14.85 | 9.26 | 3.97 | 1.08 | (0.50) |
| Starch (g) | 0.48 | 2.71 | 7.43 | 6.46 | 3.89 | 1.95 | 1.12 | 0.91 |
| Sucrose (g) | 0.01 | 0.21 | 1.64 | 2.05 | 1.93 | 1.75 | 1.50 | 1.33 |
| Glucose (g) | 0.03 | 0.27 | 1.27 | 1.39 | 1.06 | 0.75 | 0.62 | 0.59 |
| Fructose (g) | 0.01 | 0.23 | 1.80 | 2.14 | 1.85 | 1.45 | 1.14 | 0.94 |
| Malic acid (g) | 0.13 | 0.73 | 3.90 | 4.50 | 3.37 | 2.07 | 1.37 | 1.05 |
| Citric acid (g) | 0.06 | 0.38 | 3.43 | 4.19 | 2.79 | 1.20 | 0.82 | 0.69 |
| Ascorbic acid (mg) | 25 | 143 | 594 | 685 | 534 | 315 | 198 | 133 |
| Glycoalkaloids (mg) | (13) | 54 | 150 | 157 | 132 | 104 | 81 | 66 |
| Crude protein-N (g) | 0.32 | 1.34 | 3.00 | 2.88 | 2.22 | 1.50 | 1.04 | 0.81 |
| Pure protein-N (g) | 0.25 | 0.95 | 2.57 | 2.50 | 1.75 | 1.13 | 0.79 | 0.64 |
| Nonprotein-N (g) | 0.07 | 0.25 | 0.42 | 0.27 | 0.16 | 0.13 | 0.12 | 0.15 |
| Nitrate-N (mg) | 54.1 | 220.4 | 205.2 | 54.2 | 11.9 | 6.0 | 7.5 | 11.0 |
| P (mg) | 41 | 158 | 363 | 307 | 231 | 165 | 133 | 118 |
| K (g) | 0.27 | 1.13 | 2.70 | 2.38 | 1.64 | 0.84 | 0.48 | 0.34 |
| Ca (g) | 0.13 | 0.72 | 2.16 | 2.17 | 2.17 | 2.15 | 2.00 | 1.91 |
| Mg (mg) | 25 | 114 | 349 | 425 | 474 | 405 | 337 | 283 |
| Mn (mg) | 0.5 | 2.8 | 10.9 | 13.0 | 12.5 | 12.1 | 10.5 | 9.0 |
| Na (mg) | 8.4 | 32.3 | 54.7 | 54.9 | 42.4 | 32.5 | 26.6 | 23.7 |

Initially, the uptake of calcium, magnesium and manganese is comparatively low. During the time of the highest leaf biomass, the leaves of 1 hectare potato crop contain about 0.13 t nitrogen, 0.015 t phosphorus and 0.108 t potassium.

During the processes of remobilization and translocation small amounts of these components are left as leaf litter. 120 d.a.e. about 20% of the leaf fresh biomass or 50% of the maximal dry matter of the leaves is present. The amount of nonprotein nitrogen has decreased by about 65% and the amount of crude protein and pure protein by 73–75%, compared to the maximal stored values. About 0.063 t ha⁻¹ of the original leaf-stored nitrogen content is translocated at 120 d.a.e. The leaf contents of phosphorus, sodium and especially that of potassium are reduced by more than 50%. At the end of the vegetative period no similar decrease can be seen for the calcium, magnesium and manganese values (Table 1).

The stems

The accumulation of the stem dry matter including remobilization during senescence is parallel to the time course for the total leaf biomass. Altogether, the leaf dry matter is 25% higher than that of the stems (cf. Tables 1 and 2). The maximal growth of the stems takes place between 30 and 45 d.a.e. and amounts to about 0.84 t ha⁻¹ fresh matter or 0.09 t ha⁻¹ dry matter per day.

After emergence, the concentration of dry matter of young stems initially decreases from 6% to 4% and then increases up to 9–11% at complete canopy development, 60–90 d.a.e. (Fig. 4). Thereafter, the dry matter content increases because the water supply is halted during senescence.

The course of the starch content in the stems is somewhat delayed but follows the growth of the stems and it can reach a value of 3.8% just after emergence, 12.5% at the time of maximal biomass and declines to 2.5% at the end of the vegetative period. This time course is similar to that reported for roots (Wilfarth et al., 1906). The weather conditions can also markedly influence the starch content so that, for example, higher values occur during the later phases of growth and development (Randeni, 1980).

The changes in sugar contents (total sugars in fresh sap, glucose and fructose in DM of the stems) over time are also similar to the formation of dry matter. These assimilates reach maximal values some time earlier and decrease earlier than the dry matter values. The decrease of the sugar contents is nearly parallel to the course of the photosynthetically active leaf biomass (cf. Fig. 2).

According to Tsovyany & Kotikyan (1974) the upper parts of the canopy have about 0.5% higher content of sugars than the middle or lower parts during the main vegetative period. At senescence the sugar content decreases at a higher rate in stems compared to leaves and petioles (see Figs. 2 and 4).

Hofmann & Wünsch (1964) found that the concentration of sucrose follows a diurnal rhythm in stems with low values between 24.00 h and sunrise and the highest values between 15.00 h and 18.00 h. The concentrations of reducing sugars did not fluctuate strongly.

A relatively high content of ascorbic acid is obtained in young sprouts (Lampitt et al., 1945). The highest values, about 10 times the level found in stems, occur in leaves 40–80 d.a.e. because, except for sprouting tubers, the ascorbic acid content strongly depends on the light conditions. Therefore, in stems a contrary course to that in leaves is characteristic for ascorbic acid (cf. Fig. 2 and Fig. 4). With increasing shade from the leaves the concentration of this vitamin at first decreases in stems, then increases during early leaf senescence and begins to decrease again after stem senescence.

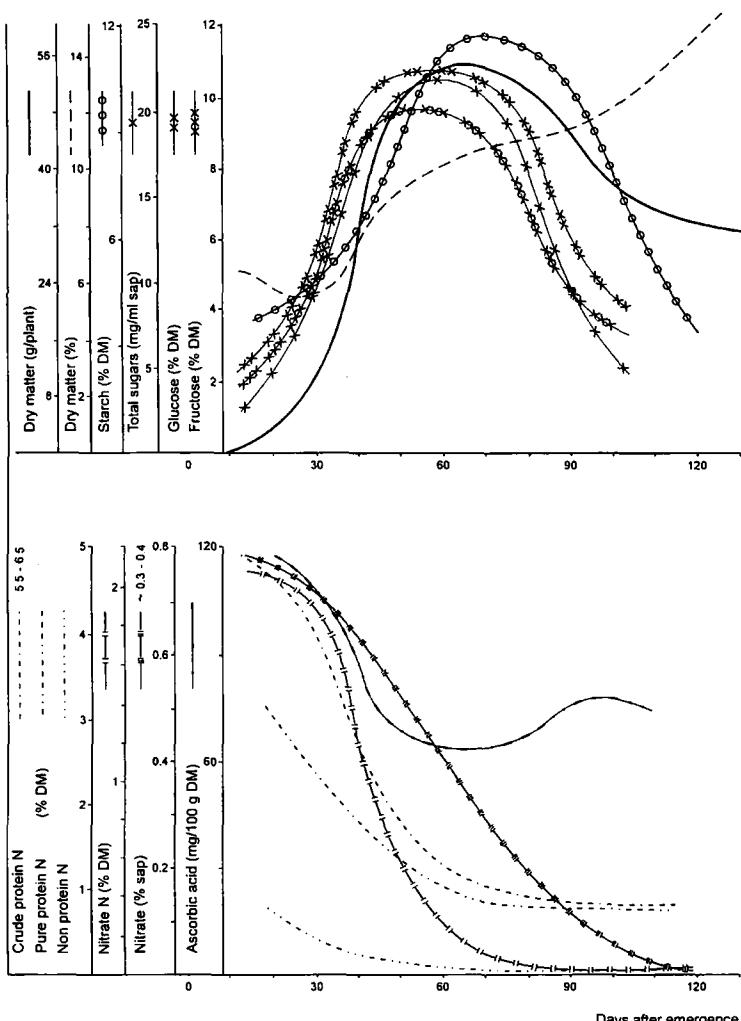


Fig. 4. Change of the dry matter and of nitrogen compounds of stems of the potato crop (contents of sufficient nutrient supply are given after Bergmann, 1993).

The time courses for nitrogenous compounds are similar to those in leaves (Fig. 4). The nitrate content (in the sap of stems or in DM) decreases in a marked reciprocal sigmoid form. During main canopy growth (30–70 d.a.e.) a huge decrease of the nitrate concentration usually can be seen. However other investigations have established that the nitrate course strongly depends on nutritional effects. Moreover, it can be used to determine the nitrogen supply of the plant (van Loon et al., 1987; Nitsch & Varis, 1991). From the projected nitrate course, it may be concluded that an exact knowledge of the phenological stages of the potato crop is necessary to assess the best method for split-dressing of nitrogen (see also Bates, 1971).

Further important minerals in stems (especially phosphorus, potassium and calcium) show a course similar to that of nitrate during the time of vegetation growth (Fig. 5) and can also be used to obtain information on the nutritional status of the plants (Copoly et al., 1971; Roberts & McDole, 1985; Bergmann, 1993). In this case, an exact description of the examined plant material is required because the mineral values for leaves and stems shown in the graphs are often different from the optimum ranges established by Bergmann (1993) which are documented in Figs. 3–5. For example, during the period 40–60 d.a.e. leaves contain higher concentrations of phosphorus and especially of calcium and lower values of potassium and manganese than estimated for stems while no marked differences in magnesium content between stems and leaves are obtained.

In the later season until senescence the contents of phosphorus and potassium in stems are usually slowly decreasing (Fig. 5). In contrast to this, the concentrations of calcium, sodium and zinc increase in the potato stems during the last stages of growth.

The strong increase of the concentrations of magnesium, manganese, iron, boron and especially of calcium and copper occurs for a different reason and is inversely related to the decrease of dry matter in stems during the second part of season. These minerals are not remobilized or translocated much and, therefore, they are left in the senescent stems.

The glycoalkaloids content of all plant parts strongly depends on the light conditions and large differences between the cultivars are found (Wolf & Duggar, 1946). Fig. 5 illustrates a mean course for glycoalkaloids in stems. Depending on the environmental conditions the values can differ from the predicted course. In young sprouts maximum contents of over 200 mg 100 g⁻¹ FM are found (Smittle, 1971). At the end of the growing period about 30 mg 100 g⁻¹ FM is usual.

Table 2 shows the development of the quantities of organic and inorganic compounds of the sprout during the vegetative period. Most of the components increase in the first part of the season while in the second part they decrease. But for calcium, magnesium, manganese, iron and sodium maximum values are found in dead stems late in the season or at the end of the growth period. In the leaves a small quantity of some of these minerals can be remobilized whereas only limited translocation into stems takes place.

This seems also to be true for nitrate. The nitrate concentration in stems is 2–3 times higher and the maximal stored nitrate amount is nearly 2 times higher than in leaves (cf. Tables 1 and 2). An intermediate storage of different organic nitrogen

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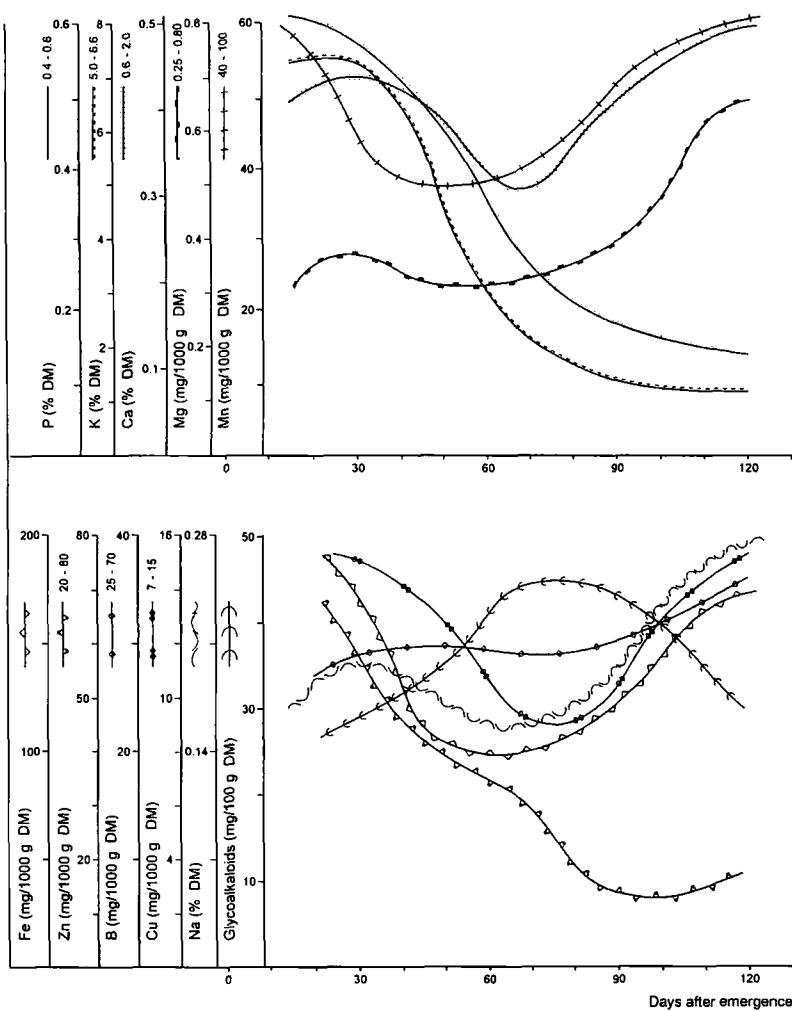


Fig. 5. Change of the concentrations of minerals and glycoalkaloids in stems of the potato crop (contents of sufficient nutrient supply are given after Bergmann, 1993).

components and of nitrate in older leaves and in stems of the potato plant has also been found by Millard & MacKerron (1986).

Table 2. Development over time of the amounts of fresh and dry matter and of organic and inorganic components of the potato stems.

| Content/plant | Days after emergence | | | | | | | |
|----------------------|----------------------|-------|-------|-------|-------|-------|-------|--------|
| | 15 | 30 | 45 | 60 | 75 | 90 | 105 | 120 |
| Fresh matter (g) | 28 | 201 | 515 | 537 | 486 | 392 | 280 | 220 |
| Dry matter (g) | 1.7 | 11.5 | 44.2 | 54.6 | 53.4 | 45.1 | 36.6 | 32.6 |
| Starch (g) | 0.07 | 0.56 | 3.29 | 6.12 | 6.25 | 4.60 | 2.35 | 1.09 |
| Glucose (g) | 0.05 | 0.67 | 4.56 | 5.88 | 5.29 | 2.71 | 1.38 | (1.30) |
| Fructose (g) | 0.04 | 0.60 | 4.08 | 5.19 | 4.30 | 2.06 | 1.15 | (1.10) |
| Ascorbic acid (mg) | 2.1 | 12.3 | 33.2 | 35.4 | 35.2 | 34.4 | 27.2 | 22.8 |
| Glycoalkaloids (mg) | 0.5 | 3.4 | 14.7 | 22.5 | 24.0 | 19.3 | 13.3 | 9.6 |
| Crude protein-N (mg) | 84 | 449 | 862 | 825 | 702 | 573 | 453 | 411 |
| Pure protein-N (mg) | 58 | 284 | 663 | 715 | 582 | 446 | 346 | 310 |
| Nonprotein-N (mg) | 17.4 | 53.6 | 101.7 | 70.9 | 42.7 | 31.6 | 22.0 | 26.1 |
| Nitrate-N (mg) | 36.6 | 226.5 | 371.4 | 152.7 | 40.6 | 19.8 | 11.8 | 14.0 |
| P (mg) | 11 | 68 | 217 | 191 | 123 | 81 | 57 | 46 |
| K (g) | 0.13 | 0.87 | 2.51 | 1.62 | 1.00 | 0.65 | 0.45 | 0.39 |
| Ca (mg) | 7 | 53 | 177 | 178 | 179 | 189 | 168 | 163 |
| Mg (mg) | 5 | 44 | 142 | 169 | 182 | 185 | 196 | 215 |
| Mn (mg) | 0.10 | 0.53 | 1.68 | 2.08 | 2.28 | 2.34 | 2.05 | 1.98 |
| Fe (mg) | 0.34 | 2.03 | 4.86 | 5.35 | 5.55 | 5.55 | 5.56 | 5.67 |
| Zn (mg) | 0.13 | 0.68 | 0.84 | 1.86 | 1.28 | 0.60 | 0.47 | 0.57 |
| B (mg) | 0.05 | 0.34 | 1.31 | 1.59 | 1.55 | 1.36 | 1.14 | 1.19 |
| Cu (mg) | 0.027 | 0.177 | 0.594 | 0.567 | 0.480 | 0.474 | 0.475 | 0.472 |
| Na (mg) | 3.0 | 22.5 | 77.8 | 84.6 | 86.0 | 87.9 | 89.8 | 89.9 |

The whole canopy

Table 3 provides data on the levels of constituents and Table 4 shows the derived rates of change for the canopy components (leaves and stems).

The maximal values of fresh and dry matter and most of the other components incorporated by the canopy are found 60 d.a.e. (Table 3). Only the nitrogenous compounds and the phosphorus and potassium nutrients reach their maximal values by 45 d.a.e. Thereafter, a marked decrease of all components can be seen because of remobilization, translocation or littering of leaves.

At the end of the season 30% of the maximal values of fresh matter and of nitrogenous compounds are found in the senescent potato canopy. The value of nitrate is reduced by more than 95% and the amounts of phosphorus, ascorbic acid and especially of starch and potassium are even more reduced than that of nitrate. The values of magnesium, manganese, sodium and calcium, however, are only decreased by 10–30% from their maxima (Table 3).

The highest rates of growth of all components listed are found between 30 and 45 d.a.e. (Table 4). At this time the plant synthesizes more than 5.0 g dry matter per day of leaves and stems (that is about 0.21 t ha^{-1} at 40,000 plants). Values of about $44.0 \text{ g plant}^{-1}$ (respectively 1.76 t ha^{-1}) water intake are usually found and, for example, the

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Table 3. Development over time of the amounts of fresh and dry matter, organic and inorganic components of the potato shoot (stems and leaves).

| Content/plant | Days after emergence | | | | | | | |
|---------------------|----------------------|------|-------|-------|-------|------|------|--------|
| | 15 | 30 | 45 | 60 | 75 | 90 | 105 | 120 |
| Fresh matter (g) | 85 | 478 | 1217 | 1235 | 1006 | 702 | 470 | 372 |
| Dry matter (g) | 7 | 35 | 113 | 128 | 116 | 95 | 77 | 69 |
| Starch (g) | 0.55 | 3.27 | 10.72 | 12.58 | 10.14 | 6.55 | 3.48 | 1.99 |
| Glucose (g) | 0.08 | 0.94 | 5.82 | 7.27 | 6.35 | 3.46 | 2.01 | (1.89) |
| Fructose (g) | 0.05 | 0.83 | 5.88 | 7.33 | 6.16 | 3.51 | 2.29 | (2.04) |
| Ascorbic acid (mg) | 27 | 156 | 628 | 721 | 569 | 349 | 226 | 155 |
| Glycoalkaloids (mg) | 13 | 57 | 164 | 179 | 156 | 123 | 94 | 75 |
| Crude protein-N (g) | 0.36 | 1.81 | 3.86 | 3.71 | 2.92 | 2.07 | 1.49 | 1.22 |
| Pure protein-N (g) | 0.30 | 1.23 | 3.24 | 3.22 | 2.33 | 1.57 | 1.14 | 0.95 |
| Nonprotein-N (mg) | 91 | 304 | 526 | 342 | 205 | 157 | 134 | 173 |
| Nitrate-N (mg) | 91 | 447 | 577 | 207 | 53 | 26 | 19 | 25 |
| Total-N (g) | 0.45 | 2.26 | 4.44 | 3.91 | 2.98 | 2.10 | 1.51 | 1.25 |
| P (mg) | 51 | 226 | 579 | 498 | 354 | 246 | 190 | 163 |
| K (g) | 0.40 | 1.99 | 5.21 | 3.99 | 2.65 | 1.49 | 0.92 | 0.73 |
| Ca (g) | 0.14 | 0.78 | 2.34 | 2.35 | 2.34 | 2.34 | 2.17 | 2.07 |
| Mg (mg) | 30 | 158 | 490 | 594 | 656 | 585 | 533 | 498 |
| Mn (mg) | 0.6 | 3.3 | 12.6 | 15.1 | 14.8 | 14.4 | 12.6 | 11.0 |
| Na (mg) | 11 | 55 | 133 | 140 | 128 | 120 | 116 | 114 |

Table 4. Daily rates of growth and change of organic and inorganic components of the potato shoot (stems and leaves).

| Content/plant | Days after emergence | | | | | | |
|----------------------|----------------------|--------|--------|---------|---------|--------|---------|
| | 15–30 | 30–45 | 45–60 | 60–75 | 75–90 | 90–105 | 105–120 |
| Fresh matter (g) | 26.23 | 49.25 | 1.18 | -15.23 | -20.25 | -15.49 | -6.55 |
| Water (g) | 24.38 | 44.06 | 0.17 | -14.43 | -18.87 | -14.30 | -6.02 |
| Dry matter (mg) | 1850 | 5195 | 1009 | -798 | -1379 | -1190 | -524 |
| Starch (mg) | 181.7 | 496.4 | 123.9 | -162.5 | -239.1 | -205.2 | -98.8 |
| Glucose (mg) | 57.5 | 325.4 | 96.7 | -61.3 | -193.0 | -96.6 | -7.9 |
| Fructose (mg) | 52.2 | 336.4 | 97.0 | -78.3 | -176.7 | -81.0 | -16.9 |
| Ascorbic acid (mg) | 8.587 | 31.472 | 6.196 | -10.116 | -14.626 | -8.252 | -4.687 |
| Glycoalkaloids (mg) | 2.942 | 7.150 | 0.9761 | -1.542 | -2.188 | -1.909 | -1.267 |
| Crude protein-N (mg) | 97.1 | 136.5 | -10.5 | -52.0 | -56.6 | -38.7 | -18.1 |
| Pure protein-N (mg) | 62.0 | 133.5 | -1.1 | -59.0 | -50.5 | -29.0 | -12.4 |
| Nonprotein-N (mg) | 14.2 | 14.8 | -12.3 | -9.1 | -3.2 | -1.5 | 2.6 |
| Nitrate-N (mg) | 23.8 | 8.7 | -24.7 | -10.3 | -1.8 | -4.3 | 3.8 |
| Total-N (mg) | 120.9 | 145.2 | -35.1 | -62.5 | -58.4 | -39.1 | -17.7 |
| P (mg) | 11.63 | 23.57 | -5.39 | -9.64 | -7.17 | -3.74 | -1.78 |
| K (mg) | 106.5 | 214.7 | -81.3 | -89.9 | -77.0 | -37.7 | -6.6 |
| Ca (mg) | 42.3 | 104.1 | 0.7 | -0.3 | -0.3 | -11.5 | -6.6 |
| Mg (mg) | 8.49 | 22.17 | 6.89 | 4.13 | -4.69 | -3.49 | -2.31 |
| Mn (mg) | 0.183 | 0.620 | 0.163 | -0.020 | -0.021 | -0.123 | -0.106 |
| Na (mg) | 2.90 | 5.20 | 0.47 | -0.74 | -0.53 | -0.27 | -1.90 |

uptake of nitrogen is about 5.81 kg ha^{-1} .

The highest rates of reduction are shown for nitrogenous compounds (especially nitrate and nonprotein nitrogen) as well as for phosphorus and potassium between respectively, 45–60 days, and 60–75 d.a.e. (Table 4). At that time period, for example, one hectare of standing canopy displaces about 2.5 kg N and 3.6 kg K per day. Other ingredients are reaching their highest negative rates 75–90 d.a.e. During this period the fresh matter can decrease by about 0.81 t ha^{-1} . The water content may decrease for 0.76 t ha^{-1} . Pätzold & Stricker (1964) also found a maximal daily decrease of $0.5\text{--}1.0 \text{ t ha}^{-1}$ of fresh matter of stems during the second part of the vegetative period.

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