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Development, growth and chemical composition of the potato crop (*Solanum tuberosum* L.). II. Tuber and whole plant

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Summary

This second paper of the review describes the development of the potato tuber and whole plant based on research data and literature. The development and growth, daily changes of fresh and dry matter, and of the contents of organic and inorganic components (dry matter, starch, sugars, organic acids, ascorbic acid, nitrogenous compounds, nitrate, crude lipid, glycoalkaloids, P, K, Ca, Mg, Mn, Na), discolouration indices, and physiological parameters (rate of assimilation and respiration, activity of enzymes) are reviewed.

Introduction

This survey presents a compendium of available information about the growth and development and chemical composition of the potato tuber and plant. Investigations of Deffner (1987) and Stephan (1989) and many additional data are quoted and documented in the first part of the review (Kolbe & Stephan-Beckmann, 1997) in which phenological stages of the potato crop and the development of biomass and chemical composition of the potato leaves and stems were described in detail.

The tubers and roots

The development of important yield characteristics, contents of chemical compounds and indices of quality of the potato tubers are shown in Figs 1–3.

After tuber initiation the tuber dry matter initially increases exponentially (Fig. 1). Thereafter, a long period of nearly linear growth can be seen, followed by a decreasing rate and finally an end to growth when the shoot senesces. Moreover, a dry matter decrease occurs before the tubers are harvested. The course of the tuber dry matter is similar to that presented for the average tuber weight, tuber number, cell diameter and cell number per tuber.

Fig. 1 also shows that the number of tubers and the cell number per tuber somewhat precedes the growth of tuber yield. In the results presented most of the tubers are initiated in a very short period of only 10 days (see also Struik et al., 1988),

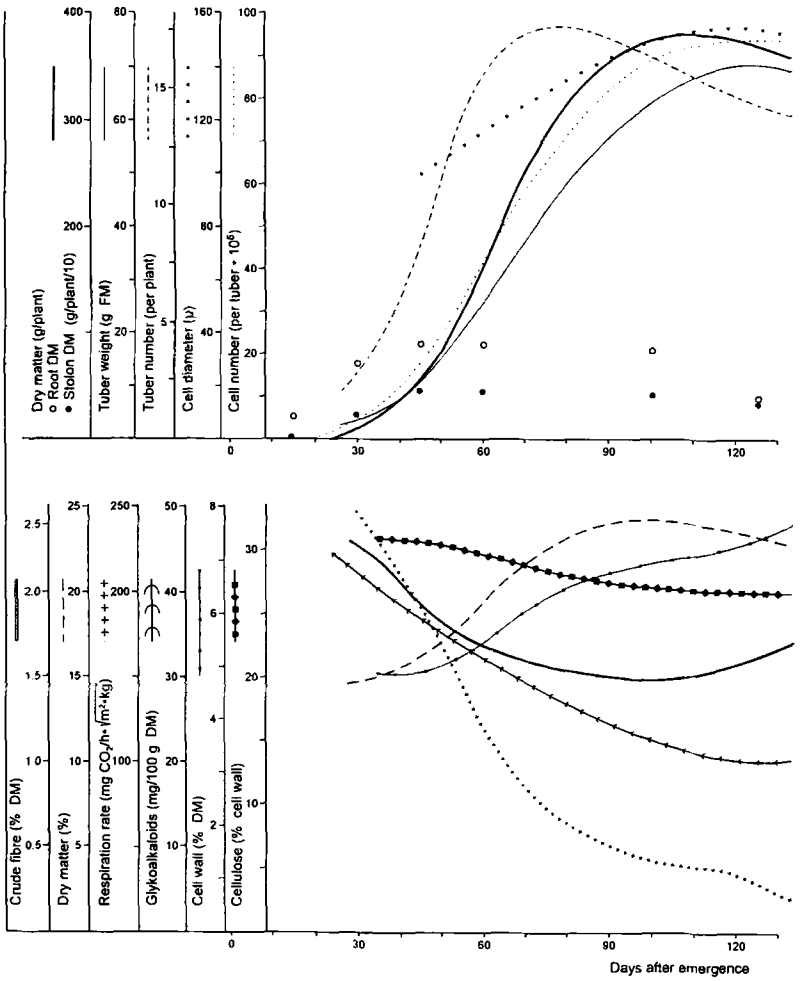

Fig. 1. Development over time of yield characteristics, cell wall components, rate of respiration and glycoalkaloid content of the potato tubers.

while the maximal number of tubers is approximately reached after the shoot dry matter begins to decrease. Thereafter, the tuber number can drop markedly until harvest (in this case from 18 to 14 tubers per plant). Also results of Krijthe (1955), Pätzold & Stricker (1964) and Moll (1992b) show that resorption of already initiated tubers take place especially during the second part of the vegetative period.

Meredith (1988b) found several initiation phases for tubers. These findings are confirmed by Heyland (1963), Frederiksen (1957), Johnston & Rowberry (1962) and Pätzold & Stricker (1964). According to results of Meredith (1988b), newly initiated

tubers are growing in cohorts. That means that tubers of similar sizes are growing over a particular period whereas other cohorts are growing at another similar rate. In contrast, Marshall et al. (1993) found a synchronous tuber growth especially when only one period of tuber initiation is usually observed.

There is a close relation between the size of the mother tuber, the number of stems and the number of daughter tubers (Haverkort et al., 1990; O'Brien & Allen, 1992; Moll, 1992a, b; von Meltzer, 1992). Usually, the largest tubers are localized at the same plant position throughout the whole vegetative period. But there are also periods of time during which small and large tubers are together increasing or decreasing in size. Therefore, this means that large tubers can be affected to a greater extent by a growth check than smaller tubers. Mechanisms of tuber size distribution have been reviewed by Struik et al. (1990, 1991).

At the time of harvest Lehmann (1926) (cf. Müller & Lehmann, 1926) obtained a relatively high positive correlation between the weight of the tubers and the diameter of the cells (see Fig. 1). Cultivar-specific differences in cell size are established early in the season.

As shown in Fig. 1 the cell number increases with diminishing rates nearly until maturity and a higher rate of assimilate storage can be observed (cf. courses of tuber yield in comparison to other parameters mentioned). Between 60 and 100 days after emergence (d.a.e.) the cell wall nearly doubles in thickness (Reeve et al., 1973). Parallel to the increase in tuber dry matter content the cell wall components (and the relative contents of pectin and lignin in the cell wall) show an inverse sigmoid increase. Cellulose in the cell wall decreases and the degree of pectin esterification increases during the vegetative period (Zgorska, 1987). According to Baumann (1957), the potential osmotic values increase by about 25% during the growth of tubers.

The content of 2.2% crude fibre in very young tubers is the highest during growth. Thereafter, the crude fibre decreases continuously because of starch accumulation until maximal tuber yields are reached (process of dilution). When compared to the respiration rate a steadily lower quantity of assimilates is synthesized during the senescence of the potato crop. Consequently, a slight increase of the crude fibre content may take place in the period leading to crop maturity.

After tuberization a distinct increase of the rate of photosynthesis can often be seen (Kolbe & Stephan-Beckmann, 1997) which is associated with an exponential tuber growth. Thereafter, when the growth rate of tubers slowly decreases, the rate of photosynthesis drops (Moll, 1982). The maximal tuber yield is reached when the major part of green leaves has died and the leaf area index reaches values lower than 1.0.

The course of tuber respiration during the vegetative period (Fig. 1) may be compared with that of the nett rate of assimilation of leaves (Fig. 2 in Kolbe & Stephan-Beckmann, 1997). After tuber initiation very high respiration rates are shown in young tubers followed by a clear decrease until the period during which rates of starch accumulation decline. After termination of starch accumulation (at the stage of maximal tuber yield, no photosynthetically active leaves are present) the

respiration rate of the senescing tubers decreases significantly.

Usually, very young tubers also have the highest glycoalkaloid contents which steadily decrease during the vegetative period (Fig. 1). According to Passeschnitschenko (1957), the major glycoalkaloid, α-chaconine, decreases at a higher rate than other alkaloid components of the tuber. High glycoalkaloid contents, which are harmful for human nutritition, can especially occur when harvest is very early, as is the case for early potatoes (Verbist & Monnet, 1979). After direct exposure of tubers to light, chlorophyll synthesis and formation of glycoalkaloids take place. Both components increase proportionally to the logarithm of light intensity and the tubers turn green (Liljemark & Widoff, 1960, cited by Schwardt, 1983).

Fig. 1 also shows the development of the root and stolon dry matter during the vegetative period (on a 1:10 scale in relation to the tuber dry matter). Comprising about 2% roots and 1% stolons these proportions are small in comparison to the total dry matter (Raeuber & Engel, 1966). The potato crop is characterized by a small and fine structured root system which is not deep-growing but wide-ranging and upper soil layers are rooted at high relative density (Brouwer et al., 1976). Usually the maximal root biomass is obtained some time before or at the time when the maximal shoot biomass is reached. In addition, after experiments of V. Schulz (unpublished) and Schulz (1994) at about 60 d.a.e. a maximal root length of 8–10 km plant^{-1} and a mean root radius of 0.135 mm is observed in sandy soils with a maximal root depth of 60 cm. Earlier, at about 30 d.a.e. the root length is 2–2.5 km plant^{-1} (0.145 mm radius) and at the end of vegetation the length is 3–4 km plant^{-1} (0.105 mm root radius).

The starch accumulation and synthesis of other organic compounds of the potato tubers are illustrated in Fig. 2. The course of starch accumulation is similar to that of dry matter (cf. Fig. 1) and reaches maximal values between 90–110 d.a.e. Thereafter, the starch content decreases slightly until maturity. The average size of starch granules is closely related to the development over time of the starch content (Putz, 1978). Hunnius (1974) found the maximal starch yield accumulated when more than half of the leaves are dead and the stems begin to die. These observations are in accordance with results shown here (cf. Fig. 2 and Fig. 4 in Kolbe & Stephan-Beckmann, 1997).

Some important enzymes of starch synthesis are marked by characteristic changes of activity during tuber growth. Parallel to increasing starch contents the levels of starch synthase, UDPG-pyrophosphorylase and phosphorylase in tubers increase (Sowokinos, 1976; Hawker et al., 1979). But only the course of starch synthase and especially that of ADPG-pyrophosphorylase is characterized by maximal activities during the stage of linear tuber growth. At the later stage of reducing rates of starch deposition the activity of ADPG-pyrophosphorylase decreases while further on starch synthase shows a high activity. Engels (1983) and Engels & Marschner (1986) showed that a close positive correlation exists between the ADPG-pyrophosphorylase/phosphorylase quotient and the activity of starch synthesis. In contrast to that, the activity of sucrose synthetase (in the sucrose splitting direction) is nearly parallel to the content of sucrose in growing tubers (Sowokinos, 1971, 1973).

The sugars (sucrose, glucose, fructose) have the highest levels in very young tubers (Fig. 2). Compared to the glucose content fructose usually reaches very low values earlier during the main vegetative period. These low contents are maintained over a period of time (Fig. 2). Only at the end of the season an increase of glucose and fructose often occurs. This may be caused by the seasonal decrease of the temperature and the reduced storage rate of assimilates.

The content of sucrose, particularly, may differ from the course shown in Fig. 2. Yamaguchi et al. (1960) and Miskovic (1987) found increasing values until flowering. In later growth stages the sucrose content decreased until harvest time. For this

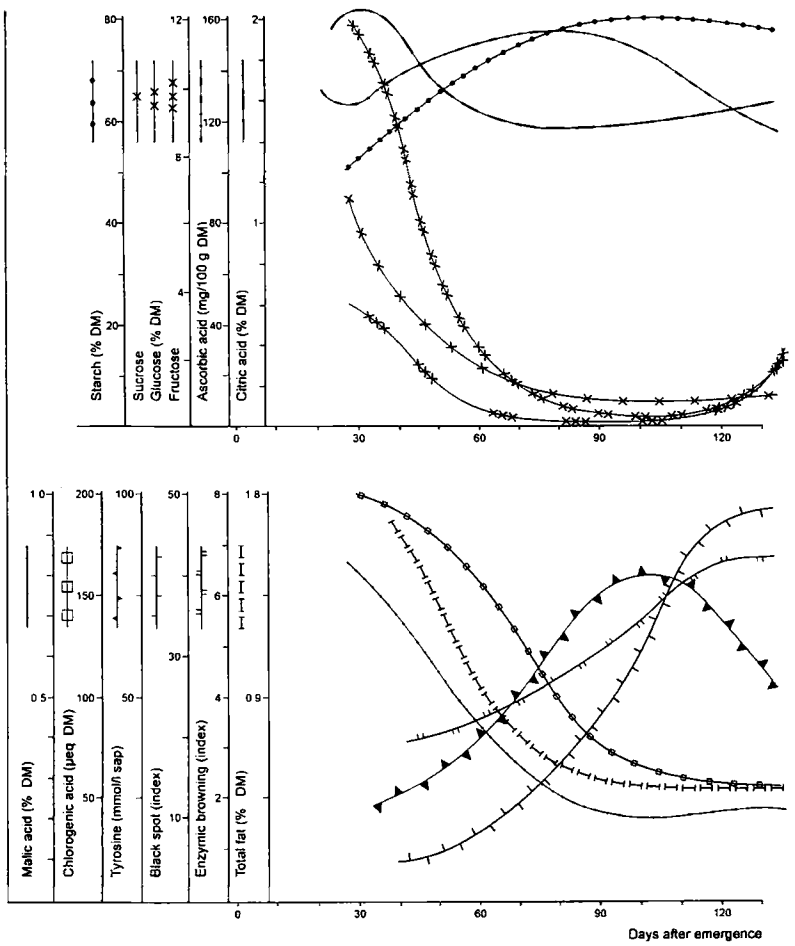

Fig. 2. Development over time of the organic compounds and of discolouration indices of potato tubers.

reason, in contrast to Putz (1981, 1984), it is suggested the sucrose content of tubers is a characteristic sign of maturity (Wünsch, 1964; Sowokinos, 1971, 1973, 1978; Müller, 1975; Sabhlok, 1975; Iritani & Weller, 1977; Reust & Aerny, 1985; MacKerron & Davies, 1986).

Throughout the vegetative period the course of the tuber glucose/fructose ratio is nearly parallel to the decrease of the sucrose content (cf. Weaver & Timm, 1983). A similar time course also occurs in tubers for malic, chlorogenic and, to a lesser extent, citric acid (Fig. 2). Establishing typical citric acid changes is difficult because tuber values show large fluctuations during the season.

According to Reust & Aerny (1985), the content of sucrose and malic acid decreases after harvesting and that of citric acid increases later during storage until dormancy break takes place. Thereafter, the values of citric acid decrease and the sucrose, malic acid and, later at sprouting, ascorbic acid concentrations increase again.

During the season the course of the ascorbic acid content in tubers is associated with the development of the shoot biomass and the highest values are reached at the time of maximal rates of tuber growth (Fig. 2). The concentration of ascorbic acid depends strongly on photoperiod and light intensity (see Kolbe, 1994). Therefore, important physiological contributions of ascorbic acid at photosynthesis, assimilation, protein biosynthesis and all processes of crop growth are described (Nanda & Tayal, 1976; Chinoy, 1984).

Calculations based on results of Yamaguchi et al. (1960) show similar courses of the content of niacin and ascorbic acid during tuber growth. At tuber initiation, contents of 3.9 mg niacin 100 g^{-1} DM are usually obtained. At the time of highest ascorbic acid contents maximal values of 4.8 mg and later on 3.4–3.5 mg niacin are found at the end of the vegetative period. The average content of vitamin B_1 of young tubers is 0.44 mg and about 0.60 mg 100 g^{-1} DM at harvest time and the content of vitamin B_2 remains nearly constant at 0.13 mg 100 g^{-1} DM during the season.

During growth of the potato crop, indices of tuber discolouration also change. Fig. 2 shows the black spot index (Aeppli et al., 1981) and the tuber browning value (value 1 = light, 9 = dark) increase throughout the season. These changes are inversely proportional to those of chlorogenic acid and of several minerals. For a long period the course follows that of the tyrosine content. After reaching maximal tyrosine content (a short time before the end of assimilate accumulation) the increase in the discolouration index is reduced. There seems to be no close correlation between the development of citric acid or ascorbic acid and the discolouration indices during the vegetative period.

The total fat content (Fig. 2) shows a large decrease, down to 1/3 of the original values of young tubers, but during the season no significant change in the fatty acid composition take place. Linolic acid amounts 50–55% and linolenic acid 16–19% of the total fatty acids. Together with palmitic acid these fatty acids totals about 90–95% of the tuber lipid composition (Galliard, 1972; Bolling & El Baya, 1973; Berkeley & Galliard, 1974). Results of Berkeley & Galliard (1974) and Schiemichen (1977) show large cultivar differences in the total lipid contents but the composition of fatty acids

is nearly constant.

During the vegetative period the course of various nitrogenous compounds is similar to most of the components shown in Fig. 3. Probably they are influenced by dilution effects caused by the storage of assimilates of growing tubers. Nevertheless, the incorporated quantities of these components usually are also increasing during the vegetative period until senescence (cf. Table 2).

The course of the concentrations of nitrate, calcium, sodium, iron, boron and aluminium is very different throughout the vegetation period (Yamaguchi et al., 1960; Sanders et al., 1972). In the examples in Fig. 3, the nitrate content of very young

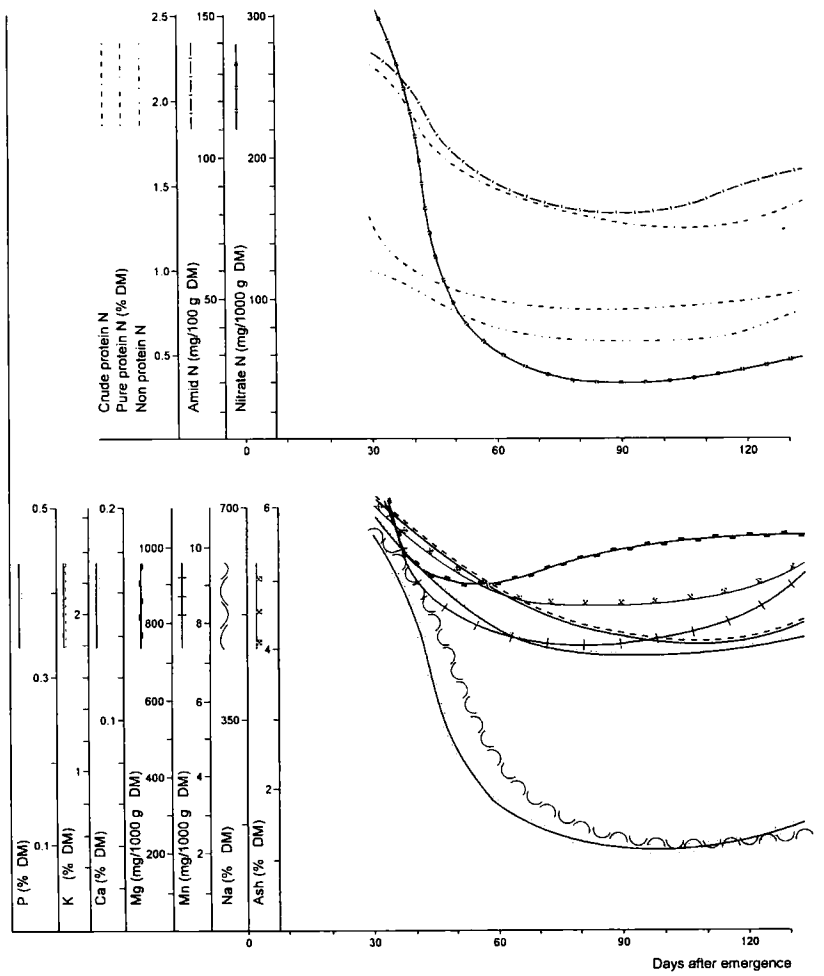

Fig. 3. Changes in the concentrations of nitrogen compounds and minerals of the potato tubers.

tubers amounts more than 300 mg (nitrate-N in 1 kg DM) and it can drop to less than 60 mg in 20 days. Dependant upon the nutrient availability of the soil, the nitrate content and also that of other minerals can change enormously during the later part of the growing season. Therefore, in mature tubers much higher nutrient concentrations can be found than presented in Fig. 3.

The change of the magnesium content clearly differs from the other minerals. During the exponential stage of growth the magnesium concentration first decreases markedly in young tubers. Thereafter, at times of relatively high growth rates, it increases (Fig. 3). The course of the growth rate and magnesium content of young leaves is similar (cf. Fig. 1 in Kolbe & Stephan-Beckmann, 1997). According to Addiscott (1976) intensively growing plant tissue is a dominant sink, especially for magnesium, which is caused by the specific antagonistic effects of potassium. After tuber initiation the tuber is the largest physiological sink of the potato crop. Therefore, in tuber materials a close positive correlation can be found between the contents of potassium and the contents of magnesium as well as of manganese (Kolbe, 1995).

The mineral content changes of the cell walls are different from the above-described time courses. The concentrations of calcium and magnesium show a particularly marked increase during the growing season (Braun, 1989). After harvest these minerals, as well as the content of pectin, increase during early storage until a certain "pseudo-climacteric" metabolic change takes place in which the contents of calcium and pectin decrease in the cell walls of stored tubers.

After reaching maximal tuber yields (cf. Fig. 1) the contents of all components shown in Fig. 3 increase slowly until harvest time. During senescence this enrichment is accentuated for the contents of acid amides and cannot be caused only by the concentrational effects of decreasing starch content. During the last part of the growing season nitrogenous compounds and several minerals are remobilized from the senescing shoot and translocated into the tuber.

In addition to these results, Table 1 reports the time courses of several chemical compounds for small (20–40 mm = s), medium (40–60 mm = m) and large tubers (60–80 mm = l). During the vegetative period small tubers usually contain the lowest concentrations of dry matter and starch, but late in the season the largest tubers seem to loose the highest quantity of starch, so that they have relatively lower starch contents. The content of dry matter is also closely related to the tuber size at harvest. Ifenkwe et al. (1974), Ifenkwe & Allen (1978) and Meredith (1988a) show a nearly non-linear increase of dry matter content until a tuber diameter of 5–6 cm is reached. At greater diameters the tuber dry matter decreases again. Mica (1970) and Haase (1993) found higher values of starch viscosity and a higher portion of amylose and larger starch granules in large tubers compared to relatively small tubers. Changes in tuber starch quality and viscosity properties during growth have been also analyzed by Madsen & Christensen (1996) and Christensen & Madsen (1996).

The small tuber sizes usually have by far the highest, and tubers of larger sizes the lowest, contents of crude and pure protein and of nonprotein nitrogen. However late in the season (120–130 d.a.e.) the crude protein and especially the nonprotein

nitrogen increases. Desborough (1985) and Hunnius (1977) found that young and small tubers in comparison to older and larger ones have relatively high protein and very high nitrate contents and only low values of starch. At harvest however large tubers can have relatively high, as well as low nitrogen concentrations, because of extreme differences in nutrient supply and weather conditions (availability of assimilates) throughout the vegetative period.

Averaged over trials, the medium tubers show the highest ascorbic acid content

Table 1. Changes of the chemical composition of small (s), medium (m) and large (l) potato tubers during the vegetative period, mean values of a two-year field trial and three cultivars in Germany (K. Müller, unpublished).

	Size	Days after emergence			
		60 – 70	80 – 90	100 – 110	120 – 130
Dry matter	s	19.0	19.5	21.2	21.2
(%)	m	19.7	19.6	21.5	21.0
	l	19.0	20.8	22.9	22.0
Starch	s	65.5	66.3	67.4	66.2
(% DM)	m	69.5	68.3	71.4	64.5
	l	69.3	67.5	71.6	63.6
Crude	s	10.63	9.86	10.44	10.16
protein	m	8.98	9.06	9.69	9.34
(% DM)	l	8.94	8.87	9.40	10.12
Pure	s	5.82	5.50	5.80	5.73
protein	m	5.34	5.11	5.27	5.40
(% DM)	l	5.19	5.06	5.11	5.45
Nonprotein	s	4.81	4.36	4.64	4.43
nitrogen	m	3.64	3.95	4.42	3.94
(% DM)	l	3.75	3.81	4.29	4.67
Ascorbic acid	s	134	151	133	102
(mg/100	m	158	134	123	145
g DM)	l	146	146	127	126
Reducing	s	0.97	0.40	0.38	0.98
sugars	m	0.35	0.45	0.26	0.81
(% DM)	l	0.32	0.22	0.27	0.32
Sucrose	s	2.28	2.33	1.33	0.95
(% DM)	m	2.16	1.99	1.12	0.87
	l	1.80	1.95	1.05	1.02
Total	s	0.55	0.58	0.46	0.59
lipids	m	–	–	–	–
(% DM)	l	0.49	0.44	0.35	0.41

and the small tubers the lowest (Table 1). Moreover, at any time throughout the season tubers of small sizes have the highest and the large sizes the lowest sugar contents, especially of reducing sugars. The same relationship is true for the total lipid concentration between small and large sizes and no important change of these relations is seen during the different growth stages. Small tubers have much higher lipid contents than larger tubers. This is especially true for the contents of unsaturated fatty acids (Schiemichen, 1977).

The change over time of several tuber components is shown in Table 2. The maximal values of most components are found at harvest. The maximal quantities of starch, total lipids, pure protein, glycoalkaloids, ascorbic and malic acid are reached at earlier stages (75–120 d.a.e.). Thereafter, these components decrease by 10–25% until senescence.

Maximal storage rates of water, fresh matter, glycoalkaloids, sucrose, malic acid, pure protein, potassium and particularly of nitrate and sodium are reached at early growth

Table 2. Development over time of the amounts of fresh and dry matter, organic and inorganic compounds of potato tubers.

		Days after emergence							
Content/plant		30	45	60	75	90	105	120	135
Fresh matter	(g)	48	335	836	1280	1487	1575	1591	1582
Dry matter	(g)	7	54	162	288	355	378	372	356
Crude fibre	(g)	0.16	1.05	2.72	4.49	5.33	5.63	5.80	5.98
Cell wall	(g)	0.4	2.6	8.8	18.0	24.0	26.6	26.9	27.1
Cellulose	(g)	0.11	0.80	2.58	5.10	6.56	7.14	7.18	7.20
Starch	(g)	4	34	115	221	281	302	293	275
Sucrose	(g)	0.41	0.81	2.27	2.30	2.13	2.08	2.23	2.49
Glucose	(g)	0.82	3.37	3.69	2.25	1.07	0.91	2.12	6.84
Fructose	(g)	0.24	0.97	0.88	0.52	0.43	0.57	1.79	7.90
Ascorbic acid	(mgt)	9	77	244	445	542	538	476	410
Citric acid	(g)	0.14	0.97	2.51	4.23	5.25	5.67	5.80	5.45
Malic acid	(mg)	57	345	693	821	763	756	744	730
Total lipids	(g)	0.12	0.81	1.56	1.89	1.95	1.97	1.93	1.89
Glycoalkaloids	(mg)	2.9	19.9	51.8	79.9	86.1	80.3	72.5	71.2
Crude protein-N	(g)	0.16	0.97	2.59	4.44	5.29	5.56	5.62	5.63
Pure protein-N	(g)	0.09	0.54	1.46	2.36	2.88	3.14	3.14	3.13
Nonprotein-N	(g)	0.07	0.44	1.09	1.87	2.31	2.42	2.46	2.49
Amid-N	(mg)	10	59	147	237	284	314	338	338
Nitrate-N	(mg)	2.2	7.4	10.2	12.9	14.2	15.7	18.1	19.6
Total-N	(g)	0.16	0.98	2.60	4.45	5.30	5.57	5.65	5.65
P	(g)	0.03	0.22	0.57	0.95	1.15	1.24	1.24	1.23
K	(g)	0.19	1.30	3.45	5.59	6.57	6.84	6.88	6.89
Ca	(mg)	13	60	96	127	139	147	164	164
Mg	(mg)	8	49	146	274	352	385	382	370
Mn	(mg)	0.08	0.46	1.25	2.14	2.65	2.91	3.20	3.20
Na	(mg)	4.7	27.6	45.4	52.4	52.9	52.9	53.2	53.4
Ash	(g)	0.4	2.9	7.8	13.5	16.6	17.9	18.3	18.6

stages (Table 3). Between 45 and 60 d.a.e. the maximal daily rate of fresh matter increase is 1.34 t ha^{-1} and of water uptake is about 1.05 t ha^{-1} (40.000 plants ha^{-1}). In addition, maximal increase rates of tuber initiation, glyoalkaloid, malic acid and crude protein synthesis are observed. A maximal daily increase of about $1.7x10^6$ cells per tuber and a maximal expansion of the cell diameter of 1.1 μ take place. At times of the highest rates of tuber dry matter growth, 60–75 d.a.e., the maximal rates of changes for most of the components are obtained (Table 3). Tubers of one hectare accumulate 0.34 t dry matter, 0.28 t starch, 4.9 kg N, 1.0 kg P, 5.7 kg K per day. In contrast to the above-ground plant parts, negative rates of change are only calculated for a few tuber components.

Table 3. Calculated daily rates of growth of fresh and dry matter and of chemical compounds of potato tubers.

		Days after emergence						
Content/plant		30–45	45–60	60–75	75–90	90–105	105–120	120–135
Fresh matter	(g)	19.10	33.41	29.61	13.77	5.89	1.07	-8.88
Water	(g)	15.97	26.21	21.21	9.31	4.36	1.47	0.48
Dry matter	(g)	3.13	7.20	8.40	4.47	1.53	-0.40	-1.07
Tuber number/plant		0.369	0.503	0.124	-0.036	-0.094	-0.073	-0.061
Cell number/tuber·10^6		0.933	1.667	1.533	1.100	0.567	0.167	-0.013
Cell diameter	(μ)	0.800	1.067	0.960	0.800	0.640	0.160	-0.267
Cell wall	(mg)	152.3	407.5	616.8	399.9	174.2	21.5	11.1
Cellulose	(mg)	46.4	118.5	167.9	97.3	38.7	2.9	1.1
Crude fibre	(mg)	59.2	111.6	118.1	55.5	20.5	11.4	11.9
Glycoalkaloids	(mg)	1.127	2.133	1.872	0.411	-0.384	-0.519	-0.089
Starch	(g)	1.987	5.415	7.099	3.999	1.416	-0.617	-1.221
Sucrose	(mg)	93.3	30.7	2.0	-11.3	-3.3	10.0	17.3
Glucose	(mg)	170.0	21.3	-96.0	-78.7	-10.7	80.7	314.7
Fructose	(mg)	48.7	-6.0	-24.0	-6.0	9.3	81.3	407.3
Ascorbic acid	(mg)	4.489	11.146	13.401	6.518	-0.278	-4.141	-4.403
Citric acid	(mg)	54.9	102.9	114.9	68.0	27.7	8.9	-7.1
Malic cid	(mg)	19.2	23.3	8.5	-3.8	-0.5	-0.8	-3.3
Total lipids	(mg)	45.8	50.0	22.2	4.0	1.3	-2.1	-3.2
Crude protein-N	(mg)	54.5	108.0	122.9	56.9	17.9	4.0	0.5
Pure protein-N	(mg)	29.7	61.5	60.3	34.3	17.4	0.4	-0.7
Nonprotein-N	(mg)	24.5	43.2	52.5	29.1	7.4	2.4	2.5
Amid-N	(mg)	3.321	5.843	6.000	3.130	2.003	1.582	0.028
Nitrate-N	(mg)	0.346	0.188	0.176	0.090	0.100	0.161	0.098
Total-N	(mg)	54.8	108.2	123.1	57.0	18.0	4.2	0.6
P	(mg)	12.5	23.5	25.1	13.6	5.7	-0.1	-0.7
K	(mg)	74.0	143.3	142.4	65.4	18.3	2.7	0.5
Ca	(mg)	3.13	2.37	2.07	0.79	0.58	0.43	0.01
Mg	(mg)	2.738	6.460	8.490	5.228	2.221	-0.199	-0.833
Mn	(mg)	0.025	0.053	0.060	0.034	0.018	0.019	0.0003
Na	(mg)	1.529	1.184	0.470	0.032	0.0027	0.018	0.014
Ash	(mg)	162.7	328.7	382.9	202.9	86.7	48.1	1.3

The whole plant

Tables 4 and 5 summarize calculated results for the development over time of the biomass and components of the whole potato crop (shoot and tubers).

Table 4 shows that maximal quantities of fresh and dry matter, of organic and inorganic ingredients are reached between 75 and 105 d.a.e. On a basis of 40,000 plants the maximal fresh matter of 91.5 t ha^{-1} is reached at an earlier growth stage than that of dry matter which amounts about 18.2 t ha^{-1}. The maxima for the nitrogenous compounds occur at characteristic, different times. The highest nitrate value is reached 45 d.a.e. whereas that of pure protein is not achieved until 30 days later. According to these calculations the maxima of nonprotein nitrogen is reached at the end of the vegetation period. At 75 d.a.e., at the time of maximal biomass production, the whole standing crop (shoot and tubers) of one hectare contains about 0.30 t N, 0.052 t P and 0.33 t K (Table 4).

In contrast, the maximal daily rates of change for most components in Table 5 have already been reached between 30 and 45 d.a.e. On the basis of 63 t ha^{-1} fresh matter of total yield, the daily growth rate is about 2.73 t ha^{-1} of fresh matter and about 0.333 t ha^{-1} dry matter. That is a mean daily rate of 0.139 t ha^{-1} dry matter during the whole vegetation period.

Raeuber & Engel (1966) calculated, for a mean tuber yield of 25 t ha^{-1} fresh matter, a daily rate of about 0.125 t ha^{-1} and for yields of 40 t ha^{-1} an increase of 0.250 t ha^{-1} of

Table 4. Development over time of dry and fresh matter and the amounts of organic and inorganic compounds of the total potato plant (shoot and tubers).

		Days after emergence								
Content/plant		15	30	45	60	75	90	105	120	135
Fresh matter	(g)	85	526	1552	2071	2286	2189	2045	1963	1911
Dry matter	(g)	7	42	167	290	404	450	455	441	423
Starch	(g)	0.6	6.9	44.2	127.3	231.3	287.7	305.9	295.1	276.7
Glucose	(g)	0.08	1.76	9.19	10.96	8.60	4.53	2.92	4.01	(8.67)
Fructose	(g)	0.05	1.07	6.85	8.21	6.68	3.93	2.86	3.83	(9.80)
Ascorbic acid	(mg)	27	165	704	964	1013	892	764	632	560
Glycoalkaloids	(mg)	13	60	184	231	236	209	175	148	140
Crude protein-N	(g)	0.36	1.97	4.83	6.30	7.36	7.36	7.05	6.84	6.84
Pure protein-N	(g)	0.30	1.32	3.77	4.68	4.69	4.45	4.27	4.09	4.07
Nonprotein-N	(g)	0.09	0.37	0.96	1.43	2.08	2.45	2.55	2.63	2.66
Nitrate-N	(mg)	90.7	449.2	584.0	217.1	62.4	40.0	35.0	43.1	43.5
Total-N	(g)	0.45	2.42	5.42	6.51	7.42	7.40	7.09	6.88	6.88
P	(g)	0.05	0.26	0.80	1.07	1.30	1.40	1.43	1.40	1.39
K	(g)	0.40	2.18	6.51	7.45	8.23	8.06	7.77	7.61	7.61
Ca	(g)	0.14	0.79	2.40	2.44	2.47	2.48	2.32	2.23	2.23
Mg	(mg)	34	166	540	740	929	937	918	881	865
Mn	(mg)	0.57	3.40	13.08	16.31	16.90	17.09	15.50	14.20	14.20
Na	(mg)	11	60	160	185	181	173	169	167	167

Table 5. Daily rates of growth of fresh and dry matter, organic and inorganic compounds of the potato plant (shoot and tubers).

Content/plant		Days after emergence								
		0–15	15–30	30–45	45–60	60–75	75–90	90–105	105–120	120–135
Fresh matter	(g)	5.64	29.45	68.35	34.59	14.38	-6.48	-9.60	-5.47	-3.49
Water	(g)	5.18	27.13	60.02	26.38	6.78	-9.56	-9.94	-4.55	-2.24
Dry matter	(g)	0.463	2.317	8.329	8.209	7.602	3.087	0.343	-0.924	-1.255
Starch	(g)	0.036	0.426	2.484	5.539	6.937	3.759	1.211	-0.716	-1.227
Glucose	(mg)	5.1	112.2	495.4	118.1	-157.3	-271.7	-107.3	72.8	310.8
Fructose	(mg)	3.2	68.2	385.0	91.0	-102.3	-182.7	-71.7	64.5	398.1
Ascorbic acid	(mg)	1.779	12.754	57.909	17.342	3.285	-8.108	-8.530	-8.827	-4.755
Glycoalkaloids	(mg)	0.864	3.138	8.278	3.109	0.330	-1.776	-2.293	-1.786	-0.549
Crude protein-N	(mg)	23.8	107.5	191.0	97.5	70.7	0.3	-20.8	-14.1	-0.2
Pure protein-N	(mg)	20.2	68.0	163.1	60.4	1.0	-16.2	-11.7	-12.0	-1.3
Nonprotein-N	(mg)	6.0	18.9	39.3	30.9	43.4	24.7	7.1	5.0	2.3
Nitrate-N	(mg)	6.1	23.9	9.0	-24.5	-10.1	-1.7	-0.3	0.5	0.03
Total-N	(mg)	29.9	131.3	200.0	73.1	60.5	-1.3	-21.1	-13.6	-0.1
P	(mg)	3.41	13.91	36.05	18.08	15.49	6.39	1.99	-1.85	-0.8
K	(mg)	26.4	119.2	288.7	62.0	52.3	-11.6	-19.4	-10.3	-0.2
Ca	(mg)	9.4	43.2	107.3	3.1	1.8	0.5	-10.9	-5.5	-0.1
Mg	(mg)	2.03	9.05	24.91	13.35	12.62	0.54	-1.27	-2.51	-1.05
Mn	(mg)	0.0377	0.1888	0.6454	0.0832	0.0293	0.0126	-0.1059	-0.0869	-0.0001
Na	(mg)	0.8	3.2	6.7	1.7	-0.3	-0.5	-0.3	-0.2	-0.1

dry matter (cf. Wittstock, 1962; Pätzold & Stricker, 1964; Kopp, 1973; Caesar et al., 1981; Feddes, 1987). For the whole potato crop Monteith (1978) cited by Loomis (1983) quoted daily maximal growth rates for short periods of 0.370 t ha^{-1}.

The period of intensive biomass gain is associated with the maximal rates of nutrient uptake of the potato crop (Table 5). Between 30 and 45 d.a.e. the daily uptake is about 8.0 kg N, 1.4 kg P and 11.6 kg K per hectare. By contrast, the maximal synthesis of nonprotein nitrogen and of starch is reached until 60–75 d.a.e. The daily maximal rate of starch synthesis is about 0.28 t ha^{-1} and an average rate of 0.09 t ha^{-1} starch is calculated for the whole vegetation period.

The rates of almost all tuber components follow an optimum curve and change to negative values during senescence. At that time, biomass and nutrient loss occurs to a different extent because of leaf litter, resorption of tubers, catabolism of organic compounds, processes of remobilization and translocation within the plant and, not least, also back into the soil. For example, at the time of maximal negative rates, about 90–120 d.a.e., the standing crop loses about 0.84 kg N, 0.07 kg P and 0.78 kg K per hectare and day (Table 5).

In relation to the maximal amounts of the whole potato crop the following relative values of fresh and dry matter and of chemical compounds remain in the shoot and tubers after senescence (Table 6). The potato crop loses a higher quantity of water than of dry matter. About 70% of the fresh matter and nearly 80% of the dry matter are located in the tubers and about 14% remains in the shoot. With different cultivars and locations comparable results were also obtained by Caesar et al. (1981).

As a starch storing organ at least about 90% of the synthesized starch is located in the tubers. The glycoalkaloids and ascorbic acid of the shoot are many times higher than the tubers, but only 29% of the glycoalkaloid and about 15% of the ascorbic acid remain in the dead shoot. A large quantity of 40–45% is catabolized during the life cycle and the tubers still contain 30% of the glycoalkaloids and about 40% of ascorbic acid at senescence.

According to these calculations a marked removal and transfer of assimilates and nutrients take place within the standing crop during the vegetative period. In addition, investigations of Millard & MacKerron (1986) show (depending of the N-nutrition) a steady translocation of dry matter and nitrogen from the first developed, relatively old leaves, into newly grown stems and leaves during the vegetative period.

Especially older and middle-old leaves and stems are, therefore, important intermediate storage locations for nitrogen and other nutrients. At harvest time 40% of the total uptake of tuber nitrogen has originated from remobilization in the leaves (34%) and the stems (6%); only 60% of the nitrogen is taken up from the soil and directly transferred into the tubers (Millard & MacKerron, 1986). According to Table 6, the portion of remobilization is 56%; 42% originates from leaves and about 14% from stems.

Altogether, during the process of senescence one hectare of standing crop (40.000 plants) loses about 21.3 kg N, 1.6 kg P and 24.9 kg K. Between 8.7–16.8% of these nutrients remain in the dead shoot and between 76–86% in the tubers. More than 93% of the nonprotein nitrogen, but only 3% of the maximal nitrate amount of the

Table 6. Calculated relative quantities of fresh and dry matter, organic and inorganic compounds of the potato shoot and tubers, and plant losses at the time of senescence (maximal quantities = 100%).

	Tuber	Shoot	Difference	
			Absolute	Relative
Fresh matter	69.2	14.4	376 g	16.4
Dry matter	78.4	12.4	32.7 g	7.2
Starch	89.9	0.6	29.2 g	9.5
Crude protein-N	76.4	16.6	517 mg	7.0
Pure protein-N	66.8	20.0	618 mg	13.2
Nonprotein-N	93.6	6.4	–	–
Nitrate-N	3.4	4.1	541 mg	92.6
Total-N	76.1	16.8	533 mg	7.2
Glycoalkaloids	30.2	29.1	96.1 mg	40.8
Ascorbic acid	40.5	14.8	453 mg	44.7
P	85.9	11.3	39.7 mg	2.8
K	83.7	8.7	623 mg	7.6
Ca	6.6	83.7	241 mg	9.7
Mg	39.5	52.8	72.5 mg	7.7
Mn	18.8	64.4	2.89 mg	16.9
Na	29.5	62.8	13.9 mg	7.7

plants, is present in tubers at harvest (Table 6).

Calculated results of Dow & Cline (1980) cited by Roberts & McDole (1985) show the following quantities of translocated nutrients, the rest remains in the shoot at senescence: nitrogen 67%, phosphorus 85%, potassium 62%, calcium 17%, magnesium 32%, zinc 50%. These findings agree with results in Table 6. According to these data mature tubers contain a large portion of nitrogen, phosphorus and potassium. In contrast, 20–40% of the total amount of sodium, magnesium, and manganese and only a low proportion of calcium is in the tubers. A corresponding, large portion of these nutrients remains in the shoot.

Concluding remarks

After reviewing the changes in concentration with time of the potato crop components characteristic courses can be identified depending on the plant organ and on the physiological function. In the canopy the concentration of several compounds change and follows a similar course to the dry matter production for leaves and stems (see Kolbe & Stephan-Beckmann, 1997). These include the direct and indirect products of photosynthesis: sugars, starch, organic acids and chlorophyll. High concentrations of these occur at phases of maximal daily dry matter production of the whole plant.

In contrast, the concentration of several minerals in the canopy reach their lowest values at phases of maximal dry matter yield. These components and the nitrogenous compounds are present in high concentrations in the young rapidly growing shoot

because of their physiological functions in cell multiplication and cell and organ differentiation. Late in the season the concentrations of these components are either present at high levels (Ca, Mg, Mn, Fe, B, Cu) or the concentrations of nitrogenous compounds, P, K and Zn are decreasing until senenscence for the reason of different translocation rates.

The growing young tubers contain relatively high, or the highest, concentrations of nearly all nitrogenous compounds and minerals. In addition, the maximum levels of cellulose, crude fibre, lipids and glycoalkaloids are found in the young tubers. Mostly because of dilution effects these components steadily decrease when the tubers are growing and to some extent increase again when the dry matter yield begins to decline at the end of the season.

Exceptions occur for components which are important to establish and expand the storage capacity. The tuber number, cell number and diameter and the cell wall material, therefore, increase markedly and reach maximal values at relatively early phases of growth. The increase in starch and dry matter content follow these and are maintained over the duration of vegetative growth and emphasize the significance of the potato tuber as a carbohydrate storing organ.

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