VARIATION IN LEAF RESPIRATION RATE BETWEEN POTATO CULTIVARS: EFFECT OF DEVELOPMENTAL STAGE

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Introduction

Although it is well-documented that a major part of photosynthates is used for maintenance of plant biomass (Penning de Vries 1975, Lambers *et al.* 1983a, Amthor 1989), knowledge about the nature of the underlying processes is poor. It has been proposed that a major part of this energy is used for maintenance of solute gradients and protein turnover (Penning de Vries 1975), but this has not been experimentally confirmed. Wilson (1982) showed that it is possible to select high-yielding ryegrass populations by screening for low respiration rate of mature leaves without knowing the underlying processes. However, more insight in the processes of maintenance respiration is required to (a) understand plant and crop production and (b) develop new plant breeding criteria. Insight in the quantitative aspects of plant and crop production may form the basis of plant breeding.

For identification of the quantitatively most important maintenance processes it would be helpful to have varieties/cultivars/lines differing in (maintenance) respiration rate. Various potato cultivars are available which differ in earliness, a commonly used index for time of tuber formation/harvest (0 = late, 10 = early). For example, Alcmaria (index 8) is an early cultivar, whereas Pimpernel (index 3.5) is about 30 days later (Spitters *et al.* 1988). Preliminary measurements showed large varietal differences in leaf respiration rate of potato (by a factor of two; F.W.T. Penning de Vries, pers. comm.). There may be several causes for these differences in respiration rate. General metabolic activity may differ due to different optima for temperature or other conditions. Alternatively, the efficiency of one or more of the many energy-consuming processes (*e.g.* growth, maintenance, ion transport) may be responsible.

We examined possible causes of the varietal differences in leaf respiration rate, hypothesizing that different energy requirements of the cultivars for growth and/or maintenance are involved.

Material and methods

Plant material

A – greenhouse and field experiments with 15 cultivars

For both the greenhouse experiment (March-May 1988) and the field experiment

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(April-June 1989), plants were grown from pre-sprouted tubers. Fifteen potato (*Solanum tuberosum* L.) cultivars were used: Alcmaria, Alpha, Bintje, Civa, Désirée, Katahdin, Kennebec, Krostar, Maritta, Multa, Pimpernel, Saturna, Spunta, Veenster and Woudster. In the *greenhouse* experiment, plants were grown on recirculating aerated Steiner nutrient solution (Steiner 1966). The growth conditions in the *greenhouse* were : 18 ± 1°C constant, and 65% RH.

B – growth room experiments with 2 cultivars

Plants of the potato (*Solanum tuberosum*) cvs Alcmaria and Pimpernel, were propagated by in vitro culture, and grown on recirculating aerated Hoagland solution (macro nutrients 1/2 strength according to Hoagland & Snijder (1933) and micro nutrients 1/2 strength according to Lewis & Powers (1941) with iron as Fe(III)-EDTA). Entangling of roots of neighbouring plants was prevented, and a uniform supply of nutrients was provided. Other conditions were: 12 hours 240 μmol m^{-2} s^{-1} PPFD (fluorescent light from Philips TLD 36W/54 and incandescent light from Pope 60W in a ratio 12:1) for growth and 6 h incandescent light (Pope 60W) for day length extension to prevent tuber induction. The temperature was maintained at 18 ± 2°C, and the air humidity at 70%. Photosynthesis was measured, and a growth analysis was carried out. Fresh and dry weight of roots, shoots and leaves and leaf area were determined.

Respiration measurements

Dark respiration rate was measured (1) manometrically with a Warburg apparatus (greenhouse, field & growth room-experiments) and (2) by infra-red gas analysis (IRGA; Analytical Development Co. Ltd., type 225-2B-SS) as described by Louwerse & van Oorschot (1969) with computerized control and data processing (growth room-exp.). Measurements were made on leaf discs, in the dark at 20°C, on humid filter paper to prevent desiccation. O_2 uptake was monitored for one hour after equilibration. No dark-decay measurements were performed, as this kind of measurements causes artefacts (data not shown). By IRGA, respiration rates were determined of leaves of intact plants or for whole shoots under growth conditions. Warburg and IRGA measurements showed no significant differences. Dark respiration rates were expressed on a dry weight basis.

Leaf respiration rate was measured on the youngest fully-expanded leaves of two months old plants (*greenhouse* and *field*-exp.) and 19, 34 and 44 days old plants (*growth room*-exp.). The respiration rate of whole shoots was determined on 34 days old intact plants (*growth room*-exp.). The *greenhouse* and *field* experiment were performed during 14 days in May 1988 and June 1989, respectively.

As it is known that previous illumination may influence respiration (Azcón-Bieto & Osmond 1983), care was taken to sample the leaves from the different cultivars in *greenhouse* and *field* at the same time of the day throughout the experimental periods.

Protein determination

Leaf tissue was boiled for 1 hour. Protein was precipitated overnight in 10% (g g^{-1}) TCA. The N content of the precipitate was determined by Kjeldahl analysis. Protein

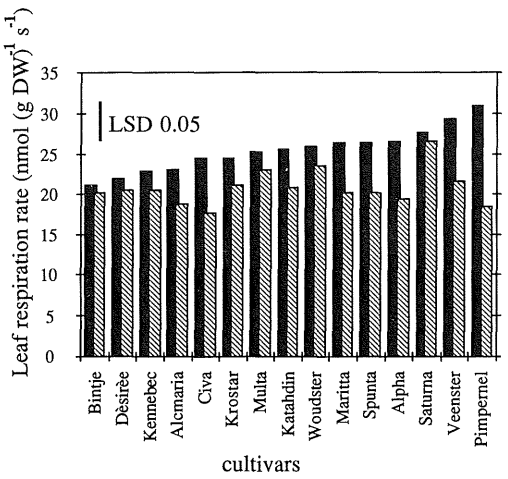

Fig. 1. Dark respiration rates (nmol O_2 (g DW)$^{-1}$ s^{-1}) of fully expanded leaves of 15 potato cultivars grown in the (■) greenhouse in 1988 and (□) field in 1989 with n = 6 and 8, respectively. The cultivars are ranked in order of ascending respiration rate in the greenhouse. LSD stands for least significant difference.

content of the leaf was calculated by multiplying the N content of the precipitated protein with 6.25.

Growth analysis and statistics

For growth analysis the following equations were used:

$$W_2 = W_1 * \exp (RGR * (t_2\text{-}t_1)) \quad (1)$$

$$RGR = NAR * LAR \quad (2)$$

$$LAR = SLA * LWR \quad (3)$$

where W_1 is plant weight at time t_i, RGR is the relative growth rate (g plant (kg plant)$^{-1}$ day^{-1}), NAR is the net assimilation rate (g m^{-2} (leaf) day^{-1}), LAR is the leaf area ratio (m^2 leaf (kg plant)$^{-1}$), SLA is the specific leaf area (m^2 leaf (kg leaf)$^{-1}$), and LWR is the leaf weight ratio (g leaf (g plant)$^{-1}$).

Cultivar differences were tested in *greenhouse* and *field* experiments by analysis of variance (ANOVA) and regression analysis. In the *growth room* experiments, cultivar differences were tested by Student's t-test (95%-probability intervals).

Results

A – greenhouse and field experiments with 15 cultivars

Figure 1 shows significant differences in leaf respiration rates between 15 potato cultivars in the greenhouse experiment ($P < 0.01$; $n = 6$). In accordance with preliminary measurements (F.W.T. Penning de Vries, pers. comm.), Alcmaria (early cv) and

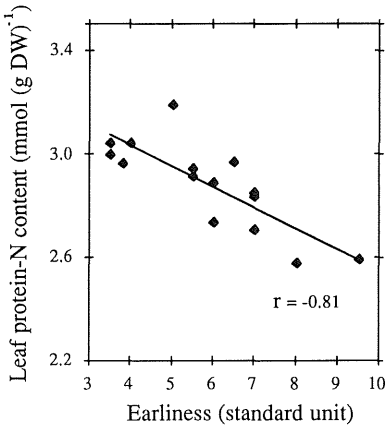

Fig. 2. Relationship between leaf protein content and earliness of 15 potato cultivars grown in the field.

Pimpernel (late cv) showed different leaf respiration rates ($P < 0.01$; $n = 6$). We found a negative trend between respiration rate on a dry weight basis and earliness ($r = -0.49$; $P < 0.07$).

Also in the field experiment significant differences in leaf respiration rate between the 15 cultivars existed (Fig. 1; $P < 0.01$; $n = 8$). However, respiration rates differed from those of the plants grown in the greenhouse. No significant correlation between respiration on a dry weight basis and earliness was found ($r = -0.32$). In contrast to the preliminary results and greenhouse experiment, Alcmaria and Pimpernel did not show a significantly different respiration rate (Fig. 1; $n = 8$).

Leaf senescence is generally accompanied by a decrease in protein content. So, leaf protein is an indicator of leaf age/developmental stage (Field 1983, Osman & Milthorpe 1971, Friederich & Huffaker 1980, Field & Mooney 1983). The relation between the protein content of the leaves of plants grown in the *field* and earliness is shown in Fig. 2. In the *field* experiment the protein content of the leaves showed a negative correlation with earliness ($P < 0.001$); the earliest cultivars (high numbers) had the lowest protein content. Thus, in this experiment cultivars appeared to develop in accordance with the earliness-index of the Dutch National Lists of Varieties.

Significant cv-differences in leaf respiration rate are not constant but change with growth conditions (Fig. 1). These differences between the cultivars might be partially due to differences in developmental stage. The correlation between leaf protein content and earliness support the idea of different developmental stages in our experiments (Fig. 2). However, differences in growth and maintenance respiration cannot be excluded. Therefore we examined the respiration rate of plants grown under controlled conditions in a growth room, where developmental rate can be regulated by manipulating the growth conditions. Tuber induction can be delayed by high nitrate nutrition and long day-lengths (Bodlaender 1963, Sattelmacher & Marschner 1978, Lorenzen & Ewing 1990). The cultivars selected for the growth room experiments, Alcmaria and Pimpernel, strongly differed in leaf respiration rate in both the preliminary and the greenhouse experiments. Growth analysis was performed (*a*) to trace

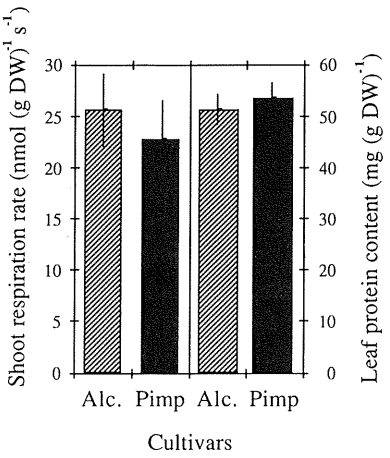

Fig. 3. The respiration rate of shoots (nmol CO_2 (g DW)$^{-1}$ s^{-1}) and the protein content of fully expanded leaves of 34 days old, intact potato plants of cv. Alcmaria (▨) and cv. Pimpernel (■) (n = 5). Bars indicate 95%-probability intervals.

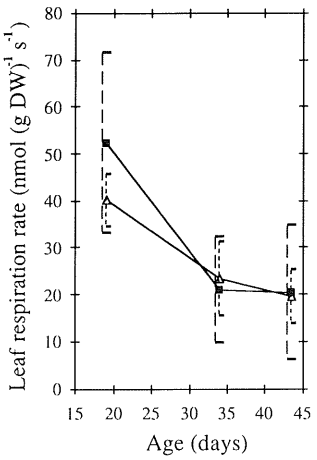

Fig. 4. Respiration rate (nmol CO_2 (g DW)$^{-1}$ s^{-1}) of fully expanded leaves of the cvs Alcmaria (▵) and Pimpernel (■). Plants of various ages (19, 34 and 44 day old plants) grown under controlled conditions (n = 4 or 5). Bars indicate 95%-probability intervals.

the causes of possible differences in respiration rate and (*b*) to check whether developmental differences occurred.

B – growth room experiments with two cultivars

Alcmaria and Pimpernel showed similar shoot respiration rates (Student's t-test with 95%-probability intervals; Fig. 3). Fully expanded leaves of young plants (19 days old) of both cultivars had a significantly higher rate of respiration than the older (34 and 44 day old) plants (Student's t-test with 99%-probability intervals; Fig. 4). However, leaves of the same age had similar respiration rates in both cultivars (Student's t-test with 99%-probability intervals; Fig. 3).

The cultivars showed similar light responses of photosynthesis (Fig. 5), leaf protein content (34 days old plants; Student's t-test with 95%-probability intervals; Fig. 3) and RGR (Fig. 6). There were also no differences in the SWR , RWR, SLA, LWR and the calculated LAR (Table 1).

Discussion

The relative variation in the leaf respiration rate between the potato cvs (Fig. 1) is of a similar magnitude as found between *Lolium perenne* populations by Wilson (1982). A quantitative comparison of our respiration measurements with values in the literature is difficult to interpret, because respiration rate strongly depends on the measuring conditions (*e.g.* temperature), and respiration rates are expressed on various bases (g DW, g FW or m^2 leaf) even though plant morphology (*e.g.* SLA, percen-

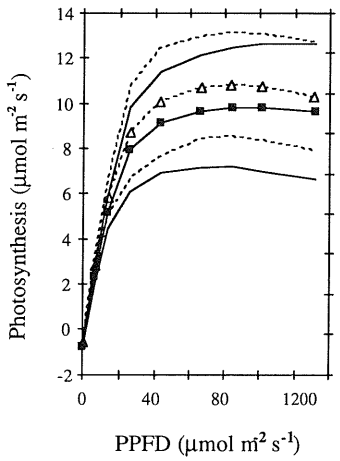

Fig. 5. Light response curves of photosynthesis (μmol CO_2 m^{-2} (leaf) s^{-1} of cvs Alcmaria (▵) and Pimpernel (■). Lines without points indicate 95%-probability intervals.

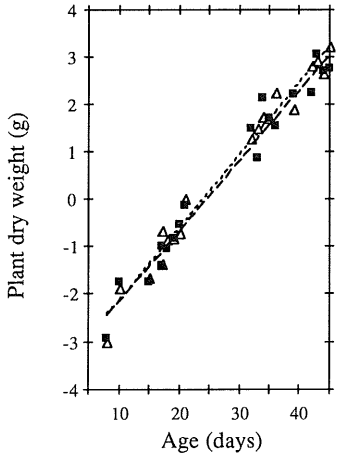

Fig. 6. Dry matter accumulation of plants of the cultivars Alcmaria (▵) and Pimpernel (■). Note that the Y-axis is a natural log (ln) scale The RGR is the slope of the line, being 0.153 for Alcmaria and 0.149 g g^{-1} day^{-1} for Pimpernel, respectively.

tage dry matter) is influenced by growth conditions. Recalculated respiration rates of the potato cultivars on a leaf area basis are for both the *field* experiment (0.7-1.1 μmol O_2 m^{-2} s^{-1}; average SLA 30 m^2 kg^{-1}) and *greenhouse* experiment (0.4-0.6 μmol O_2 m^{-2} s^{-1}; average SLA 50 m^2 kg^{-1}) quantitatively of a similar magnitude as the leaf respiration rates of 8 plant species mentioned by Lambers *et al.* (1983b; 0.6-1.2 μmol O_2 m^{-2} s^{-1}).

The results of the growth analysis show that development is identical for Alcmaria and Pimpernel when grown under long day conditions in a *growth room*. No tuber induction or flower initiation occurred during the experiment. Respiration rates of leaves (Fig. 4) and shoots (Fig. 3) of both cultivars were also similar under these growth conditions. Table 1 shows that RGR and LAR (measured or calculated from the SLA and LWR) are similar for both cultivars. This results in a similar NAR (RGR = NAR * LAR). However, NAR is the difference of leaf gross photosynthesis and total plant respiration. As can be seen in Fig. 5, the cultivars have similar light responses of leaf photosynthesis. Therefore we conclude that at a similar light interception, due to identical LAR, SLA, LWR and irradiance, total plant respiration rates of both cultivars must be equal during the experimental period. This is in agreement with the respiration measurements on both leaves and intact shoots (Figs. 4 and 3).

In case of a similar total respiration rate, differences in maintenance and growth respiration between the two cultivars can only exist if a higher growth respiration is accompanied by lower maintenance costs or vice versa for one of the cultivars. Differences in growth respiration are not likely, as the cultivars have similar leaf protein contents (Fig. 3), one of the most abundant, energetically important compounds (Penning de Vries *et al.* 1974). Furthermore, in the growth room experiment no

Table 1. Growth parameters of cvs Alcmaria and Pimpernel, with 95%-probability intervals; n = 11 to 18. The RGR is calculated from the data in Fig. 6.

Cultivar:	Alcmaria	Pimpernel
measured:	mean	mean
LAR (m^2 (kg DW plant)$^{-1}$)	26.5 ± 1.7	25.9 ± 1.4
SLA (m^2 (kg DW leaf)$^{-1}$)	47.0 ± 3.5	46.1 ± 2.7
LWR (kg DW leaf (kg DW plant)$^{-1}$)	0.57 ± 0.03	0.56 ± 0.02
SWR (g DW shoot (g DW plant)$^{-1}$)	0.82 ± 0.02	0.80 ± 0.02
RWR (g DW roots (g DW plant)$^{-1}$)	0.17 ± 0.01	0.18 ± 0.01
RGR (g DW (kg DW)$^{-1}$ day^{-1})	153	149
calculated:		
NAR (g m^{-2} day^{-1})	5.8	5.8

differences in respiration rate were found for (*a*) full-grown leaves (34 and 44 day old plants; Fig. 4) and (*b*) shoots consisting of both growing and fully developed parts (Fig. 3). It is not clear why the respiration rate of the fully expanded leaves of 19 day old plants is higher than the respiration rate of similar leaves in 34 and 44 day old plants (Fig. 4). Nevertheless, again no differences between the cultivars existed. Therefore, we conclude that differences in growth and/or maintenance respiration between the cultivars Alcmaria and Pimpernel can be excluded, as long as they are in the same stage of development.

The varietal differences in respiration rate measured on plants grown in the *greenhouse*- and *field*, are probably related to different developmental stages of the cultivars, caused by the interaction between genotype and environmental conditions. It cannot be excluded that differences in respiration for growth and maintenance are absent for all cultivars. Also, energy costs for maintenance and/or growth may depend on the growth conditions. To answer such questions, a detailed study of growth, development, and respiration with various cultivars under various conditions is needed.

Differences in respiration rate do not necessarily originate from different energy costs of maintenance and/or growth costs. Therefore the outcome of selecting for low respiration rate cannot be predicted. In order to select for low maintenance costs, identification of the processes and a direct method of selection are required.

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