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Components of relative growth rate and nitrogen productivity of Brussels sprouts and leeks grown at two widely differing light intensities

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† Shortly after the experiments our colleague Tessa Enserink unfortunately died. She greatly contributed to this work.

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Abstract

Early in the season, Brussels sprouts have a higher rate of biomass production than leeks at recommended fertilizer (nitrogen) application rates. Furthermore, they have a considerably higher annual biomass production and a higher annual biomass production per unit of nitrogen taken up. In this paper we explore and discuss the possible explanations for these field observations, using information obtained from growth chamber studies and the literature.

Young vegetative plants of Brussels sprouts and leeks were grown in a growth chamber at a light intensity of 550 μmol m^{-2} s^{-1} and at a light intensity which was 20% of that of the high-light treatment. At both light treatments, Brussels sprouts had an approximately 90% higher relative growth rate than leeks. At both light treatments the higher relative growth rate of Brussels sprouts was mainly explained by its higher leaf area ratio. Only minor differences in the physiological component, the net assimilation rate, between the two species within a light treatment were observed. The higher leaf area ratio of Brussels sprouts was mainly explained by its higher specific leaf area. Brussels sprouts had a higher rate of biomass production per unit of internal nitrogen (nitrogen productivity) than leeks. This was mainly explained by a higher allocation of nitrogen to leaves and a higher rate of biomass production per unit leaf nitrogen. We suggest that the higher biomass production per unit of nitrogen taken up of Brussels sprouts compared to that of leeks as observed in the field is explained by its higher nitrogen productivity. The results obtained from the growth chamber studies are discussed in relation with field experiments and data from the literature.

Keywords: Brussels sprouts, growth analysis, leeks, net assimilation rate, nitrogen productivity, relative growth rate, specific leaf area

Introduction

At recommended fertiliser (nitrogen) application rates, Brussels sprouts produce ap-

proximately 16–17 tons of dry matter per ha, whereas leeks only produce 9–11 tons. The most striking differences in the rate of dry matter production were observed early in the growing season. Furthermore, the annual production of dry matter per unit of nitrogen taken up was higher for Brussels sprouts than for leeks. In addition Brussels sprouts showed a higher recovery of the applied fertiliser nitrogen (Smit & Van der Werf, 1992; Booij *et al.*, 1993,1996). This low recovery of nitrogen may lead to high losses of nitrogen to the environment.

Smit *et al.* (1995, 1996) showed in their Wageningen Rhizolab studies that roots of leeks penetrated the soil profile slower than Brussels sprouts do. Moreover, the volumetric rooting density of Brussels sprouts in the greatest part of the soil profile was higher than that of leeks. The question now arises whether the lower rooting density of leeks compared to that of Brussels sprouts is responsible for its relatively low growth rate or if its low root density is merely a consequence of a lower potential growth rate. The first evidence that the differences in dry matter production between the two vegetable crops are not explained by differences in rooting density comes from a series of field experiments with different rates of fertiliser nitrogen application (Booij *et al.*, 1993, 1996). Reducing the fertiliser application rate of nitrogen from over 200 to approximately 100 kg ha^{-1} hardly influenced the annual biomass production and the uptake of nitrogen of leeks in 1991, whereas that of Brussels sprouts was significantly reduced. In 1992, even a reduction in the fertiliser application from approximately 200 to zero kg ha^{-1} hardly influenced biomass production or nitrogen uptake in leeks. In Brussels sprouts both dry matter production and nitrogen uptake were greatly reduced in that year. If, under recommended fertiliser application rates, the root system would have been responsible for the relatively low dry matter production in leeks, a reduction in the rate of fertiliser nitrogen application should have been accompanied by a reduction in dry matter production. Secondly, simulation studies have shown that root densities of approximately 1 cm cm^{-3} can sustain an uptake rate of nitrogen of 0.2–0.3 g m^{-2} day^{-1}, even at very low concentrations of nitrate in the soil (De Willigen & Van Noordwijk, 1987). This uptake rate is sufficient to support the maximum demand of leeks at recommended fertiliser rates (cf. Smit *et al.*, 1995). This again suggests that the morphology of the root system of leeks is not limiting nitrogen uptake and thus biomass production under an ample supply of nitrogen. Generally, under an ample supply of nitrogen, the activity of the uptake system is far less than its capacity , i.e. nitrogen uptake is down-regulated to the 'demand of the plant' (e.g. Lee & Drew 1986; Mattson *et al.*, 1988). All the information given above suggests that the relatively low biomass production of leeks compared to that of Brussels sprouts is not limited by an inferior root system. Consequently, we hypothesise that differences between the two vegetable crops in dry matter production are explained by differences in their potential growth rate.

Generally, nitrate uptake is controlled by the growth rate and not the other way around (Touraine *et al.*, 1994). A high growth rate is generally highly correlated with a high uptake rate (e.g. Garnier, 1991; Van der Werf *et al.*, 1993c; Touraine *et al.*, 1994). Thus, species with a high potential growth rate have a higher 'demand for nitrogen' than species with a low potential growth rate. The magnitude of this differ-

ence in 'demand' now strongly depends on the rate of biomass production per unit of internal nitrogen present in the plant (nitrogen productivity), i.e. on the realised plant nitrogen concentration given a certain potential growth rate.

In this paper we test the hypothesis that Brussels sprouts have an inherently higher relative growth rate than leeks. Secondly we give explanations for these differences in growth rate in underlying morphological and physiological characteristics of both species. Thirdly we give explanations for the differences in the rate of biomass production per unit of nitrogen taken up, as observed in field experiments, using the concept of nitrogen productivity. These three objectives are analysed for both Brussels sprouts and leeks under controlled-environmental conditions in a growth chamber at a relatively high and relatively low photosynthetic photon flux density. The high light intensity treatment approximates (20% less than ambient) the average daily light intensity in June (7.8 MJ m^{-2} day^{-1}) in the years 1991 and 1992 in the vicinity of field-experiments in Wageningen carried out by Booij *et al.* (1996). We assume that the high light intensity enables us to determine the potential growth rate (Pons, 1977; references cited in Björkman, 1981). The low light treatment (20% of the high light treatment) was used to analyse if differences in plant characteristics between the two vegetable species observed under more or less non-limiting light conditions also hold under low light conditions.

Materials and methods

Plant growth

For the experiments we used plants of the monocotyledonous vegetable *Allium porrum* L. (leeks) and the dicotyledonous vegetable *Brassica oleracea* var. *gemmifera* (Brussels sprouts).

The experimental conditions of the growth room were: photosynthetic photon flux density, 100–120 µmol m^{-2} s^{-1} and 530–570 µmol m^{-2} s^{-1} at average plant height, provided by 400W HPI lamps; light period, 14 h; day and night temperature 20°C; RH 75%.

Seeds (obtained from Sluis & Groot, Enkhuizen, The Netherlands) of Brussels sprouts and leeks were germinated on river sand, moistened with one fourth of the concentration of the nutrient solution as described below. When the first leaf was expanded (in the case of Brussels sprouts) or when the second leaf had reached a length of approx. 5 cm. (in the case of leeks), seedlings were transferred to 33-L tanks containing an aerated solution. Nutrient concentrations were: 1.1 mM KNO_3, 1.0 mM Ca $(NO_3)_2$, 0.6 mM $MgSO_4$, 0.25 mM KH_2PO_4, 45 µM Fe-EDTA, 20 µM H_3BO_3, 20 µM $MnSO_4$, 6 µM $ZnSO_4$, 0.5 µM Na_2MoO_4 and 0.5 µM $CuSO_4$. The nutrient solution was renewed each week, to prevent nutrient depletion. The pH of the solution was maintained between 5.8 and 6.6 and was adjusted regularly with H_2SO_4. Only minor differences in light intensity and temperature occurred in the growth room. To minimize these effects plants were rotated within the growth room twice a week. During the experimental period mutual shading was prevented, by spacing the plants with time.

Growth analysis

In both light treatments, five harvests over a period of 15 days were carried out, with 6 plants per harvest. Plants were separated into leaves (blades), stems (leaf sheaths) and roots, and the dry weight (48 h at 70 °C) and the leaf area (Leaf Area Meter, Licor, model 3100, Lincoln, USA) was determined.

Chemical analyses

The organic and inorganic nitrogen content was determined for the above mentioned plant parts on three harvest days and per harvest three plants were pooled. Total nitrogen was determined with an elemental analyser according to the Dumas method (ROBOPREP-CN, Biological Sample Converter, Europe Scientific, Crewe, UK). Nitrate was determined with a continuous-flow analyser system (TRAACS 800, Bran + Luebbe Analyzing Technologies, Elmsford (NY), USA).

Statistical analysis

The mean RGR during the experimental period was determined as the slope of the linear regression of natural logarithm of total plant dry weight versus time. Differences in RGR were tested using the multiple linear regression method in GENSAT (Payne et al., 1993). Mean values of parameters in equations. 1–4 were analyzed with an ANOVA.

Theoretical background

The relative growth rate (RGR; mg g^{-1} day^{-1}) can be factored into a 'physiological component', the net assimilation rate (NAR; g m^{-2} day^{-1}) and a morphological component, the leaf area ratio (LAR; m^2 kg^{-1} (plant)).

$$RGR=NAR*LAR \quad (1)$$

The leaf area ratio can be further broken down into two components: specific leaf area (SLA; m^2 kg^{-1}(leaf)) and the leaf weight ratio (LWR; g (leaf) g^{-1}(plant)):

$$LAR=SLA*LWR \quad (2)$$

The net assimilation is determined by the carbon gain in photosynthesis per unit leaf area and carbon utilisation in respiration in all organs, also expressed per unit leaf area. Therefore, net assimilation rate, actually represents an overall expression for both physiological processes (photosynthesis and respiration) and morphological characteristics (biomass partitioning and leaf area characteristics) (cf. Van der Werf, 1996).

To obtain further insight in differences between Brussels sprouts and leeks in dry matter production per unit of nitrogen taken up, as observed in field experiments (Booij *et al.*, 1996), the following analysis can be applied:

$$NP=RGR/PNC \quad (3)$$

where NP is the nitrogen productivity (g mol^{-1} (N) day^{-1}). The nitrogen productivity gives the amount of biomass that can be produced per unit of nitrogen present in the plant and per unit of time, and PNC is the nitrogen concentration of the whole plant. Hirose (1988) proposed to rewrite equation 3 into:

$$NP = N_l/Np * N_lP \quad (4)$$

N_l over N_p represents the ratio of leaf nitrogen to plant nitrogen (LNR; leaf nitrogen ratio) and N_lP the rate of biomass production per unit leaf nitrogen. It can fairly easy be demonstrated that both NP and N_lP strongly depend on the carbon gain in photosynthesis expressed per unit leaf nitrogen (photosynthetic nitrogen use efficiency), the respiratory utilisation of carbon, expressed per unit organ nitrogen, and the partitioning of nitrogen over all the organs (e.g. Lambers *et al.*, 1990; Van der Werf *et al.*, 1993a; Garnier *et al.*, 1995).

The three objectives of this paper, as mentioned in the introduction, can now be analysed according to equations 1–4.

Results

With decreasing light intensity, the RGR of both species decreased. Within a light treatment the RGR of Brussels sprouts was approximately 90% higher than that of leeks (Table 1). The differences in RGR between the two species within a light treatment were mainly explained by differences in LAR, whereas only minor differences within a treatment were observed in NAR. The higher LAR of Brussels sprouts was explained both by a higher LWR and a higher SLA, be it that under both light conditions, SLA contributed more to the higher LAR than LWR did.

Under both light conditions the organic nitrogen concentration of leaves and roots was higher for Brussels sprouts than for leeks. This also holds when the nitrogen

Table 1. Mean values during the experimental period of relative growth rate (RGR; mg g^{-1} day^{-1}), leaf weight ratio (LWR; g (leaf) g^{-1} (plant), root weight ratio (RWR; g (root) g^{-1} (plant)), specific leaf area (SLA; m^2 (leaf) kg^{-1} (leaf)), leaf area ratio (LAR; m^2 (leaf) kg^{-1} (plant)) and net assimilation rate (NAR; g m^{-2} (leaf) day^{-1}) of leeks (L) and Brussels sprouts (B) grown at two photosynthetic photon flux densities (PPFD; µmol m^{-2} s^{-1}). NAR calculated from equation 1. LSD: least significant difference.

Parameter	PPFD 500		100		
	Species L	B	L	B	LSD
RGR	124	230	78	155	*
LWR	0.57	0.73	0.63	0.67	0.02
RWR	0.24	0.14	0.16	0.14	0.01
SLA	12.6	20.9	20.8	32.4	0.7
LAR	7.2	15.2	13.1	21.8	0.5
NAR	17.0	15.2	6.0	7.1	

* Relative growth rates are statistically different at $P < 0.01$.

Table 2. Mean values during the experimental period of leaf organic nitrogen concentration (LNC; mmol N g^{-1}), root organic nitrogen concentration (RNC), total organic plus inorganic plant nitrogen concentration (PNC_t), organic plant nitrogen concentration (PNC_{org}), the leaf nitrogen ratio (LNR; mol (leaf N) mol^{-1} (plant N), nitrogen productivity (NP; g mol^{-1}(plant N) day^{-1}) and leaf nitrogen productivity (N_lP; g mol^{-1} (leaf N) day^{-1} of leeks (L) and Brussels sprouts (B) grown at two photosynthetic photon flux densities (PPFD; µmol m^{-2} s^{-1}). NP and N_lP calculated from equations 3 and 4. LSD: least significant difference.

Parameter	PPFD 500		100		
	Species L	B	L	B	LSD
LNC	2.78	3.31	2.61	3.53	0.30
RNC	2.26	2.95	1.73	2.72	0.40
PNC_t	3.19	3.92	3.15	4.39	0.45
PNC_{org}	2.55	3.06	2.43	3.12	0.28
LNR	0.6	0.78	0.70	0.76	0.04
NP	48.5	74.9	32.1	49.7	
N_lP	80.8	96.2	45.8	65.3	

concentration per unit of plant weight is compared (Table 2). Within a light treatment, also the total organic plus inorganic nitrogen concentration of leaves, roots or plant was higher in Brussels sprouts (data for leaves and roots not shown).

Brussels sprouts had an approx. 50% higher rate of biomass production per unit of internal organic nitrogen (NP) than leeks, irrespective of the light intensity at which the plants were grown (Table 2). The higher NP of Brussels sprouts was explained both by a higher LNR and a higher rate of biomass production per unit of organic leaf nitrogen (N_lP, Table 2).

Discussion

Based on field trials and simulation studies we hypothesized that the relatively low annual rate of biomass production of leeks is not explained by an inferior rooting system compared to that of Brussels sprouts, but by inherent differences in relative growth rate. This study further demonstrates that both at high and at low light intensity, the RGR of Brussels sprouts was approximately 90% higher than that of leeks (Table 1). At the high light intensity the potential RGR probably is approximated (cf. Evans & Hughes, 1961; Hiroi & Monsi, 1963; Pons, 1977; Van Dobben *et al.*, 1981, Hunt & Halligan, 1981; Corré, 1983). At both light intensities, the higher RGR of Brussels sprouts was mainly explained by its higher LAR. The SLA contributed most to the higher LAR of Brussels sprouts. Only minor differences between the two vegetable species in the net assimilation rate (NAR) were observed within a light treatment. Similar results were obtained when a wider range of species was compared: differences in RGR are highly correlated with differences in SLA and less with differences biomass partitioning, NAR or the rate of photosynthesis per unit

leaf area (e.g. Poorter & Remkes, 1990; Poorter *et al.*, 1990; Garnier, 1992; Van der Werf *et al.*, 1993a,b; Van der Werf, 1996).

Also in the field studies (Booij *et al.*, 1996), the physiological component hardly determined the difference in biomass production between the two vegetable crops. Both species had a more or less equal light use efficiency (LUE; approx. 2.3 g MJ^{-1}). In fact LUE is strongly correlated with NAR: LUE=NAR/IPARL, where IPARL represents the daily amount of intercepted radiation per unit leaf area. Under conditions of a LAI less than one, the SLA of Brussels sprouts in the field experiments was also significantly higher than that of leeks (27 versus 12 m^2 kg^{-1}, R. Booij unpublished results). Even though these field SLAs slightly differ from those observed in the growth chamber experiments, a general tendency can be observed. Within a light treatment (Table 1) or in field-experiments, Brussels sprouts have a higher SLA than leeks. Only small differences in the physiological components (NAR and LUE) are observed. Thus, the higher SLA enables Brussels sprouts to grow faster in the young vegetative phase, leading to faster canopy closure and consequently to a higher biomass production.

Touraine *et al.* (1994) proposed that uptake is down-regulated by a satiety signal which informs the roots on the N-status of the plant, rather than a demand-signal. Irrespective of this regulation it is generally assumed that nitrogen uptake is regulated by the growth rate and not the other way around. Thus a higher RGR consequently leads to a higher demand for nitrogen. This was also observed in the field experiments: Brussels sprouts absorb considerably more nitrogen than leeks (Booij *et al.*, 1996). Therefore, fertiliser application should be partly adjusted to the growth rate, as excessive nitrogen will to a certain extent not be absorbed, due to down-regulation of nitrogen uptake. This mechanism of down-regulation, however, does not regulate growth and uptake to such an extent that they match perfectly. Oscarson et al. (1989) showed that nitrate addition above the one to sustain maximum growth, did increase the nitrogen concentration, but did not increase RGR. In our experiments, both Brussels sprouts and leeks have a considerable amount of nitrate-N (Table 2). Similar results were observed in the field experiments. In a young vegetative phase, approximately 25 and 10% of the total N-concentration was in the form of nitrate in field-grown plants of Brussels sprouts and leeks, respectively (R. Booij unpublished data).

Despite the higher demand for nitrogen in Brussels sprouts in the field, they have a higher annual biomass production per unit of nitrogen taken up than leeks (Booij *et al.*, 1996). Based on the growth chamber experiments we suggest that this is mainly explained by the higher nitrogen productivity of Brussels sprouts, i.e. they have a higher rate of biomass production per unit of nitrogen present in the plant (Table 2). Next these differences in NP between the two species can be analysed according to equation 4. The higher NP of Brussels sprouts was both explained by a higher allocation of nitrogen to leaves (Table 2) and a higher leaf nitrogen productivity (N_lP). Garnier *et al.* (1996) showed that differences between species in NP and N_lP are mainly explained by differences in the rate of photosynthesis per unit leaf nitrogen. Explanations for differences in the photosynthetic nitrogen use efficiency are discussed in Lambers & Poorter (1992) and Pons *et al.* (1994).

Based on the information obtained from our experiments, field- (Booij *et al.*, 1996) and Rhizotron-experiments (Smit *et al.*, 1996), it becomes evident that if we want to reduce the possibility of nitrogen leaching to the environment, information on the physiological and morphological components, determining growth and nitrogen productivity have to be taken into account. Fertiliser application should be adjusted to these characteristics. An example of such an approach is given in Booij *et al.* (1996). The mechanisms determining growth and nitrogen productivity under reduced nitrogen fertilisation input can be incorporated into models and give explanations for differences in N-demand and N-uptake curves, either between species or between treatments.

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