DIFFERENCES IN GROWTH AND METABOLISM OF POTATOES GROWN IN THE MOUNTAINS AND IN THE LOWLANDS

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1. INTRODUCTION

Following the classical work of BONNIER (1895), numerous studies have been made of the influence of mountain climate on the development of both wild and cultivated plants. For many years these were concerned mainly with morphological differences, particularly in growth, between plants growing at various altitudes; yield being taken into consideration in the case of cultivated species. More recently, LUNDEGÅRDH (1957) and WINKLER (1959) made detailed investigations of the effect of light and temperature on the growth of plants in the mountains and in the lowlands. The interrelation between climate and soil, as well as uptake of anions and cations at different altitudes, provided another wide field of research. Little work has, however, been done on the effect of altitude on the metabolic processes of plants (LASCOMBES, 1954, 1958).

The potato is a plant in which the environment can exert a distinct influence on the progeny, this being due, at least partly, to its vegetative propagation. The long established procedure of importing seed from coastal or mountainous areas for planting in the lowlands arose not only because of the lower virus content of such seed but also because of its more vigorous growth. The present paper gives the results of ecophysiological and virological research, which has been carried out for a number of years, on the reaction of the potato plant to the varying environmental conditions consequent on its cultivation at different altitudes.

2. MATERIALS AND METHODS

West Pomerania is one of the best potato-seed producing areas in Europe. Winds off the sea ensure a low aphid population and mean temperatures not exceeding 13 °C, combined with a fairly high relative humidity, provide excellent growing conditions.

In 1955, seed (1st class) of three varieties, *Epoka*, *Ackersegen* and *Voran*, was imported from Pomerania and planted in 53 different localities in south-west Poland, both in the lowlands, at an alititude of about 200 m and in the Carpathians, at altitudes ranging from 300 to 1290 m (some 300 m above the normal upper limit of cultivation). At each location, 30 plants of each variety were grown, seed from each being saved and replanted each year for three successive years. The plants were examined

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individually at the time of flowering, when the height of the haulm and the incidence of virus diseases were recorded. This information, together with subsequent data on yield, provided an estimate of their development. In this way it was possible to separate two independent problems, that of virus infection and the subsequent development or inhibition of the disease, and that of the physiology of the general development of the plant as defined by a number of factors acting in a given environment.

3. EXPERIMENTAL

3.1. Climate and soil factors

More than 150 years ago, HUMBOLDT (1817) formulated a general rule. This was expressed in terms of temperature only, with which all other simultaneously operating factors were causally connected. This rule is as follows: "the air temperature throughout the year decreases 0,5 °C for every 100 m increase in altitude, independently of latitude". More recent investigations have altered this but little. ROMER (1939–1946) estimated the fall in the Carpathians in summer to be 0,62 °C/100 m and stated that it was accompanied by a simultaneous rise in precipitation. The establishment of this correlation led to the formulation of another general rule: "the amount of slowly decomposing organic matter in the soil increases proportionally to the falling air temperature and increasing precipitation consequent on rising altitude" (JENNY, 1941).

During the present investigation, regression coefficients were calculated for both percentage organic matter in the soil on altitude and soil pH on altitude, in the Carpathians. For every 100 m rise in altitude, soil organic matter can be expected to increase by 1.08 % and pH decrease by 0.093 of a unit. The correlations were significant at the 1 % level. At the highest experimental site (1295 m) the organic-matter content of the soil was about 13.8 % and the pH 4,2.

3.2. Development and yield of the crop

For the purpose of demonstrating the relation between the development of the plants, particularly their yield, and the ecological conditions prevailing, only those plants without symptoms of virus infection were considered. In the course of the three years of the experiment, the yields on the 53 experimental plots fluctuated considerably. The differences in yield between varieties and between years at any one centre were significant.

A close negative correlation was established between altitude and average yield per plant for all three varieties. The regression coefficients of yield on altitude, for each of the three years, are given in TABLE 1a. The correlations are significant at the 1 % level. It will be seen that there is close agreement between all the figures.

Further confirmation of this effect was provided by the establishment of a negative correlation between height of haulm, measured at the time of flowering, and altitude, in the variety *Epoka*. The regression coefficient for each of the three years is given in TABLE 1b.

TABLE 1. Coefficients of regression of yield and haulm height of potatoes on altitude above sea level

Variety	1955	1956	1957
a. yield (g/plant/100 m)[1]			
Epoka	– 0,60	– 0,57	– 0,48
Ackersegen	– 0,54	– 0,69	–
Voran	– 0,55	– 0,43	– 0,52
b. haulm height (cm/plant/100 m)[2]			
Epoka	– 0,27	– 0,43	– 0,27

[1] *Knollenertrag (g Pflanze 100 m) - rendement en tubercules (g plante 100 m)*
[2] *Staudenhöhe (cm Pflanze 100 m) - hauteur des tiges (cm plante 100 m)*

TABELLE 1. *Regressionskoeffizienten zwischen Knollenertrag bzw. Staudenhöhe von Kartoffeln und Höhenlage über Meer*

TABLEAU 1. *Coefficients de régression du rendement en tubercules respectivement de la hauteur des tiges de pommes de terre en altitude*

The marked dwarfing of the plants which accompanies increasing altitude is, of course, a common phenomenon which has been studied by many workers since it was first recorded by BONNIER (1895).

3.3. The relation of altitude to virus infection

The dwarfing effect of altitude is linked with another important phenomenon, that of weaker reaction to virus infection. FIG. 1 shows the percentage virus infection in potatoes grown on experimental fields at three altitudes: $>$ 400 m, 300–400 m and $\leq$ 300 m.

Plants grown from seed imported from Pomerania and planted at various levels in the mountains had a very similar health status during the first year of cultivation. Field inspection in July indicated no more than 5% of primary virus infection in any one of the three varieties. Secondary symptoms appeared earlier and were more pronounced in the mountains than in the lowlands.

During the second and third years, considerable differences in the health of the plants at different altitudes were noted. These were mainly due to lower aphid infestation at the higher sites but, apart from this effect on the intensity of infection, there was a distinct inhibitory effect of mountain environment on the development of virus diseases within the plant itself.

Mosaic and crinkle symptoms, usually denoting a progressive disease (mainly virus Y), appeared on fewer plants in the second than in the first year of cultivation at sites above 400 m. In the third year the number increased only slightly. In the lowlands, on the contrary, there was a steady increase in the number of plants with secondary symptoms of virus Y infection throughout the period of the experiment. This phenomenon of inhibition of virus development in plants grown in the mountains has been observed frequently before. Sunny, dry summers make the Carpathians

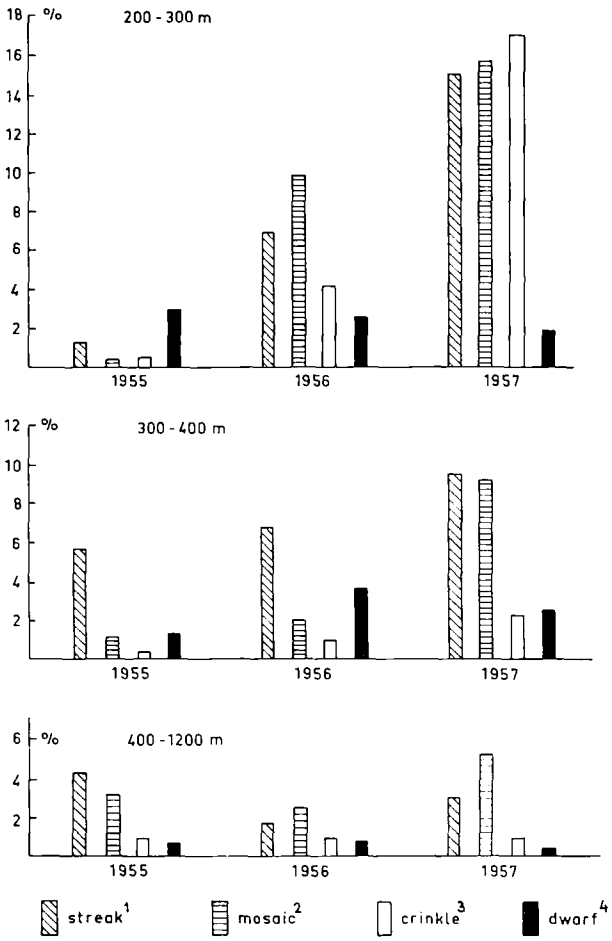


FIG. 1
Percentage virus infection in potatoes grown at different altitudes over a period of three years

ABB. 1
Prozent Virusbefall in Kartoffeln, die in drei aufeinanderfolgenden Jahren in verschiedenen Höhenlagen angebaut wurden

FIG. 1
Pourcentages d'infection virologique dans des pommes de terre poussées à différentes altitudes pendant une période de trois ans

[1] *Strichelkrankheit – la bigarrure.*
[2] *Mosaikkrankheit – mosaïque.*
[3] *Kräuselkrankheit – la frisolée.*
[4] *Kümmerwuchs – plantes naines.*

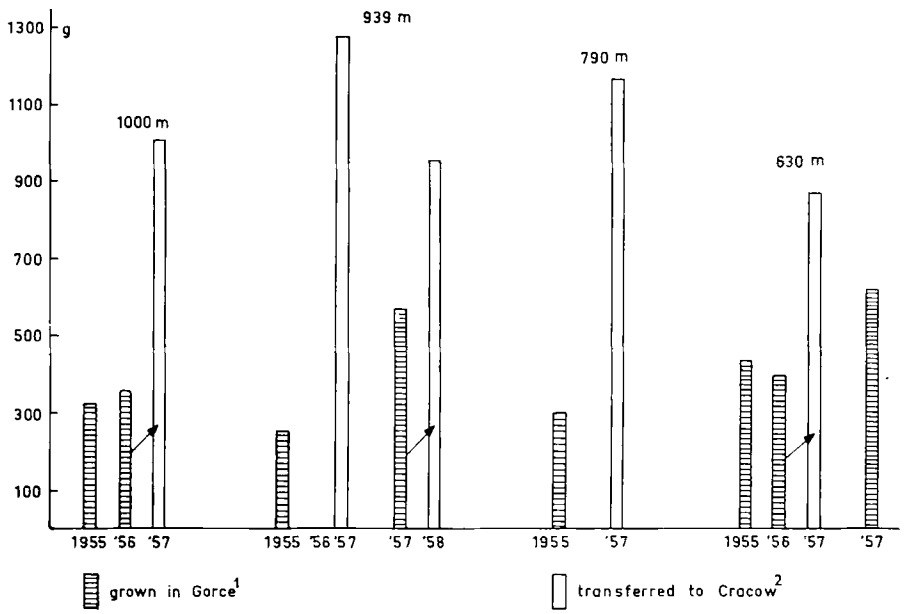
particularly suitable for potato cultivation and, in the course of nine years of experiments at Zakopane, starting in 1947, stocks of varieties originally infected with virus Y (mosaic and crinkle symptoms and dwarfing) showed no symptoms in 1950, which was unusually dry and sunny. The virus appeared to have changed to a latent form detectable only on test plants (KOZLOWSKA, 1957).

3.4. The effect of transferring stocks from the mountains to the lowlands

Sixty tubers from 30 marked plants of each of the three varieties were taken from each of the 53 experimental sites after the second and again after the third year of cultivation. These were planted for comparison in 10 randomised blocks on a site in the lowlands near Cracow. Incidence of disease, development of haulm and yield were recorded for each plant. Considerable differences in the rate of development

were noted and these were subsequently reflected in the yield in both years. Those potatoes obtained from sites above 400 m showed more vigorous growth than did either the parental stocks in the mountains or healthy selected seed from stocks grown in the lowlands. This vigorous growth was reflected in the yields (FIG. 2).

FIG. 2. Average yield per plant of *Epoka* potatoes grown over a number of years in the Gorce mountains compared with that of the same stock transferred at intervals to the lowlands near Cracow



[1] *Angebaut in Gorce = poussées en Gorce.* [2] *Nachbau in Krakau = transférées à Cracovie.*

ABB. 2. *Durchschnittlicher Ertrag je Pflanze der Sorte* Epoka, *die während einer Anzahl Jahre in den Gorce-Bergen angebaut wurde, verglichen mit dem Ertrag von Knollen des gleichen Bestandes, die in Intervallen im Tiefland bei Krakau ausgepflanzt wurden*

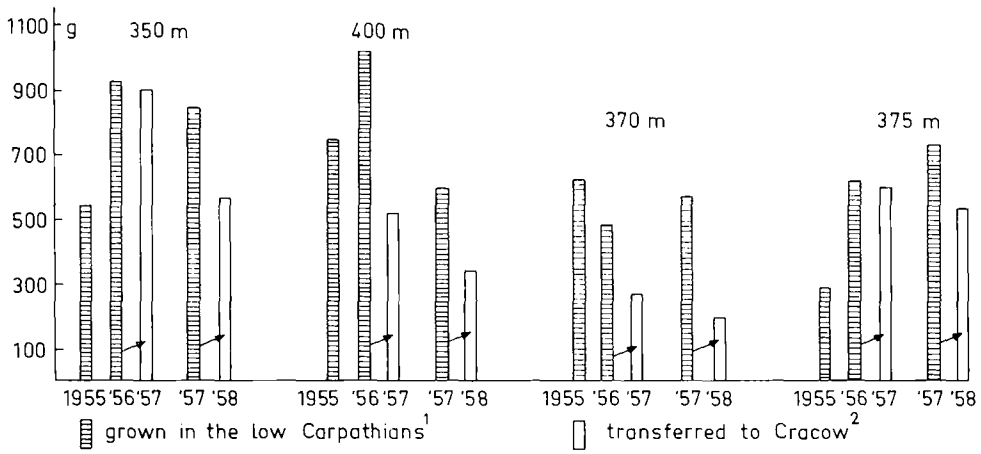
FIG. 2. *Productions moyennes par plantes de la variété* Epoka *poussées pendant un certain nombre d'années dans les montagnes "Gorce" comparées avec celles du même lot, transférées à intervalles dans la plaine près de Cracovie*

In *Epoka*, the mean increase in yield/plant at Cracow, over the parental stocks grown in the Carpathians, was 31.1 g in 1957 and 15.8 g in 1958. In *Voran*, the corresponding differences were 29.9 g and 16.5 g respectively. The smallest differences were found in *Ackersegen*, namely 12.0 g and 0.9 g in the two years. All these differences were significant at the 1 % level.

Potatoes transferred to Cracow from 13 sites below 400 m showed some decrease in yield but the differences were not significant (FIG. 3).

From this data it would seem that, in the west Carpathians, the 400 m contour

FIG. 3. Average yield per plant of *Epoka* potatoes grown over a number of years in the low foothills of the Carpathians compared with that of the same stock transferred at intervals to the lowlands near Cracow



[1] *Angebaut im Vorgebirge der Karpaten – poussées dans les basses Carpathes.*
[2] *Nachbau in Krakau – transférées à Cracovie.*

ABB. 3. *Durchschnittlicher Ertrag je Pflanze der Sorte* Epoka, *die während einer Anzahl Jahre im niederen Vorgebirge der Karpaten angebaut wurde, verglichen mit dem Ertrag von Knollen des gleichen Bestandes, die in Intervallen im Tiefland bei Krakau ausgepflanzt wurden*

FIG. 3. *Productions moyennes par plantes de la variété* Epoka, *poussées pendant un certain nombre d'années dans les coteaux inférieurs des Carpathes comparées avec celles du même lot transférées à intervalles dans les plaines près de Cracovie*

is a very important threshold in a whole series of ecological factors which influence all the vital processes in the plant. Returning to HUMBOLDT's concept of climate, we find that the difference in mean temperature during the vegetative period between Cracow and elevations of 400 m is –1.24 °C; at 800 m and above it is from –3.72° to over –4 °C. Evidently this relatively small difference of –1.24 °C, combined with the differencies in soil acidity and organic-matter content seem to induce dwarfing of the haulm and the enhanced vigour of stocks transferred to the lowlands, only some 200 m lower.

3.5. The influence of altitude on the uptake of potassium and phosphorus

In order to obtain further information both on the dwarfing effect of altitude and its stimulatory effect on stocks transferred to the lowlands, an investigation was made of the comparative rate of uptake of various anions and cations by potatoes growing under different conditions. In the first instance, a study was made of potassium and phosphorus uptake.

The results obtained on the potassium content of tubers have been published elsewhere (KOZLOWSKA, 1960). They showed a constant yearly increase in percentage

K_2O proportional to the altitude of cultivation and a simultaneous decrease in yield. It may be possible to interpret this on the basis of a general decrease in the fresh weight of the plant in the mountains.

If the % K_2O in the tuber depends on the fresh weight of the plant, which decreases with increasing altitude, it would be reasonable to expect a similar increase in the content of other compounds. The antagonistic behaviour of K and Ca in plants is widely known. In the lowlands and on calcareous soils, the increase in calcium in the tuber is accompanied by a decrease in potassium. In the Carpathians, however, the situation is different. Tubers formed by dwarfed plants growing at high altitudes in the Tatra or Gorce mountains usually contain an increased amount of *both* calcium and potassium.

Determinations of phosphorus, carried out during the last few years on all the available tuber material under investigation, gave very different results to those obtained with potassium. The phosphorus content was determined in samples of tubers from each of the 53 experimental sites in each of the three years of cultivation. TABLE 2

TABLE 2. P_2O_5-content of *Epoka* potato tubers grown in Pomerania (original source of seed used), in the lowlands and in the mountains

Locality *Standort Localité*	Altitude *Höhe Altitude* (m)	% organic matter in soil – % *organische Substanz im Boden* – % *matière organique dans le sol*	P_2O_5-content (% dry wt) – P_2O_5-*Gehalt* (% *Trockengew.*) – *teneur en* P_2O_5 (% *poids sec*)		
			1st year *1. Jahr 1re année*	2nd year *2. Jahr 2e année*	3rd year *3. Jahr 3e année*
Pomerania – *Pommern – Poméranie*					
Chojnice	175	2,1	0,437	0,454	0,444
Lowlands – *Tiefland – plaines*					
Mydlniki	215	1,8	0,528	0,541	0,646
Głogoczów	230	4,0	0,508	0,481	0,586
Polanowice	260	2,8	0,729	0,622	0,506
Pszczyna	270	3,5	0,659	0,627	–
Lodygowice	350	5,2	0,646	0,545	0,536
Carpathian Mts. – *Karpaten – Monts Carpathes*					
Milówka	450	7,6	0,376	0,531	–
Ludźmierz	610	14,5	0,458	0,435	0,376
Zawadka	720	7,3	–	0,329	0,350
Pietraszonka	750	9,5	0,465	–	0,428
Potrójna	800	10,6	0,330	0,361	0,350
Zawoja	900	7,8	0,394	0,348	0,330
Magórka	900	12,1	0,364	0,408	0,554
Obidowa	900	5,4	0,444	0,408	0,361
Pilsko	1200	13,8	0,522	0,577	0,479
Kopieniec	1295	12,4	–	0,405	0,506

TABELLE 2. *P_2O_5-Gehalt von Kartoffelknollen der Sorte* Epoka *angebaut in Pommern (Herkunftsort des verwendeten Saatgutes), im Tiefland und in den Berggebieten*

TABLEAU 2. *Teneur en P_2O_5 de tubercules de la variété* Epoka *grandis en Poméranie (origine des plants utilisés) en plaine et en montagne*

shows the results for *Epoka*. These indicate that in crops grown continuously in the mountains, at elevations ranging from 400–1200 m, the phosphorus content of the tubers remained at the same low level throughout the three years as it did in the parental stocks grown continuously in the seed-producing area of Pomerania. On the other hand, where the stocks were grown in the lowlands at elevations ranging from 207–390 m, there was often a distinct increase in phosphorus content over the same period. Only plants free from all signs of virus infection were included in the samples taken for this analytical work.

The mean % P_2O_5-content of tubers of *Epoka* grown in 1955 on the mountain (400–1295 m) sites was 0.467 and on the lowland sites 0.533. *Ackersegen* gave somewhat higher values but showed similar differences, the corresponding figures being 0,524 and 0,622. Similar values and differences were maintained in both varieties during the three years of the experiment.

The transference of stocks from the mountains to the lowlands, which was shown earlier in this paper to increase both vigour and yield, also affects uptake of potassium and phosphorus. TABLE 3 shows that there was a distinct decrease in potassium and an increase in phosphorus content when potatoes were transferred to the lowlands from altitudes above 400 m, compared with the parental material grown in the mountains.

TABLE 3. K_2O and P_2O_5-content of *Epoka* potato tubers grown in the mountains (1956) and transferred to Cracow (1957)

Locality *Standort* *Localité*	Altitude *Höhe* *Altitude* (m)	In % dry wt. – *in % Trockengew.* – *en % poids sec*		Transferred to Cracow – *Nachbau in Krakau* – *transférés à Cracovie* In % dry wt. – *in % Trockengew.* – *en % poids sec*	
		K_2O	P_2O_5	K_2O	P_2O_5
Lubień	440	2,32	0,437	1,86	0,510
Tenczyn	550	2,18	0,398	1,88	0,678
Harklowa	600	2,36	0,472	2,10	0,682
Ludźmierz	610	2,40	0,435	1,88	0,629
Kluszkowce	710	2,30	0,472	1,90	0,565
Zawadka	720	2,28	0,329	1,94	0,500
Potrójna	800	2,32	0,361	1,99	0,687
Zawoja	900	2,26	0,348	1,82	0,568
Magórka	900	2,10	0,364	1,46	0,563
Obidowa	900	2,56	0,408	2,12	0,604
Gubałówka	1008	2,64	0,508	2,16	0,518
Pilsko	1200	2,47	0,479	2,01	0,581
Kopieniec	1295	3,03	0,444	2,16	0,645

TABELLE 3. *K_2O- und P_2O_5-Gehalt in Kartoffelknollen der Sorte* Epoka, *die in Berggebieten gewachsen sind (1956) und nachher in Krakau (1957) nachgebaut wurden*

TABLEAU 3. *Teneur en K_2O et P_2O_5 de tubercules de la variété* Epoka *poussés en montagne (1956) et transférés à Cracovie (1957)*

3.6. The relation of altitude to the organic-acid content of the tubers

The organic acids occupy a key position in plant metabolism. An increase in metabolic activity is usually accompanied by a simultaneous increase in organic-acid content of the tissues which, in turn, is linked with respiration and phosphorus metabolism. Samples of tubers were taken from an experimental field at Zakopane on the slopes of Gubalówka, at an elevation of 1008 m, and from one in the lowlands near Cracow and their organic-acid content determined by means of silica gel column-chromatography. Extracts for analysis were prepared according to the method of Awapara, as quoted by LINSKENS (1955).

The organic acids were then analysed according to the method of BULEN *et al.* (1952), NYKAMP (1954) and VENEKAMP (1959). Identification of the acids was verified by paper-chromatography (BUSCH *et al.*, 1952). The acids found were predominantly oxalic, malic and citric.

The analyses were mainly done on dormant tubers between November and April. Control analyses on tubers of the same plants in January and again in April, when sprouts were already 1 cm long, showed no difference in their organic-acid content. Most of the work was on *Epoka* and the related *clone 926*, but comparative studies were made on *Ackersegen* which, it will be remembered, differed somewhat from *Epoka* in its reaction to mountain environment.

Evidence obtained in our laboratory confirmed the results of BOSER (1957) who stated that the organic-acid content of the tuber varied according to the health of the plant. Tubers infected with viruses X or S and Y, in the later stages of the disease, *i.e.* plants with mosaic and crinkle symptoms, usually showed a decrease in organic acids. Tubers from plants with primary virus Y infection (streak symptoms), however, showed a distinct increase. In the experiments detailed here, except where otherwise stated, only those tubers were used which came from plants without virus symptoms and which had not shown any such symptoms in both the preceeding and succeeding generation. The presence or absence of viruses X and S was determined by the precipitin method.

Epoka

Tubers were taken from the following sources:

1. The parental seed stock in Pomerania.
2. Potatoes grown for 1, 2, 4 and 7 years at Zakopane.
3. Potatoes transferred from Pomerania and grown in the lowlands near Cracow, both healthy and virus-infected.
4. Potatoes transferred from Zakopane to Cracow, healthy in the first year but virus-infected in subsequent years.

In parallel with the estimations of organic-acid content, oxygen uptake by tuber tissue was measured, using Warburg's apparatus. The potassium and phosphorus content was also determined. TABLE 4 shows the results obtained with healthy tubers. After the first year at Zakopane, the content of organic acids, potassium and phos-

TABLE 4. Organic acids, K_2O and P_2O_5-content and O_2-uptake of *Epoka* potato tubers grown in Pomerania, Zakopane and Cracow

Locality / *Standort* / *Localité*	O_2-uptake ($\mu l\ O_2$/g dry wt.)[1]	Organic acids (µg equiv./g fresh wt.)[2]				In % dry wt. / *in % Trockengew.* / *en % poids sec*	
		oxalic[3]	malic[4]	citric[5]	total	K_2O	P_2O_5
Pomerania	224,2	1,5	1,5	9,2	12,2	2,1	0,444
Zakopane 1 year[6]	151	1,03	1,00	9,53	11,56	2,16	0,446
Zakopane 4 years[6]	134	0,5	1,8	1,7	4,0	2,52	0,423
Zakopane 7 years[6]	146,8	1,02	1,05	1,32	3,34	2,62	0,412
Transferred to Cracow	377,6	0,8	4,1	14,3	19,2	2,11	0,710
Cracow 4 years[6]	339,3	2,34	3,05	14,2	19,56		0,693

[1] *O_2-Aufnahme ($\mu l\ O_2$ g Trockengew.) – O_2 prélevé ($\mu l\ O_2$/g poids sec.).*
[2] *Organische Säuren (µg Äquivalent/g Frischgew.) – acides organiques (µg équiv. g poids frais).*
[3] *Oxalsäure – oxalique.*
[4] *Apfelsäure – malique.*
[5] *Zitronensäure – citrique.*
[6] *Jahr(e) – année(s).*

TABELLE 4. *Organische Säuren, K_2O- und P_2O_5-Gehalt und O_2-Aufnahme in Kartoffelknollen der Sorte* Epoka *von den Anbauorten Pommern, Zakopane und Krakau*

TABLEAU 4. *Teneurs en acides organiques, K_2O, P_2O_5, et prélèvements de O_2 sur tubercules de la variété* Epoka *poussés en Poméranie, à Zakopane et Cracovie*

phorus and the respiration rate were substantially the same as in the parental material from Pomerania. After 4 and 7 years growth in the mountains, the content of phosphorus was very low, that of potassium was consistently rising and that of organic acids had decreased to a very low level which was reflected in a very low rate of respiration. Transferring stocks from the mountains to the lowlands had the effect of increasing the organic-acid content, the rate of respiration and the yield. At the same time there was an increase in phosphorus and a decrease in potassium. Similar results were obtained with healthy potatoes grown throughout at Cracow. FIG. 4 shows the average yields per plant of a stock of the variety *Epoka* during each of the eight years it was grown at Zakopane and the effect of transferring it to Cracow in both the seventh and eighth years. The serological tests for viruses X and S remained negative throughout the eight years of the experiment and the plants showed no signs of virus infection; there was only the dwarfing associated with the mountain environment. No signs of virus were detected after the transference of stocks to Cracow.

Investigations carried out on virus-infected tubers of *Epoka* were mainly concerned with viruses S and Y, in the later stages of attack, *i.e.* 2, 3 and 4 years after infection. Such tubers showed a definite decrease in organic-acid content accompanied by a similar fall in respiration rate compared with healthy ones (TABLE 5). The difference between these virus-infected tubers and healthy ones from crops grown for many

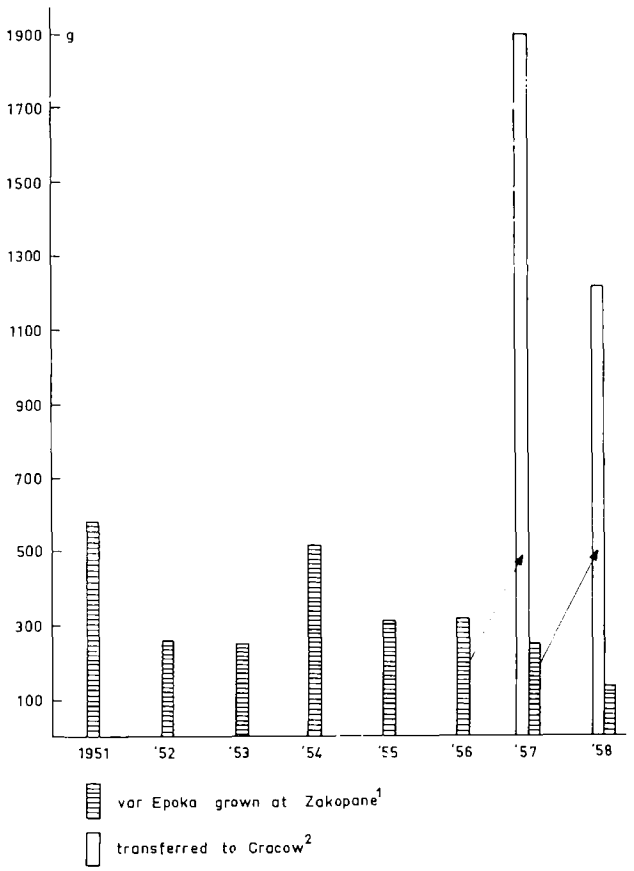


FIG. 4
Average yield per plant of *Epoka* potatoes grown for eight years at Zakopane (Carpathian Mts.) compared with that of the same stock transferred in the seventh and eighth year to the lowlands near Cracow

ABB. 4
Durchschnittlicher Ertrag je Pflanze der Sorte Epoka, *die während acht Jahre in Zakopane (Karpaten) angebaut wurde, verglichen mit dem Ertrag von Knollen des gleichen Bestandes, die im siebten und achten Jahr im Tiefland bei Krakau ausgepflanzt wurden*

FIG. 4
Productions moyennes par plantes de la variété Epoka *poussées pendant huit ans à Zakopane (Carpathes), comparées avec celles du même lot transférées la 7e et la 8e année dans les plaines près de Cracovie*

[1] *Sorte* Epoka, *angebaut in Zakopane – variété* Epoka, *poussée à Zakopane.*
[2] *Nachbau in Krakau – transférées à Cracovie.*

years in the mountains, which also show a low organic-acid content and a low respiration rate, is the phosphorus content. The diseased tubers have a P_2O_5-content of over 0,8 % of the dry matter, while in the healthy but dwarfed plants from the mountains the level is only about 0,45 %.

As can be seen from TABLE 6 the results obtained with *clone 926* gave results similar to those obtained with *Epoka*.

Ackersegen

This variety gave very different results from the other two, both when grown in the mountains and in the lowlands. TABLE 7 shows that healthy stocks grown in the mountains for 1, 2 and 6 years showed, in comparison with those grown in the lowlands, not a decrease but an increase in organic acids, due mainly to a higher content of citric acid. Their yields, however, as with *Epoka*, were much lower than in the low-

TABLE 5. Organic acids, K_2O and P_2O_5-content and O_2-uptake of *Epoka* potato tubers, healthy and virus-infected, grown at Cracow

Virus diseases *Viruskrankh. Viroses*	O_2-uptake (µl O_2/g dry wt.)[1]	Organic acids (µg equiv./g fresh wt.)[2]				In % dry wt. – *in* % *Trockengew.* – *en* % *poids sec*	
		oxalic[3]	malic[4]	citric[5]	total	K_2O	P_2O_5
Healthy[7]	339,3	2,34	3,05	14,2	19,56	2,65	0,693
Virus S 1 year[6]	120	2,28	2,41	2,06	8,77	2,62	0,728
Virus Y 3 years[6] (mosaic)		1,15	0,88	4,52	7,16	3,08	0,806
Virus Y 4 years[6]	175,4	0,88	0,74	4,77	6,4	2,82	0,723
Virus Y + virus S 2 years[6]		0,16	1,88	3,68	5,72	3,02	0,730
Virus Y + virus S 3 years[6]		0,908	0,67	0,45	2,03	2,9	0,825

[1–6] *Zur Erklärung siehe* TABELLE 4 – *pour l'explication voir* TABLEAU 4.
[7] *Gesund – sains.*

TABELLE 5. *Organische Säuren, K_2O- und P_2O_5-Gehalt und O_2-Aufnahme in Kartoffelknollen der Sorte* Epoka, *gesund und virusinfiziert, gewachsen in Krakau*

TABLEAU 5. *Teneurs en acides organiques, K_2O, P_2O_5 et prélèvements de O_2 sur tubercules de la variété* Epoka, *sains et infectés de virus, poussés à Cracovie*

TABLE 6. Organic acids, K_2O and P_2O_5-content of potato tubers, *clone 926*, grown at Zakopane and Cracow

Locality *Standort Localité*	Organic acids (µg equiv./g fresh wt.)				In % dry wt. – *in* % *Trockengew.* – *en* % *poids sec*	
	oxalic	malic	citric	total	K_2O	P_2O_5
Cracow (healthy) 8 years	2,55	4,21	8,22	14,98	2,26	0,664
Cracow (mosaic) virus Y	2,83	5,01	1,83	9,67	2,20	0,774
Zakopane (healthy) 10 years	2,26	1,8	0,85	4,91	2,32	0,41

Zur Erklärung siehe TABELLE 4 – *pour l'explication voir* TABLEAU 4.

TABELLE 6. *Organische Säuren, K_2O- und P_2O_5-Gehalt in Kartoffelknollen*, Klon 926, *gewachsen in Zakopane und Krakau*

TABLEAU 6. *Teneurs en acides organiques, K_2O, P_2O_5 de tubercules du* clone 926, *poussés à Zakopane et Cracovie*

TABLE 7. Organic acids, K_2O and P_2O_5-content and O_2-uptake of *Ackersegen* potato tubers grown at Cracow and Zakopane

Locality / *Standort* / *Localité*	O_2-uptake (µl O_2/g dry wt.)	Organic acids (µg equiv./g fresh wt.)				In % dry wt. / *in %, Trockengew.* / *en % poids sec*	
		oxalic	malic	citric	total	K_2O	P_2O_5
Cracow	350	1,73	4,4	14,06	20,45	2,75	0,852
Zakopane 1 year	396	3,74	3,17	18,86	26,54	2,24	0,5315
Zakopane 2 years	410	1,58	3,42	24,92	29,01	2,57	0,532
Zakopane 6 years	418	2,08	3,32	16,73	22,13	2,68	0,6414
Transferred to Cracow	–	1,1	5,4	14,0	20,5	3,01	0,893

Zur Erklärung siehe TABELLE 4 – *pour l'explication voir* TABLEAU 4.

TABELLE 7. *Organische Säuren, K_2O- und P_2O_5-Gehalt und O_2-Aufnahme in Kartoffelknollen der Sorte* Ackersegen, *gewachsen in Krakau und Zakopane*

TABLEAU 7. *Teneurs en acides organiques, K_2O, P_2O_5 et prélèvements de O_2 sur tubercules de la variété* Ackersegen *poussés à Cracovie et Zakopane*

lands. This accumulation of organic acids in the tubers of *Ackersegen* in the mountains is very similar to that described by LASCOMBES (1954) for beet, a lowland plant, when grown at higher altitudes. There also was an increase in the citric-acid content. It seems probable that varietal differences in the metabolism of potatoes are responsible for this effect. Both *Epoka* and *clone 926* have in their pedigree *Solanum demissum*, a wild South American species which normally grows at altitudes of from 2000–3500 m. This suggests that both these varieties adapt themselves more readily to the mountain environment than does the old variety *Ackersegen* which nowadays undergoes rapid degeneration in our fields.

The decrease in yield normally associated with increasing altitude of cultivation could not be confirmed statistically in *Ackersegen* in the third year. Moreover, the increase in yield which follows transference of a stock from the mountains to the lowlands was much less marked than in *Epoka*. A very striking feature is the high level of P_2O_5 in tubers of *Ackersegen*. Even in the mountains this is much higher than the comparable figure for *Epoka*.

3.7. A possible explanation of the enhanced resistance of potatoes to virus infection in the mountains

The differences between healthy and virus-infected tubers which exist independently of variety and methods and altitude of cultivation are those of phosphorus and potassium content. TABLE 8 shows that the increase of P_2O_5 in virus-infected tubers of *Epoka* is independent of yield.

TABLE 8. Average K_2O and P_2O_5-content of potato tubers, healthy and virus-infected, in relation to yield

		Av. crop p. plant[1] (kg)	In % dry wt. – *in % Trockengew.* – *en % poids sec*	
			K_2O	P_2O_5
Potatoes with similar crops	healthy[2]	0,94	2,18	0,614
Kartoffeln mit ähnlichen Erträgen	*diseased*[3]	0,93	2,64	0,695
P. de t. avec productions semblables	*difference*[4]	– 0,01	+ 0,46	+ 0,081
Potatoes with differing crops	healthy[2]	1,42	2,25	0,081
Kartoffeln mit unterschiedl. Erträgen	*diseased*[3]	0,23	2,76	0,748
P. de t. avec productions différentes	*difference*[4]	– 1,19	+ 0,51	+ 0,199
Potatoes with differing crops	healthy[2]	1,43	2,26	0,622
Kartoffeln mit unterschiedl. Erträgen	*diseased*[3]	0,69	2,23	0,601
P. de t. avec productions différentes	*difference*[4]	– 0,74	– 0,03*	– 0,021*

* Not significant, other differences significant at the 1 % level – *nicht gesichert, andere Unterschiede gesichert zu 1 % – non significative, les autres différences étant significatives au niveau 1 %.*
[1] *Mittlerer Ertrag je Pflanze – récolte moyenne par plante.*
[2] *Gesund – saines.*
[3] *Krank – malades.*
[4] *Unterschied – différence.*

TABELLE 8. *Durchschnittlicher K_2O- und P_2O_5-Gehalt in Kartoffelknollen, gesund und virusinfiziert, in bezug auf Ertrag*

TABLEAU 8. *Teneurs moyennes en K_2O et P_2O_5 de tubercules sains et virosés en relation avec la production*

The two varieties investigated, *Epoka* and *Ackersegen*, differ considerably in the phosphorus content of their tubers. Both in the mountains and in the lowlands and in virus-infected and healthy plants, tubers of *Ackersegen* always show a higher phosphorus content than those of *Epoka*.

At the same time, *Ackersegen* is liable to degeneration through virus disease at whatever elevation it is grown. Nevertheless, in this variety also, phosphorus content of the tubers decreases with the altitude at which the crop is grown.

The dwarfing associated with growth at higher altitudes is purely physiological and, as has been stated, is to some extent linked with inhibition of virus multiplication within the plant. Decrease in phosphorus uptake is also linked with increasing altitude. In comparison with potassium and other cations, potatoes, particularly the variety *Epoka*, take up too little phosphorus. As one of the main components of the nucleic acids, which in turn form the framework of the virus particle, phosphorus is usually absorbed more rapidly by a diseased plant. In the mountains, however, due to the combined action of a whole set of environmental factors, uptake of phosphorus is impeded, the growth of the plant is restricted and, at the same time, virus multiplication within the plant is inhibited.

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SUMMARY

In parallel with the dwarfing effect of mountain environment on potatoes, virus development within the plants was inhibited. Tubers from crops grown in the mountains consistently had a low phosphorus and organic-acid content. When seed from these crops was grown in the lowlands the content of both phosphorus and organic acids in the tubers was higher as was their respiration rate.

The probability that virus multiplication within the plant is dependent on factors affecting growth is discussed.

ZUSAMMENFASSUNG

UNTERSCHIEDE IN WACHSTUM UND STOFFWECHSEL VON KARTOFFELN IN BERGLAGEN UND IM TIEFLAND

Eine enge negative Korrelation wurde festgestellt zwischen den Höhenlagen der Karpaten und dem durchschnittlichen Ertrag der Kartoffelsorten *Ackersegen*, *Voran* und *Epoka* (TAB. 1). Wurde Pflanzgut aus Lagen über 400 m ü. M. in einer Region von 200 m ü. M. ausgepflanzt, so führte dies zu einer beträchtlichen Ertragserhöhung im Nachbau (ABB. 2 und 4).

In Höhen zwischen 400 und 1200 m ü. M. war die Virusvermehrung in Kartoffelpflanzen gehemmt (ABB. 1).

Neben der Wachstumshemmung durch die Umweltsverhältnisse in den Höhenlagen und der stimulierenden Wirkung auf das Saatgut (wenn es im Tiefland ausgepflanzt wurde), konnten auch Unterschiede im Stoffwechsel der Knollen in Abhängigkeit von der Höhenlage beobachtet werden. Knollen aus Beständen, die in drei aufeinanderfolgenden Jahren in Höhenlagen zwischen 400–1200 m ü. M. gewachsen waren, wiesen im Vergleich zu jenen aus dem Tiefland einen niedrigen Phosphorgehalt (TAB. 2) und einen hohen Kaligehalt auf. Wenn Knollen aus Lagen über 400 m ins Tiefland versetzt wurden, stieg der Phosphorgehalt, und der Kaligehalt nahm ab (TAB. 3).

Parallel mit dem Phosphor- und Kaligehalt wurden auch der Gehalt an organischen Säuren und die Respirationsrate der Knollen durch die Umweltsverhältnisse in den Höhenlagen beeinflusst. In Berglagen zeigte die Sorte *Epoka* einen sehr niedrigen Gehalt an organischer Säure und eine kleine Respirationsrate der Knollen (TAB. 4); wenn die Knollen jedoch in Krakau ausgepflanzt wurden, stiegen beide Werte beträchtlich, ebenso der Ertrag. Die Sorte *Ackersegen* reagierte unterschiedlich (TAB. 7).

Verglichen mit gesunden Knollen war bei virusinfizierten Kartoffeln eine deutliche Zunahme im Phosphor- und Kaligehalt festzustellen, begleitet von einer Abnahme an organischen Säuren und einem Absinken der Respirationsrate (TAB. 5).

Die Wahrscheinlichkeit, dass die Virusvermehrung in der Pflanze von Faktoren abhängt, die das Wachstum beeinflussen, wird diskutiert.

RÉSUMÉ

DIFFÉRENCES DANS LA CROISSANCE ET LE MÉTABOLISME DE POMMES DE TERRE POUSSÉES EN MONTAGNES ET EN PLAINES

Il existe une étroite corrélation négative entre l'altitude dans les monts Carpathes et la production moyenne des variétés de pomme de terre *Ackersegen*, *Voran* et *Epoka* (TABLEAU 1). Le transfert de plants de sites au-dessus de 400 m dans une région à 200 m cause un considérable accroissement de production dans les récoltes suivantes (FIG. 2 et 4).

Le développement des viroses est inhibé dans les plants de pomme de terre poussés à des altitudes entre 400 et 1.200 m (FIG. 1).

Outre l'effet de nanisme du milieu "montagne" et son action stimulante sur les plants transférés en plaine, des différences s'observent dans le métabolisme des tubercules poussés à de différentes altitudes. Les tubercules issus de récoltes poussées pendant trois années successives à des niveaux variant entre 400 et 1.200 m avaient une basse teneur en phosphore et une haute teneur en potassium comparativement à ceux poussés en plaine (TABLEAU 2). Quand les plants étaient transférés en plaine à partir de sites au-dessus de 400 m, la teneur en phosphore du tubercule augmentait et la teneur en potassium diminuait (TABLEAU 3).

Parallèlement aux teneurs en phosphore et en potassium, la teneur en acide organique et la vitesse de respiration étaient également affectées par le milieu "montagne". Chez la variété *Epoka*, poussée en montagne, la teneur en acides organiques et la vitesse de respiration des tubercules se trouvaient à un niveau très bas (TABLEAU 4); mais, après transfert à Cracovie, les deux caractères montraient un accroissement considérable, ainsi d'ailleurs que la production. La variété *Ackersegen* réagissait différemment (TABLEAU 7).

Comparés aux tubercules sains, les tubercules infectés de virus montraient un accroissement limité en phosphore et potassium qui s'accompagnait d'une diminution des acides organiques et d'une chute de la vitesse de respiration (TABLEAU 5).

Est discutée la probabilité que la multiplication du virus dans la plante dépend des facteurs affectant la croissance.

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