PHYSIOLOGIA PLANTARUM 83: 469–475. Copenhagen 1991

Respiratory energy requirements of roots vary with the potential growth rate of a plant species

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Poorter, H., Van der Werf, A., Atkin, O. K. and Lambers, H. 1991. Respiratory energy requirements of roots vary with the potential growth rate of a plant species. – Physiol. Plant. 83: 469–475.

The rates of growth, net rate of nitrate uptake and root respiration of 24 wild species were compared under conditions of optimum nutrient supply. The relative growth rate (RGR) of the roots of these species varied between 110 and 370 mg g^{-1} day^{-1} and the net rate of nitrate uptake between 1 and 7 mmol (g root dry weight)$^{-1}$ day^{-1}. The rate of root respiration was positively correlated with the RGR of the roots. Root respiration was also calculated from the measured rate of growth and nitrate uptake, using previously determined values for the costs of maintenance, growth and ion uptake of two slow-growing species. The calculated rate of respiration was slightly lower than the measured one for slow-growing species, but twice as high as measured rates for rapid-growing species. This discrepancy was not due to a relatively smaller electron flow through the alternative pathway and, consequently, a more efficient ATP production in the fast-growing species. Neither could variation in specific costs for root growth or maintenance explain these differences. Therefore, we conclude that fast-growing species have lower specific respiratory costs for ion uptake than slow-growing ones. Due partly to these lower specific costs of nutrient uptake, the fraction of respiration that rapid-growing species spend on anion uptake is lower than that of slow-growing species, in spite of the much higher rate of ion uptake of the fast-growing ones.

Key words – Nutrient uptake, relative growth rate, respiration.

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Introduction

Plant species from contrasting environments may differ considerably in growth potential. When grown under similar, close to optimal conditions, species naturally occurring in nutrient-rich habitats grow faster than those found in nutrient-poor sites (Grime and Hunt 1975, Poorter and Remkes 1990). These differences in growth rate are associated with differences in biomass allocation, chemical composition and leaf area formation (cf. Potter and Jones 1977, Mooney et al. 1978, Poorter 1989a). Also the rates of shoot and root respiration per unit shoot dry weight and root dry weight, respectively, vary in a systematic way, such that fast-growing species have higher rates than slow-growing ones (Dijkstra and Lambers 1989, Poorter et al. 1990).

What causes these differences in respiration? To obtain insight into this process, respiration has been partitioned into one component that correlates with the growth rate of a plant, and another that correlates with the amount of biomass (McCree 1970, Thornley 1970, Lambers and Steingröver 1978). In this manner respiratory costs for growth and for maintenance have been estimated. More recently, a third respiratory component, related to the rate of ion uptake, has been quantified (Veen 1980, Johnson 1983, Van der Werf et al. 1988). An analysis of root respiration allowing separation of three components (growth, maintenance and

Received 7 March, 1991

ion uptake) is generally less prone to errors than one where only two components (growth, which includes ion uptake, and maintenance) are discerned (Lambers et al. 1983). The various methods have been evaluated in a number of recent papers (Lambers et al. 1983, Amthor 1986, Lambers and Van der Werf 1988).

Using a three-component analysis and making allowances for any change in the contribution of the alternative path in respiration, values for the energetic costs of root growth, ion uptake and maintenance of root biomass have been obtained for two inherently slow-growing *Carex* species from nutrient-poor, floating fens (Van der Werf et al. 1988). However, it is not known if the respiratory costs for growth, ion uptake and maintenance vary between species with different growth rates. Therefore, the aim of our work was to compare the root respiration of a range of fast-growing and slow-growing species. Such a comparison allows us to test if the specific respiratory costs for root growth, ion uptake or the maintenance of root biomass vary between species, perhaps in a systematic manner depending on the inherent potential relative growth rate (RGR) of the species.

Abbreviations – NNUR, net nitrate uptake rate; RGR, relative growth rate; SHAM, salicylhydroxamic acid.

Materials and methods

Growth of the plants

Plants of 24 wild species, from a wide range of habitats in western Europe, were grown in nutrient solution in a growth chamber. These species were the monocotyledons *Brachypodium pinnatum* (L.) Beauv., *Briza media* L., *Corynephorus canescens* (L.) Beauv., *Cynosurus cristatus* L., *Dactylis glomerata* L., *Deschampsia flexuosa* (L.) Trin., *Festuca ovina* L., *Holcus lanatus* L., *Lolium perenne* L., *Phleum pratense* L. and *Poa annua* L., and the dicotyledons *Anthriscus sylvestris* (L.) Hoffm., *Galinsoga parviflora* Cav., *Geum urbanum* L., *Hypericum perforatum* L., *Lysimachia vulgaris* L., *Origanum vulgare* L., *Pimpinella saxifraga* L., *Plantago major* L. ssp. *major* L., *Rumex crispus* L., *Scrophularia nodosa* L., *Taraxacum officinale* Weber, *Trifolium repens* L. and *Urtica dioica* L.

Details about collection of the seeds and germination conditions are given in Poorter and Remkes (1990). After germination the seedlings were placed in a growth room with the following conditions: Day 14 h, photosynthetic photon flux density 315 ± 30 μmol m^{-2} s^{-1}, temperature 20 ± 0.5°C, relative humidity ca 70%. Night 10 h, temperature 20 ± 0.5°C, relative humidity ca 70%. Light was provided by fluorescent lamps (Philips TL-33-RS, 215 W) and incandescent bulbs (Philips, 40 W) in a ratio of 4:1. Plants were grown without mutual shading. The nutrient solution, a modified Hoagland solution with a NO_3^- concentration of 2 m*M* Poorter and Remkes 1990), was replenished at least once a week. With this frequency of replenishment the NO_3^- concentration in the nutrient solution never dropped below 1 m*M*. Plant dry weight was determined 6 times (8 replicates per harvest) during a period of 17 days, starting when plants had a fresh weight of approximately 100 mg. Full details are given in Poorter and Remkes (1990).

Root respiration and alternative path activity

Root respiration was determined on detached roots of 8 plants as the decrease of oxygen concentration in an airtight cuvette containing a nutrient solution, which was identical to that used for growing the plants and air-saturated before the start of the measurements. The temperature of the solution was 20 ± 0.5°C, the pH was set to 5.8. The oxygen concentration was measured with a Clark-type electrode (Yellow Springs Instruments, OH, USA). Root respiration was determined between 5 and 15 minutes after severance from the shoot. In a pilot experiment with 4 species no effect of shoot excision on root respiration was found during this period.

In separate experiments with a number of species (listed in Tab. 1), the activity of the alternative, non-phosphorylating pathway was determined using salicylhydroxamic acid (SHAM), an inhibitor of the alternative path. Prior to these determinations, titration curves were made for each species, to exclude possible side effects of SHAM, such as stimulation of peroxidases (Møller et al. 1988, Van der Werf et al. 1991) or inhibition of the cytochrome path (Bingham and Farrar 1987, Møller et al. 1988). In all cases SHAM was dissolved in a nutrient solution without Fe and set to a pH of 5.8.

Chemical analyses

Prior to the chemical analyses, all plants were dried and combined into two independent bulk samples. Total organic nitrogen was determined with a modified Kjeldahl method using concentrated sulfuric acid and Na_2SO_4, K_2SO_4 and Se in a ratio of 62:1:1 (w/w) as a catalyst. The N-content was determined colorometrically using indophenol blue. The nitrate content was determined according to Cataldo et al. (1975). Lipids were determined gravimetrically after extraction in a 2:2:1 (v/v) mixture of chloroform, methanol and water (Bligh and Dyer 1969). Soluble phenol content was determined colorometrically in the methanol-water phase as indicated in Singleton (1988). Soluble and insoluble sugars were determined using anthron reagent (Fales 1951), after extraction of root material with 80% (v/v) ethanol and 3% HCl, respectively. Ash content was measured by combustion at 550°C, and the ash alkalinity was then determined acidimetrically. Organic acid content was derived from ash alkalinity, after correcting for oxides stemming from combustion of NO_3^-. Mineral content was calculated by subtracting the total

ash alkalinity, multiplied by 30 g eq^{-1}, from the total ash content and adding the nitrate content. Crude cell wall material was considered to be the rest fraction after extraction with chloroform, methanol, water, ethanol and 3% HCl. The cell wall content was considered to be the crude cell wall material, after subtracting the organic N content of this fraction multiplied by 6.25. The lignin content in this fraction was determined colorimetrically at 280 nm after treatment with acetylbromide in acetic acid (Morrison 1972). Full details are given in Poorter and Bergkotte (1991).

Net nitrate uptake

The net rate of nitrate uptake per unit root weight (NNUR) was calculated from the RGR, the total nitrogen content of plant biomass and the fraction of total biomass invested in roots (Garnier 1991). The rate of NO_3^- uptake is considered to be a good approximation of the total anion uptake (cf. Veen 1981).

Statistical analysis

Data were analyzed with the SAS statistical package (Joyner 1985). Equations for the time trend of RGR and its components were obtained by a stepwise regression as described by Poorter (1989b). To avoid comparison of species with totally different plant weights, the values of all parameters were calculated over the period the plants had a dry weight ranging from 30 to 100 mg. These weighted values were obtained by dividing the integral of the polynomial over the period that a species had the above-mentioned range in weight, by that interval. Relations between the several parameters under investigation and RGR were tested with linear regression equations, except for the data of Fig. 4A, in which a power function was used to fit the data. Differences in slope were tested with a *t*-test.

Results and discussion

Compared to slow-growing species, fast-growing species absorbed nitrate at a higher rate per unit root weight ($P < 0.001$; Fig. 1A; cf. Garnier et al. 1989). This is associated with their higher RGR, their higher nitrogen content ($P < 0.001$; Fig. 1B) and their relatively smaller root weight (Poorter and Remkes 1990). Roots of fast-growing species also respired at a higher rate ($P < 0.01$; Fig. 2), as to be expected from their higher rates of growth and anion uptake (Veen 1980, Van der Werf et al. 1988). However, the rate of root respiration differed only by a factor of 1.7 between the fast- and slow-growing species, whereas the rate of growth and nitrate uptake differed by a factor of as much as 3 and 7, respectively.

To gain further insight why the variation in the rate of respiration of the 24 species is relatively small, we recalculated the data of Van der Werf et al. (1988) on a dry

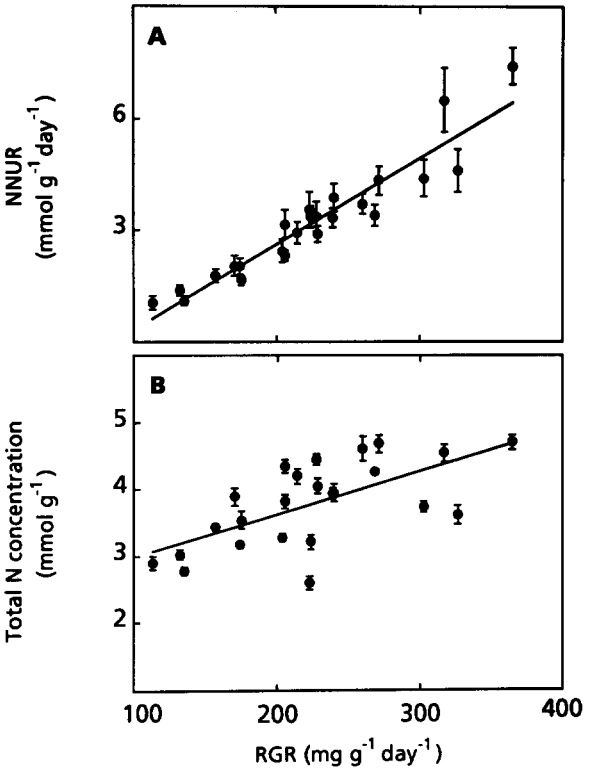

Fig. 1. A. The net influx of nitrate into roots (NNUR), expressed per unit root dry weight, B. Total plant nitrogen concentration (organic N plus NO_3^-, expressed per unit plant dry weight, of 24 species differing in growth rate. Mean values from two independent bulk samples ± SE.

weight basis. Thus, we arrived at specific respiratory costs for root growth [6.3 mmol O_2 (g dry weight)$^{-1}$], maintenance of root biomass [6.4 nmol O_2 (g dry weight)$^{-1}$ s^{-1}] and anion uptake [1.25 mol O_2 (mol

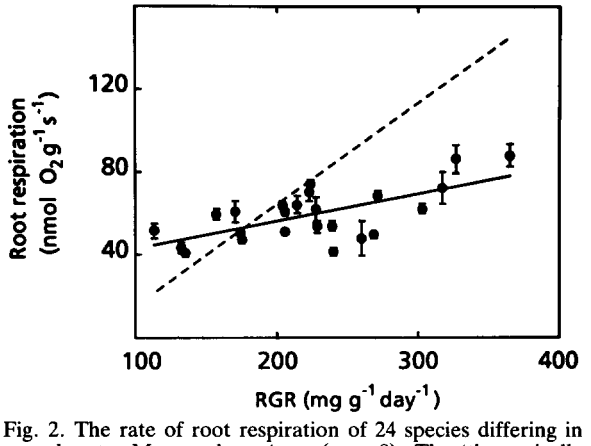

Fig. 2. The rate of root respiration of 24 species differing in growth rate. Mean values ± SE (n = 8). The 'theoretically expected' rate of root respiration (broken line) was determined using actual rates of growth and ion uptake of the 24 species and previously determined specific costs for maintenance, root growth and ion uptake for two slow-growing *Carex* species (Van der Werf et al. 1988).

ions)$^{-1}$], which are average values of the two *Carex* species. Assuming that the costs for the construction and maintenance of one gram of root biomass and for the uptake of one mol of ions are the same for all these 24 species as for the two *Carex* species determined previously, and also that there is a similar ratio between the uptake of nitrate and the uptake of other anions, we calculated a 'theoretically expected' rate of root respiration. The 'theoretically expected' rate of respiration (Fig. 2, broken line) was lower than the 'experimentally determined' rate in the RGR range of the extremely slow-growing species and considerably higher than the 'experimentally determined' rate for fast-growing species. The difference in slope between the lines is significant ($P < 0.001$).

What could be the physiological basis for this discrepancy between the 'theoretically expected' and 'experimentally determined' values? Firstly, the ADP:O ratio of root respiration, the production of ATP per atom of oxygen respired, might be lower for slow-growing species. Apart from the cytochrome pathway, with an ADP:O ratio of 3.0, plants also have an alternative pathway, which has an ADP:O ratio of 1.0 in vitro (Douce 1985), as well as in vivo (Roberts et al. 1984). Variation in the extent to which the alternative pathway contributes to root respiration would affect the ADP:O ratio. Table 1 provides information on the contribution of the alternative path to root respiration for a number of species, varying in RGR. These species are partly the same as those for which data are presented in Fig. 2. On average the alternative path represented 32% of the root respiration, which results in an ADP:O ratio of 2.37. However, there was no systematic trend of the extent of the contribution of the alternative path with RGR ($P > 0.75$; Tab. 1). Hence, variation in the contribution of the alternative path cannot explain why roots of fast-growing species respire at a relatively low rate.

An alternative explanation for the observed discrepancy is that specific respiratory costs for growth, maintenance and/or ion uptake are not identical for all 24 species, but rather lower for fast-growing species than for slow-growing ones. Are the costs for synthesis of biomass lower? This will depend on the chemical composition of the various species. Based on the biochemical pathways of synthesis, Penning de Vries et al. (1974) calculated values for the oxygen consumption associated with the production of one unit of the main compounds of plant biomass: proteins, carbohydrates, lipids, lignin and organic acids. We analyzed each of these fractions in the roots of the 24 species, as well as the soluble phenol content and minerals. Mean values for a typical slow-growing species and a typical fast-growing one are given in Tab. 2 (full data are given in Poorter and Bergkotte 1991). Combining the data on the chemical composition of the 24 species with the values given by Penning de Vries et al. (1974), and assuming an ADP:O ratio of 2.37, we calculated the oxygen consumption needed for the production of 1 g of root biomass. This respiration varied from 5.5 to 8 mmol O_2 (g dry weight)$^{-1}$, which compares rather well with the values found for the *Carex* species in the regression approach of Van der Werf et al. (1988) [on average 6.3 mmol (g dry weight)$^{-1}$]. Growth respiration increased with increasing RGR ($P < 0.01$; Fig. 3), mainly due to the higher protein levels in the roots of the faster growing species (cf. Tab. 2). Thus, fast-growing species have higher respiratory costs for growth. However, if the specific costs for growth were to explain the discrepancy between the calculated and measured rate of root respiration, their value would have to be lower for the fast-growing species. Hence, the respiratory costs for synthesis of root biomass cannot explain the relatively low respiration rate of rapid-growing species.

We have little information on the biochemistry and physiology of 'maintenance processes'. Protein turnover and the maintenance of solute gradients are considered major processes (Penning de Vries 1975), but for roots quantitative information on both of them is lacking. Assuming the same turnover rate per unit protein, we expect the maintenance requirement of fast-growing species, which have a higher protein content (Tab. 2), to be higher than that of slow-growing ones. On the other

Tab. 1. The contribution of the alternative path to root respiration (% of total root respiration) for a number of species differing in RGR (mg g^{-1} day^{-1}) at an optimum nutrient supply (SE values in parentheses, n = 4–8). SHAM, an inhibitor of the alternative path was used at a concentration that did not affect the cytochrome path or a peroxidase, as demonstrated in titration experiments (cf. Møller et al. 1988, Van der Werf et al. 1991). Some of the data have been obtained from the literature. The correlation between RGR and the contribution of the alternative path is non-significant ($P > 0.75$).

Species	RGR	Alternative path (%)	Reference
Carex tumidicarpa	82	34 (3)	
Carex flacca	104	30 (4)	
Briza media	113	19 (3)	
Carex acutiformis	129	34 (2)	
Deschampsia flexuosa	135	36 (4)	
Plantago lanceolata	145	39 (4)	Blacquière et al. 1987
Carex diandra	148	23 (3)	
Brachypodium pinnatum	150	14 (2)	
Poa pratensis	185	41 (2)	
Festuca ovina ssp. *ovina*	203	28 (3)	
Plantago major ssp. *major*	212	38	Dijkstra and Lambers 1989
Dactylis glomerata	217	54 (2)	
Pisum sativum	229	28	Blacquière and De Visser 1984
Holcus lanatus	268	40 (1)	
Plantago major ssp. *pleiosperma*	280	36	Dijkstra and Lambers 1989
Rumex maritimus	281	26 (4)	
Rumex obtusifolius	300	19 (3)	

hand, the relatively rapid turnover of carbohydrate pools in slow-growing species as compared to fast-growing ones (Farrar 1989) may enhance maintenance costs of the roots of slow-growing species. However, even in the 'theoretically calculated' respiration of fast-growing species, maintenance only accounts for 4% of the total respiration. A lower maintenance respiration rate, therefore, will hardly change the total respiration rate of these plants. Hence, we dismiss variation in maintenance requirement as a significant factor explaining the observed discrepancy between 'theoretically calculated' and 'experimentally determined' values of respiration.

By exclusion of other possibilities, we reach the conclusion that variation in the specific costs of nutrient acquisition is likely to be the major explanation for the unexpectedly low rate of root respiration of rapid-growing species (Fig. 2). To obtain an impression of the variation in these costs, the following calculation was made. We assumed the costs of maintenance for all species to be equal to the mean value found by Van der Werf et al. for the two *Carex* species [6.4 nmol O_2 (g dry weight)$^{-1}$], a fixed ratio between the uptake rate of nitrate and other anions as observed for the *Carex* species (3:1) and an ADP:O ratio of 2.37 (cf. Tab. 1). For each species we used the growth respiration as given in Fig. 3. From these data, combined with the rates of respiration, growth and nitrate uptake, we calculated the oxygen consumption necessary for the uptake of one mol of anions (Fig. 4A). These values compare well with those for the slow-growing *Carex* species as given above [1.25 mol O_2 (mol anions)$^{-1}$], for maize (1.04; Veen 1981) and for sunflower (0.69; Johnson 1990, assuming a respiratory quotient of 1.2 and a ratio of nitrate efflux to total nitrate uptake of 0.25). The main conclusion, which can be drawn from Fig. 4A, is that the computed value for the costs of anion uptake is approximately 3 times as low for the rapid-growing species as for the slow-growing ones.

What could form the physiological basis for differences in the specific costs of ion uptake? Firstly, the relatively large respiratory losses of slow-growing species might be associated with a low ratio between ion influx and efflux (cf. Pearson et al. 1981). Secondly, the stoichiometry of proton entry and anion absorption may be higher for slow-growing species (cf. Clarkson 1986). E.g., in barley two transport systems for NO_3^- were found, one energyrequiring system operating at low external concentrations; and a second one, which does not require energy and works at high external concentrations (Glass et al. 1990, Siddiqi et al. 1990). Differences in the proportion of the two uptake systems could explain the variation in specific uptake costs between species, when grown under these conditions. Thirdly, slow-growing species may exude specific compounds, like organic acids (Dinkelaker et al. 1989). Slow-growing species normally occur in unproductive environments (Grime and Hunt 1975, Poorter and Remkes 1990), where nutrients are sparingly soluble due to complexation with carbonates or humic substances, or in substrates where nutrients are very dilute. If the higher costs for nutrient uptake of the slow-growing species are related to some kind of adaptation, we expect the last two explanations to be more likely than the first one, as they will either decrease the investment for slow-growing species of building an uptake system that will hardly be used in nutrient-poor conditions (the second alternative), or enhance ion uptake under such conditions (the third).

Tab. 2. Chemical composition (mg g^{-1}) of roots of a typical slow-growing and a typical fast-growing species. Mean recovery was 104 ± 5%. For each of the 24 species, data were first normalized to 100%. Thereafter, linear regressions were computed with RGR as independent variable and the different components as dependent variables. From these regression values the predicted compositions at a very low (110 mg g^{-1} day^{-1}) and a very high (370 mg g^{-1} day^{-1}) RGR were calculated. *P*-values indicate whether the slope of the regressed line differs significantly from zero (NS, non-significant).

Compound	Typically slow-growing species	Typically fast-growing species	*P*
Lipids	16	24	NS
Lignin	41	24	NS
Proteins	177	284	<0.01
Carbohydrates	605	439	<0.01
Organic acids	18	41	NS
Minerals	140	185	<0.05
Soluble phenolics	3	3	NS

The relative share in respiration of energy-requiring processes like growth and uptake does not only depend on the specific costs but also on the associated rates. Based on the coefficients as given above, we calculated the fraction of respiration involved in the three processes discerned. Figure 4B shows that for these young

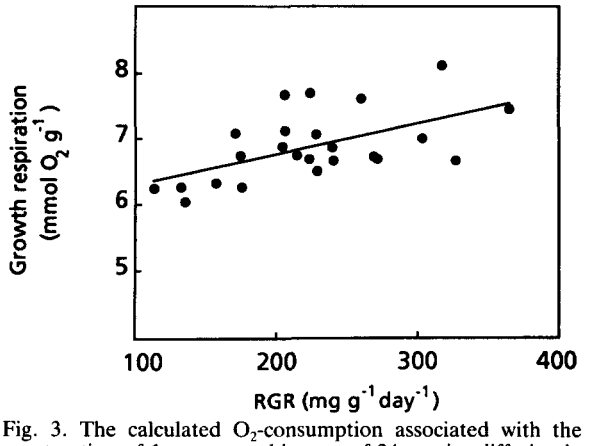

Fig. 3. The calculated O_2-consumption associated with the construction of 1 gram root biomass of 24 species differing in growth rate. These values are based on chemical analysis for lipids, lignin, proteins, carbohydrates, organic acids, minerals and soluble phenolics of the roots of the 24 species, and values for the associated oxygen consumption (cf. Penning de Vries et al. 1974).

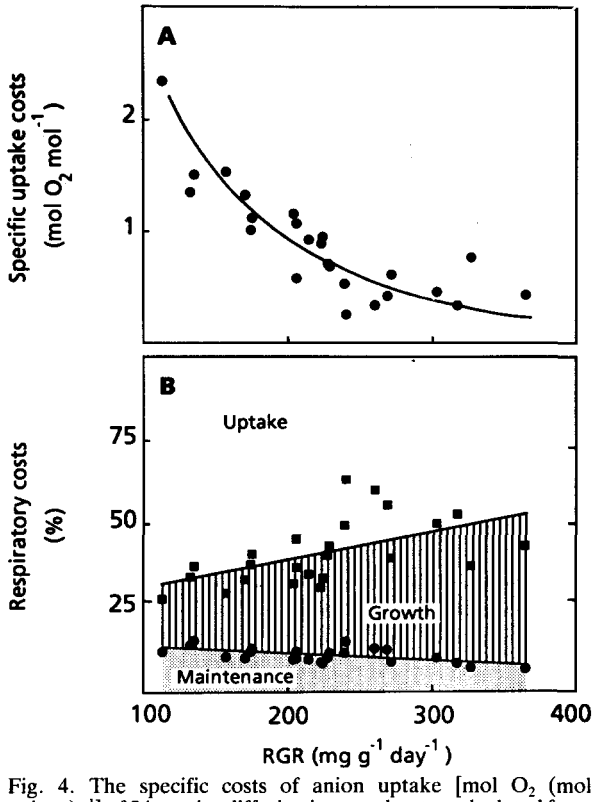

Fig. 4. The specific costs of anion uptake [mol O_2 (mol anions)$^{-1}$] of 24 species differing in growth rate, calculated from ured rate of respiration, NNUR and RGR, a maintenance respiration assumed to be equal to that found by Van der Werf et al. (1988) and specific costs for growth as given in Fig. 3. B. The percentage of root respiration used for maintenance, growth and nutrient uptake for the different species, as estimated from the specific costs and rates as used in Fig. 4A.

plants, grown under conditions of high N-availability, maintenance is only a minor component of root respiration (approximately 10%). Growth is more important (20-45%), but most of the respiration is involved in the nutrient uptake process (50-70%). The values found here agree well with those of Veen (1981) for young maize plants, in which nutrient uptake comprised 60% of total respiration, growth 24% and maintenance 16%. Van der Werf et al. (1988) found higher proportions of maintenance respiration in the *Carex* species than here, but their plants were much older and had rather low NNUR's and RGR's. Johnson (1990) found growth to be a more important factor in respiration than ion uptake. However, he calculated respiration on a carbon dioxide basis, thus including the production of reducing power for NO_3^- reduction, whereas we measured O_2 consumption, which is predominantly related to ATP production.

Conclusions

Slow-growing species have lower rates of root respiration than rapid-growing ones. However, in view of their low rates of growth and nutrient uptake, the respiration rate of slow-growing species is relatively high. We conclude that this can be explained neither by a higher contribution of the alternative pathway in respiration, nor by higher specific costs for growth or maintenance. Therefore, we infer that the relatively high respiration of slow-growing species is most probably related to their cost of nutrient acquistion.

Acknowledgements – We thank Marc Bergkotte, Peter Laan and Carlo Remkes for their technical assistance and Jeroen van Arendonk and Henk Konings for allowing us to use some of their unpublished data. Ad Borstlap, Eric Garnier, Edwin Kraus, Thijs Pons and Ries de Visser made valuable comments on a previous version of this manuscript.

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Edited by A. Kylin