Netherlands Journal of Agricultural Science 44 (1996) 3-19

Effect of nitrogen availability on dry matter production, nitrogen uptake and light interception of Brussels sprouts and leeks

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Received 26 April 1995; accepted 17 September 1995

Abstract

To analyse differences in nitrogen utilisation, field experiments with Brussels sprouts and leeks were carried out. Dry matter production and nitrogen uptake during crop growth were studied at different nitrogen application rates. Nitrogen fertilizer application rate stronger affected dry matter production, leaf area expansion and nitrogen uptake in Brussels sprouts than in leeks. When applying all nitrogen before transplanting, Brussels sprouts showed a higher recovery of nitrogen fertilizer than leeks. This was explained by a higher rate of dry matter production of Brussels sprouts, as a consequence of a faster development of leaf area. A late nitrogen application, whether as a part of a split application or not, increased nitrogen uptake stronger than dry matter production, so that tissue nitrogen concentrations increased.

The relationship between nitrogen uptake and dry matter production depended on nitrogen availability and the crop growth stage, and if all nitrogen was applied before transplanting, the relationship could be described by an asymptotic function. Plasticity of the plants allowed 'luxury consumption' of nitrogen taking place when the availability was ample and 'dilution' of nitrogen when shortage of nitrogen developed during later growth stages. This implies an increasing tissue nitrogen concentration with increasing nitrogen application and a decreasing nitrogen concentration with increasing age. To achieve a near-maximum dry matter production at any time, the nitrogen concentration in the dry matter should be kept on 2.8–3.1% during the whole growing period for Brussels sprouts as well as for leeks. On the other hand a minimum concentration of 1.2–1.5% in the dry matter was found that still allowed growth in Brussels sprouts.

In both crops nitrogen uptake increased linearly with leaf area index until maximum leaf area (LAI=4–5) was reached and this relationship was neither affected by nitrogen application rate nor by the experimental year. Irrespective of nitrogen application rate or species 2.3 g above ground biomass per MJ intercepted radiation was produced. Therefore measurement of radiation interception by the canopy can be used as a tool to estimate the nitrogen status of the crop.

Keywords: nitrogen, fertilization, *Brassica oleracea* L. var *gemmifera*, *Allium porrum* L., radiation use efficiency, nitrogen uptake, leaf area, apparent fertilizer recovery.

Introduction

In most horticultural crops nitrogen fertilizer is applied to obtain optimum marketable yield and quality. For most crops recommendations of nitrogen fertilizer application rates are given. Although the optimum rate can be determined experimentally, a large variation in optima can be observed, due to the strong influence of environmental conditions (Van Keulen & Stol, 1991). In most field grown vegetables the range of optima is relatively broad, because the economic optimum is difficult to establish due to the low costs of fertilizer in relation to the financial yield (Uthe, 1990). Moreover, in many crops there is no clear yield optimum with dose-response curves having a plateau. These two aspects allow the grower to apply high amounts of fertilizer, partly as an insurance, and when applied at recommended rates, crops differ in their use of applied nitrogen fertilizer (Smit & Van der Werf, 1992). A low utilisation of N-fertilizer means that nitrogen is lost to the environment. In the last decade the insight has gained, that the current practise adversely affects the environment due to high losses of nitrogen (leaching, denitrification) to the environment (Greenwood, 1990).

To reduce or prevent these losses it is necessary to know the processes underlying differences in nitrogen utilisation. As most of the nitrogen is applied before the onset of crop growth, the uptake rate from this supply will determine the risk of losses. The uptake rate is determined by the development of the crop nitrogen demand during crop growth.

Especially during the early crop growth phase, most of the nitrogen taken up is recovered in the leaves (Greenwood, 1990). Within the leaf it has two roles in relation to the crop CO_2 fixation. *i*) Most of the nitrogen within the leaves is found in enzymes involved in photosynthesis (Evans, 1989). The maximum photosynthetic rate per unit of leaf area is related to the nitrogen concentration in the leaf (Van Keulen *et al.*, 1989). Lambers *et al.* (1989) showed that relative growth rate was directly related to nitrogen concentration in the plant due to its effect on photosynthesis and respiration. *ii*) The nitrogen concentration of the leaf affects the leaf expansion rate, and thus soil covering and radiation interception by the canopy (Van Keulen et al., 1989).

So there is a high correlation between nitrogen uptake and dry matter production. Nitrogen uptake is also possible without resulting in a higher dry matter production but in luxury consumption (Greenwood *et al.*, 1991, Van Keulen & Stol, 1991). And on the other hand, dry matter increase can occur without nitrogen uptake (dilution of nitrogen) (Justes *et al.*, 1994). If nitrogen supply should be in agreement with the crop demand to prevent nitrogen losses, it is necessary to define the demand. Nitrogen demand can be defined now as the amount of nitrogen, which needs to be taken up to achieve maximum dry matter yield (Greenwood, 1982).

Greenwood *et al.* (1990) proposed a general relationship between the minimum nitrogen concentration, which is required at any time during crop growth to obtain maximum dry matter production at that time, with the equation:

$$\ln(\%N)=5.697-0.5\ln(W)$$

where %N = N concentration in the dry matter; W= crop dry weight.

The aim of the present paper is 1) to quantify the influence of the nitrogen availability in Brussels sprouts and leeks, differing in nitrogen utilisation, on nitrogen uptake and growth, 2) to establish the relationships between nitrogen uptake and dry matter production, leaf area development and radiation interception, 3) to find crop characteristics that can be used to establish the nitrogen demand during growth and are able to explain differences in nitrogen utilisation of the two crops.

Materials and Methods

In 1991 and 1992 field experiments were carried out with Brussels sprouts and leeks. Growth was analysed by assessing at regular intervals the above ground biomass for each fertilizer application rate. In 1991 and 1992 fertilizer rate, applied before transplanting, varied in both crops. Moreover, time of application varied in 1992 in leeks (Table 1). Details of the experiments are given in Table 1.

For each crop a trial was laid out on a sandy soil. The experimental layout was a randomized complete block design with four replicates. Fertilizer treatments and harvest dates were randomized completely. Module raised transplants of Brussels sprouts were transplanted manually at 75 × 40 cm. Bare-rooted transplants of leeks were planted at a depth of 16 cm and at a distance of 40 × 14.5 cm. Plot size was 3 × 4 m. Nitrogen fertilizer was applied as calcium ammonium nitrate. Potassium and phosphate fertiliser were applied in early spring, according to recommended rates based on soil analysis. Husbandry, pest and disease control accorded to common practice.

During crop growth interception of photosynthetic active radiation (PAR) by the canopy was measured weekly in leeks, with a line sensor (TFDL-DLO, Wageningen). In Brussels sprouts the proportion of soil cover by green leaves was estimated weekly using the method described by Haverkort & Harris (1986) with a frame, divided into 100 rectangles and with dimensions that were a multiple of the planting pattern. During the first part of the growing period in 1991, also interception of PAR was measured in Brussels sprouts. As both methods correlated well, for

Table 1. Experimental set-up.

Crop (cultivar)	Transplanting date	Fertilizer treatment (kg N ha^{-1})	Harvest date (DAP[2])
Brussels sprouts (Kundry, Sluis & Groot, Enkhuizen, NL)	28 May 1991	0, 100, 200, 300 (b.t.[1])	43, 77, 104, 132, 160, 188
	19 May 1992	0, 50, 100, 200 (b.t.[1])	24, 56, 84, 111, 139, 174
Leeks (Arcona, Royal Sluis, Enkhuizen, NL)	18 June 1991	0, 125, 250 (b.t.[1])	43, 91, 126, 155
	11 June 1992	0, 250 (b.t.[1]); 125+125, 0+60 respectively b.t.[1] and on 17 September	25, 55, 95, 130, 158

[1] before transplanting.

[2] days after transplanting.

convenience only soil cover was measured in Brussels sprouts and the soil cover was transformed into the fraction intercepted PAR. In plots of Brussels sprouts, which were assigned to the final harvest, a frame with wire-netting was installed 10 cm above the soil, to catch shed leaves. These were collected weekly and dry matter and total nitrogen content were determined.

At each harvest, 8 Brussels sprouts plants were divided into leaves (blades and petioles), stem and buds and 24 leeks plants were divided into leaf shafts and blades. Their fresh weight was determined and a sub-sample was taken for determination of dry matter content and for chemical analysis. Leaf area of the sub-sample was measured with a Li-cor 3100 area meter (Li-cor, Lincoln).

Dry matter content was determined after drying 24 hours at 105 °C. Total N concentration (nitrate + organic N) in the dry matter was determined using the Dumas-method. Nitrate in the plant material was extracted with a 1N KCl solution and determined colorometrically.

Nitrogen uptake was calculated by multiplying total dry matter yield with the nitrogen concentration. At each harvest date given cumulative dry matter and nitrogen uptake included the dry matter and nitrogen taken up observed in the dropped leaves.

Weather data were obtained from a meteorological station situated 1 km from the experimental field.

Results

Dry matter production

Dry matter production of Brussels sprouts increased with time, until a maximum was reached at about 160 days after transplanting (Figure 1 a,b). Dry matter production of leeks increased at a much lower rate than the production of Brussels sprouts. At the final harvest in November yet no clear maximum had been reached for the fertilized leek crop. In Brussels sprouts, the maximum rate of dry matter production increased with increasing nitrogen rate up to 200 kg ha^{-1} from 91 kg ha^{-1} d^{-1} up to 188 kg ha^{-1} d^{-1}. Contrary to the results obtained in Brussels sprouts, dry matter production rate of leeks was hardly affected by the nitrogen application rate during early growth and the maximum growth rate was 90 kg ha^{-1} d^{-1}. Only during the second part of the growing period in 1991 the rate of dry matter production of leeks was significantly reduced, when no fertilizer N was applied (Figure 1c). The total dry matter yield, when nitrogen fertilizer was applied, was much higher in Brussels sprouts than in leeks. Without the application of nitrogen fertilizer the dry matter yield of Brussels sprouts and leeks hardly differed at the final harvest. Maximum dry matter production rate of unfertilized plots was higher in both crops in 1992 than in 1991 (Figure 1).

Nitrogen uptake

In Brussels sprouts nitrogen uptake increased during crop growth until about 130 days after transplanting (Figures 2 a,b). Maximum uptake rate increased from 1.2 kg

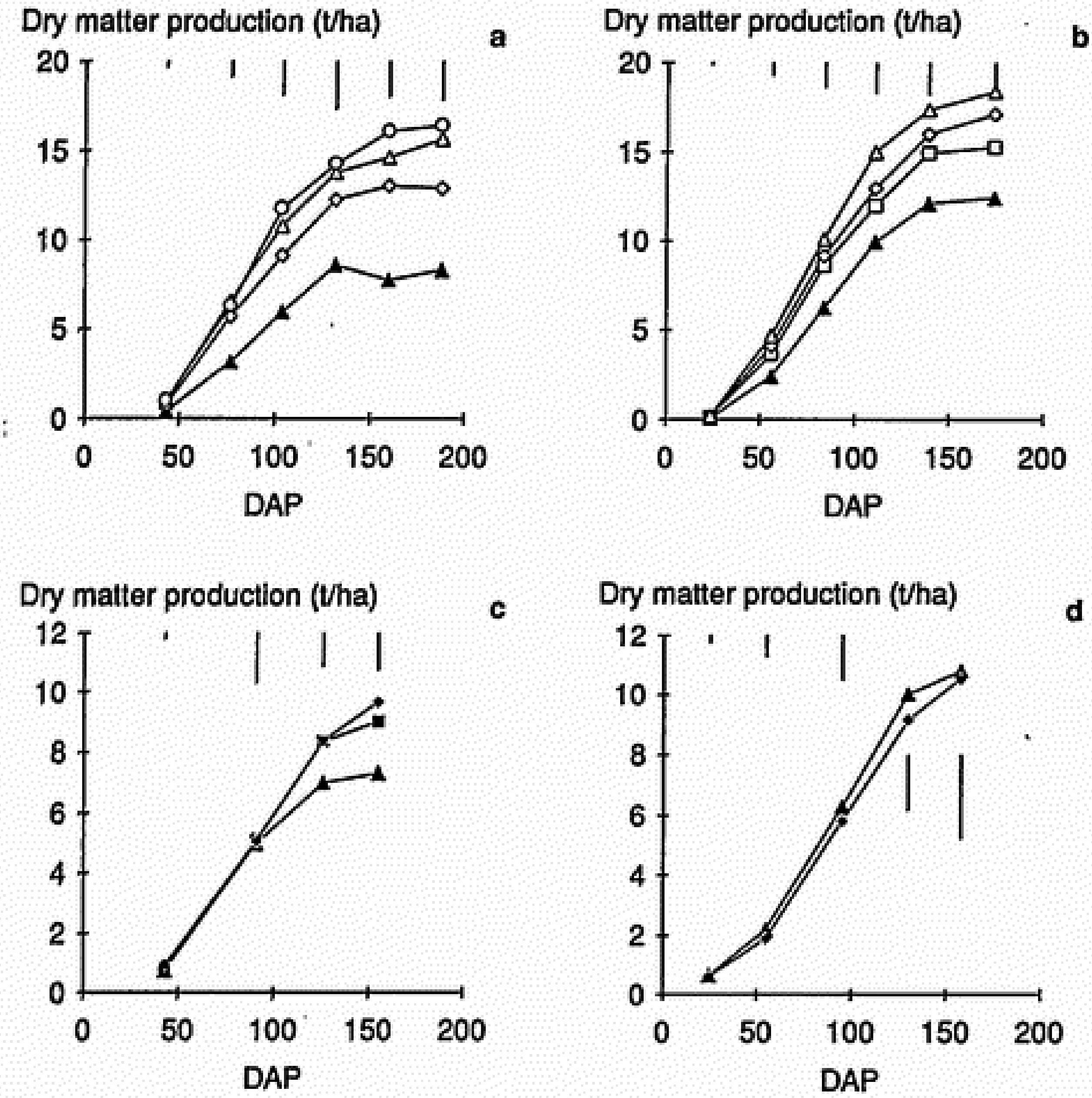

Figure 1. Dry matter production of Brussels sprouts (a,b) and leeks (c,d) in 1991 (a,c) and 1992 (b,d) after 0 (▲), 50 (□), 100(◇), 125 (■), 200 (△), 250 (◆) or 300 (○) kg N /ha had been applied before transplanting. DAP=days after transplanting. Vertical bars indicate LSD (0.05).

ha^{-1} d^{-1} in unfertilized plots up to 6.1 kg ha^{-1} d^{-1} after a nitrogen application rate of 200 kg ha^{-1}. The 'apparent fertilizer recovery'

$$REC= (U_F-U_0)/N_F$$

where U_F is the uptake of N when the amount N_F of fertilizer-N is applied and U_0 is the corresponding uptake when no fertilizer is applied, informs about the utilisation of fertilizer N (Greenwood *et al.*, 1989). At the final harvest of Brussels sprouts the 'apparent fertilizer recovery' at all fertilizer rates was 80% or higher (Table 2).

The maximum nitrogen uptake rate was lower in leeks than in Brussels sprouts and only in the unfertilized leek plots a clear maximum total uptake was reached before the final harvest (Figures 2 c,d). Maximum uptake rate increased from 1.5 kg ha^{-1} d^{-1} in unfertilized plots up to 2.5 kg ha^{-1} d^{-1} at 250 kg ha^{-1}. The lower N-uptake during the last part (Figure 2d) was overcome in 1992 by applying 60 kg ha^{-1} N at 95 days

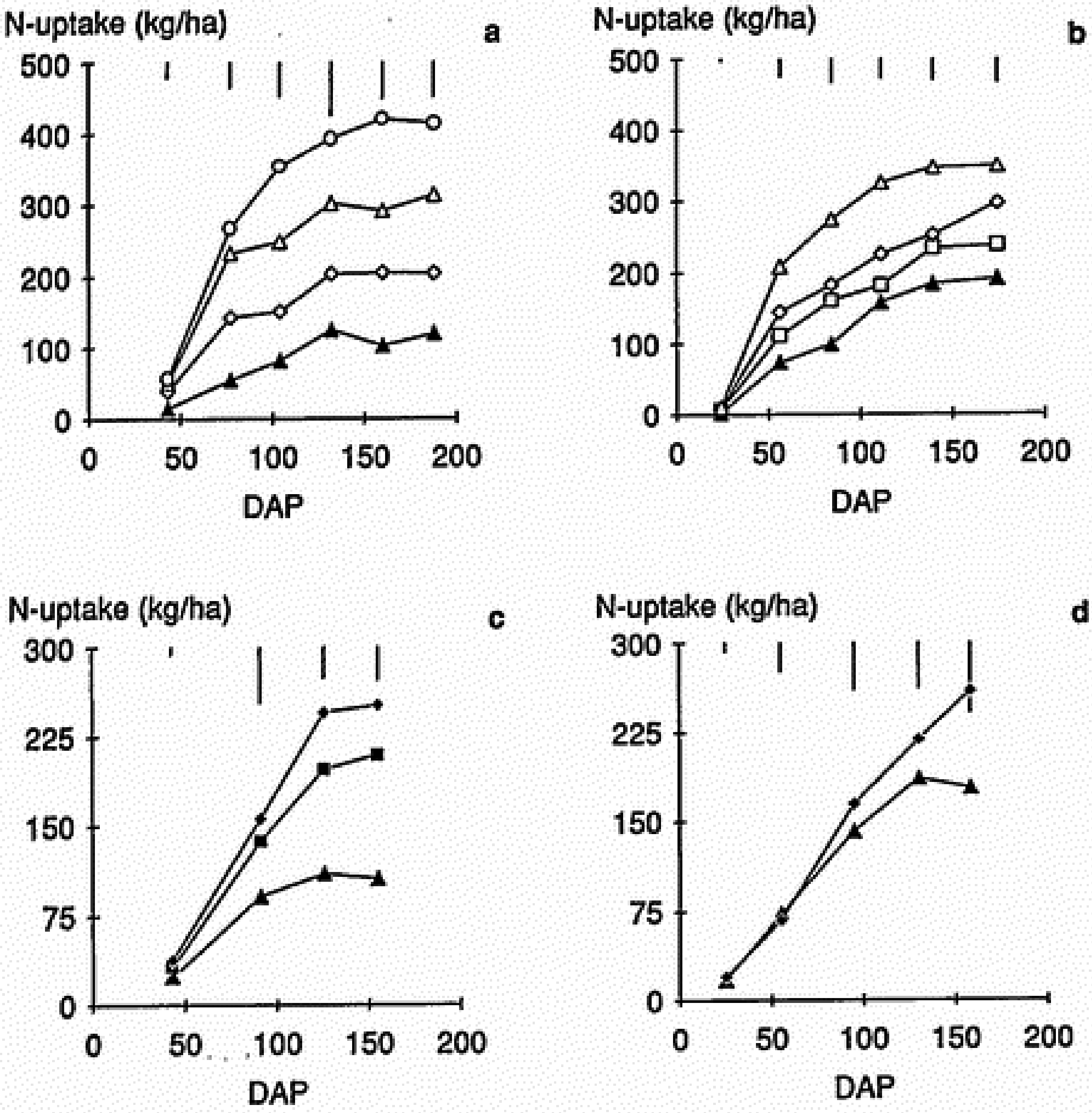

Figure 2. Nitrogen uptake of Brussels sprouts (a,b) and leeks (c,d) in 1991 (a,c) and 1992 (b,d). For symbols see Figure 1. Vertical bars indicate LSD (0.05). DAP=days after transplanting.

after transplanting (Figure 5b). For leeks the 'apparent fertilizer recovery' at a rate of 125 kg ha^{-1} N was close to the range found in Brussels sprouts (Table 2), but was much lower when higher amounts were applied (Table 2). In particular in 1992, when the nitrogen uptake in the unfertilized plot was much higher (Figure 2), due to a higher mineralisation. Splitting the amount of 250 kg ha^{-1} N in two portions only slightly increased the recovery (Table 2). A late application of 60 kg ha^{-1} was almost completely recovered in a crop having received no nitrogen at transplanting (Table 2). The total nitrogen uptake at the final harvest of unfertilized plots with leeks was only slightly lower than for Brussels sprouts (Figure 2). For both crops the total N-uptake in the crop was higher in 1992 than in 1991, due to a higher N mineralisation as is shown by the higher N-uptake in unfertilized plots (Figure 2).

Part of the total amount of nitrogen in the crop is nitrate. During early crop growth in Brussels sprouts up to 25% of the total nitrogen was present as nitrate, against

Table 2. The apparent fertilizer recovery (Greenwood *et al.*, 1989) for the different fertilization treatments (Basic data were obtained from Figures 2 and 5).

Crop	Year	Treatment (kg N ha^{-1})	Apparent fertilizer recovery (%)
Brussels sprouts	1991	100	85
		200	97
		300	98
	1992	50	95
		100	100
		200	79
Leeks	1991	125	83
		250	58
	1992	250	32
		125+125	37
		0+60	99

10% in leeks. The percentage declined during crop growth until 1–5% at the final harvest. Especially in Brussels sprouts most of the nitrate was recovered in the oldest leaves, that dropped first. Consequently at the later harvests hardly any nitrate was found in the Brussels sprouts plant.

Relationship between nitrogen uptake and dry matter production

Dry matter production and nitrogen uptake of the crop are both affected by the nitrogen application rate and the growth stage of the crop (Figures 1 and 2). So a broad range of tissue nitrogen concentrations was observed. In Figure 3 for Brussels sprouts and the leeks the dry matter production is plotted against the corresponding nitrogen uptake for each harvest and nitrogen application rate. The highest tissue nitrogen concentration in the dry matter was 6.6% in Brussels sprouts and 4.0% in leeks and the lowest concentration 1.2–1.5% in both crops. The highest values were found at the highest nitrogen rate at the first harvest and the lowest when no fertilizer was applied and for the lower application rates at the later harvest dates. Data points can now be related in two ways, namely for all harvest dates or for all fertilizer application rates. The first shows the effect of fertilizer rate at a set time (crop growth stage) and the second the effect of crop growth stage at a set fertilizer application rate. At each harvest date dry matter production increased with increasing nitrogen uptake, until dry matter production approached a maximum. At a set fertilizer rate, dry matter production increased with increasing nitrogen uptake until more or less maximum nitrogen uptake was achieved. An asymptotic function (Landsberg, 1977) seemed appropriate to describe the relationship. For each harvest date the best fitting curve could be described by the equation:

$$W = W_m(1-e^{-kN_u}) \qquad (1)$$

where W = dry matter weight, W_m= maximum dry matter weight, N_u = nitrogen up-

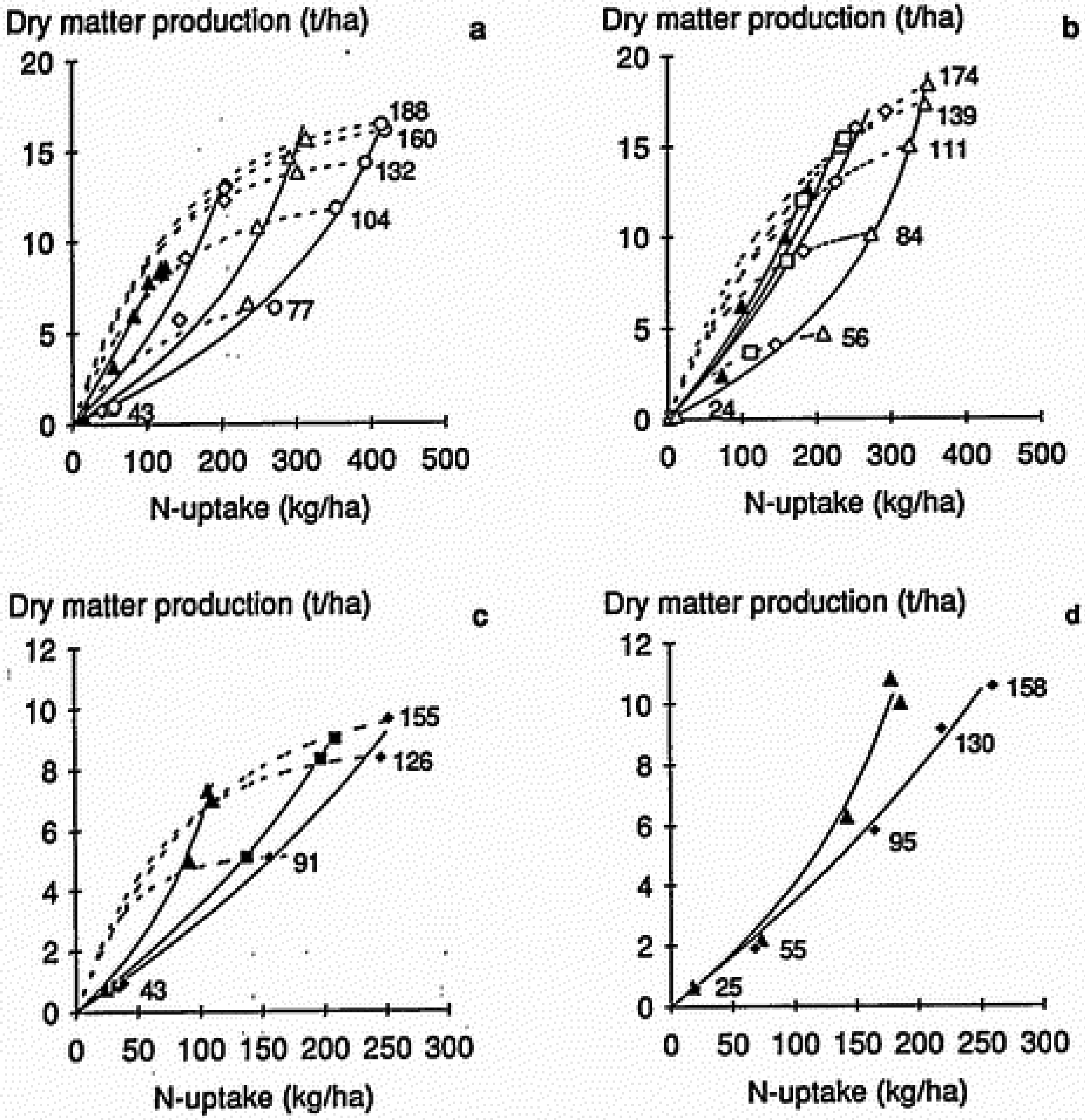

Figure 3. Relationship between nitrogen uptake and dry matter production of Brussels sprouts (a,b) and leeks (c,d) in 1991 (a,c) and 1992 (b,d) at pre-transplanting rates of 0 (▲), 50 (□), 100(◇), 125 (■), 200 (△), 250 (◆) or 300 (○)kg N /ha. For each periodic harvest date (days after transplanting) the line was fitted according to equation 1 (------) and at each fertilizer application rate according to equation 2 (——). Data values are the number of days after transplanting of periodic harvests.

take and k = constant. For each fertilizer level the best fitting curve was found by fitting the inverse relationship

$$W = -\ln(1 - N_u/N_m)/m \qquad (2)$$

where N_m = maximum N uptake, m = constant) (Figure 3). From the relationship between nitrogen uptake and dry matter production at each harvest date (equation 1), the amount of nitrogen needed to be taken up to achieve near maximum dry matter yield, can be calculated. We have defined near maximum yield as 95% of the asymptotic value (W_m) of the function. The fitted curves for the relationship are also given in Figure 4 and extended beyond the data values. On each curve the combination of near maximum dry matter production ($0.95W_m$) and the corresponding N-uptake is plotted (Figure 4). These points indicate the nitrogen uptake needed at each harvest date resulting in near maximum dry matter production at that time. Although in most cases the points could be obtained by extrapolation only, and are therefore subjected to substantial variation, there was a significant ($P<0.001$) linear relationship between the N-uptake at near maximum dry matter yield and the corresponding dry matter yield, with correlation coefficients higher than 0.75 in all experiments (Figure 4). The slope of the regression line represents the inverse of the nitrogen concentration needed to obtain maximum yield at any time during crop growth. The required nitrogen concentration appeared to be for both crops 2.9–3.1%. For comparison the relationship of Greenwood *et al.* (1990) between N-uptake and dry matter production is given, after being transformed into

$$\ln(N_u)=1.09 + 0.5 \ln(W) \quad (3)$$

where N_u=N-uptake and W= crop dry weight.
This curve (equation 3) is plotted in Figure 4 and it shows that our data points were for Brussels sprouts not according to this relationship, but the agreement was better for leeks, in particular at a lower dry matter production.

Also the line representing a nitrogen concentration of 1.2% in the dry matter is drawn in Figure 4 and it is shown that in both crops this can be regarded as the minimum nitrogen concentration which still allows growth, as all curves deliver nitrogen concentrations higher than this value (Figure 4).

The curves in Figure 3 describing the relationship between nitrogen uptake and dry matter production at a set fertilizer application rate show the change of tissue nitrogen concentration during crop growth. If nitrogen was applied before transplanting, the nitrogen concentration decreased with crop growth (Fig. 3). The question was, whether this dilution of nitrogen was due to increasing dry matter production (Greenwood *et al.*, 1990) or to nitrogen depletion later during crop growth. Therefore, in leeks nitrogen was also applied later (95 DAP). Dry matter production was not affected by the late application, but only nitrogen uptake. It also shows that curvation, indicating dilution of nitrogen within the plant during growth, was due to a shortage of available nitrogen during the last part of the growing period, as a late application resulted in a deviation from the curve (Figure 5).

Leaf area and radiation interception

Nitrogen application rate had a pronounced effect on development of leaf area (LAI) of Brussels sprouts (Figure 6a,b). Maximum LAI increased from 2.3 in the unfertilized plots up to 5.3 at the highest fertilizer application rate. Leaf area increased until a maximum was reached at about 80 days after transplanting, followed by a strong decrease and the differences in LAI became much smaller towards the final harvest. A higher N application rate enhanced both the rate of increase and the later rate of decrease (Figure 6 a,b). Maximum leaf area was reached later in the unfertilized plots than in the fertilized ones. The higher maximum leaf area was due to a higher area per leaf as the number of green leaves at maximum leaf area was not affected by

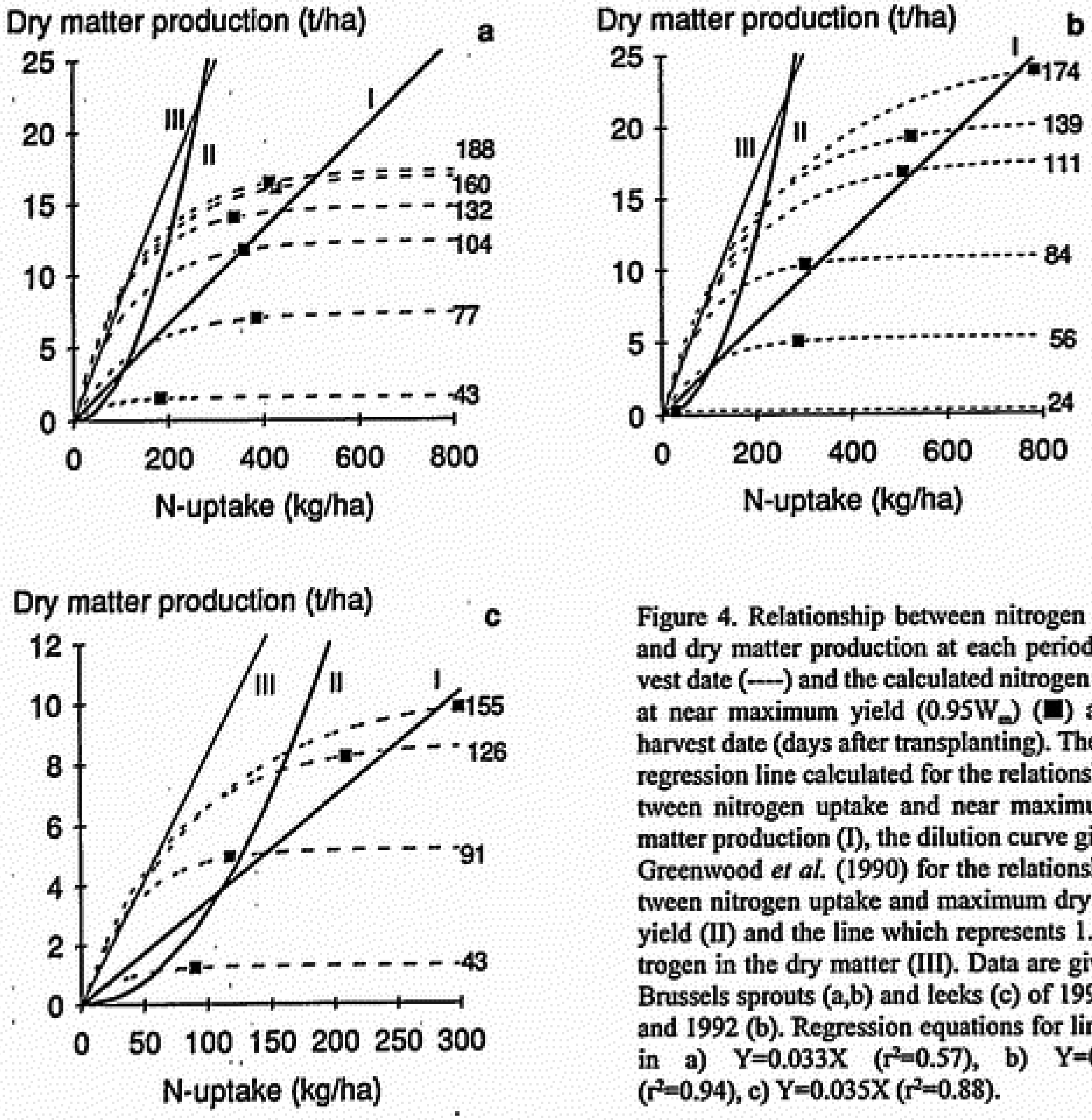

Figure 4. Relationship between nitrogen uptake and dry matter production at each periodic harvest date (----) and the calculated nitrogen uptake at near maximum yield ($0.95W_m$) (■) at each harvest date (days after transplanting). The linear regression line calculated for the relationship between nitrogen uptake and near maximum dry matter production (I), the dilution curve given by Greenwood *et al.* (1990) for the relationship between nitrogen uptake and maximum dry matter yield (II) and the line which represents 1.2% nitrogen in the dry matter (III). Data are given for Brussels sprouts (a,b) and leeks (c) of 1991 (a,c) and 1992 (b). Regression equations for line I are in a) $Y=0.033X$ ($r^2=0.57$), b) $Y=0.032X$ ($r^2=0.94$), c) $Y=0.035X$ ($r^2=0.88$).

the fertilizer application rate. Also in leeks leaf area increased, until a maximum was reached, but this maximum was lower and took 6–7 weeks longer to reach than in Brussels sprouts (Figure 6 c,d). Only in the unfertilized plots of the 1991 experiment, LAI was significantly lower in the unfertilized plots from 91 days after transplanting. There was no difference in leaf area of leeks, when 125 or 250 kg ha^{-1} was applied. For both crops maximum leaf area in unfertilized plots was higher in 1992 than in 1991 (Figure 6).

The development of leaf area affects the interception of incoming radiation by the canopy. The fraction of incoming photosynthetically active radiation, intercepted by the canopy $\left(1-\frac{I_L}{I_O}\right)$, increased exponentially with increasing LAI in both crops (Figure 7) according to Beer's Law:

$$\frac{I_L}{I_O} = e^{-kL}$$

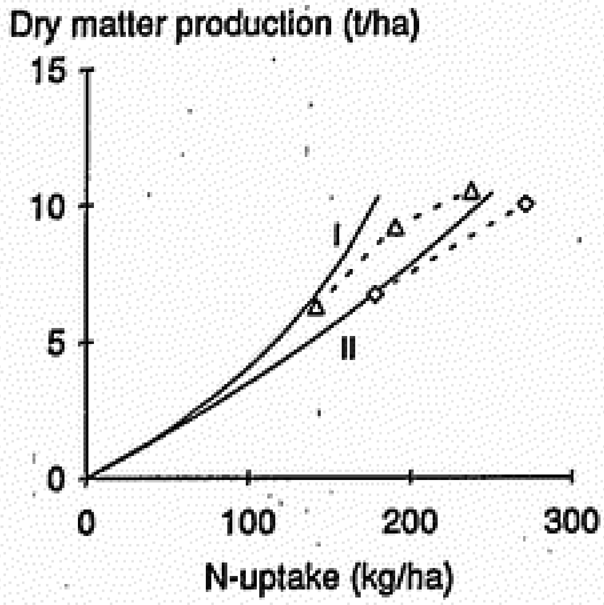

Figure 5. The relationship between nitrogen uptake and dry matter production of leeks, when 60 kg/ha N was applied at 95 DAP (△) or 125 kg/ha N before transplanting and 125 kg/ha N at 95 DAP(◇). The fitted lines (——) for the unfertilized plot (I) or when 250 kg/ha N was applied before transplanting (II), from Figure 3d are also given.

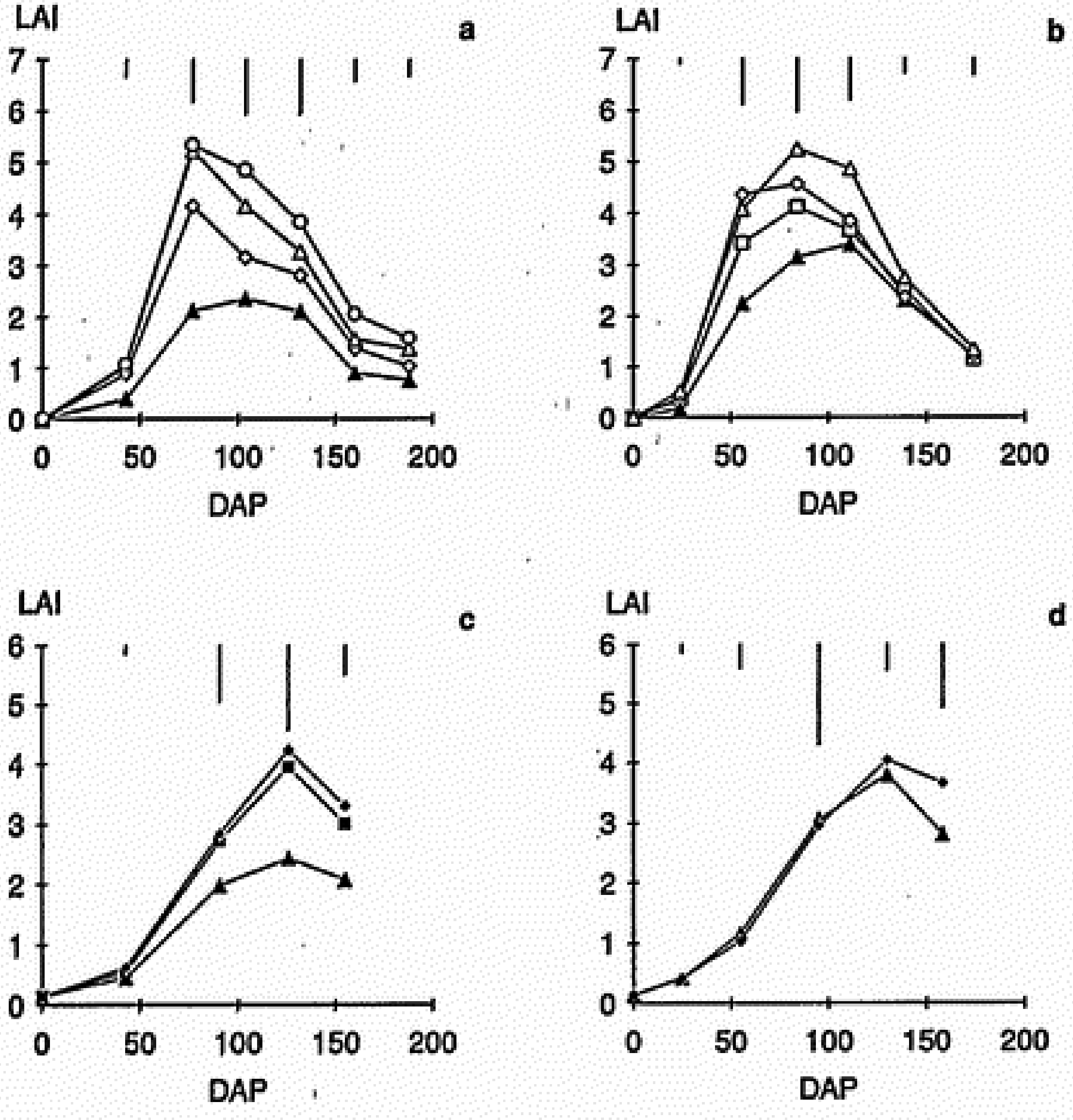

Figure 6. Development of the leaf area index (LAI) at different times after transplanting (DAP) of Brussels sprouts (a,b) and leeks (c,d) in 1991 (a,c) and 1992 (b,d). For symbols see Figure 1. Vertical bars indicate LSD (0.05).

where I_L = radiation below the canopy with a leaf area index L, I_o = radiation at the top of the canopy and k = extinction coefficient. No significant effects of nitrogen supply were found and the curves were the same in both years. The estimated value for the light extinction coefficient was lower for Brussels sprouts (Figure 7a) than for leeks (Figure 7b). More than 90% of the incoming photosynthetically active radiation was intercepted at a LAI of 3.8 for Brussels sprouts and 4.3 for leeks.

Relationship between N-uptake and LAI

According to Greenwood (1990) a large proportion of nitrogen is recovered in the crop canopy, especially during the first part of the growing period. Therefore the LAI at different times was plotted against the nitrogen uptake by the crop, until the maximum LAI was reached. A significant ($P<0.001$) linear relationship appeared for each crop, which was independent of the experimental year and the nitrogen application rate (Figure 8). The slope of the relationship was significantly higher for Brussels sprouts than for leeks. It means that for the formation of 1 unit of leaf area a N-uptake of 4.21 g m^{-2} N was required for Brussels sprouts and 5.14 g m^{-2} for leeks.

Relationship between radiation interception and dry matter production

Rate of leaf area development during crop growth determines the radiation interception by the canopy. The development of leaf area was affected by nitrogen supply and was different for each crop (Figure 6). Consequently, the cumulative interception of photosynthetically active radiation by the canopy during crop growth was different. Total intercepted radiation at the end of the growing period was twice as high in Brussels sprouts than in leeks (Figure 9). For each crop, in both ex-

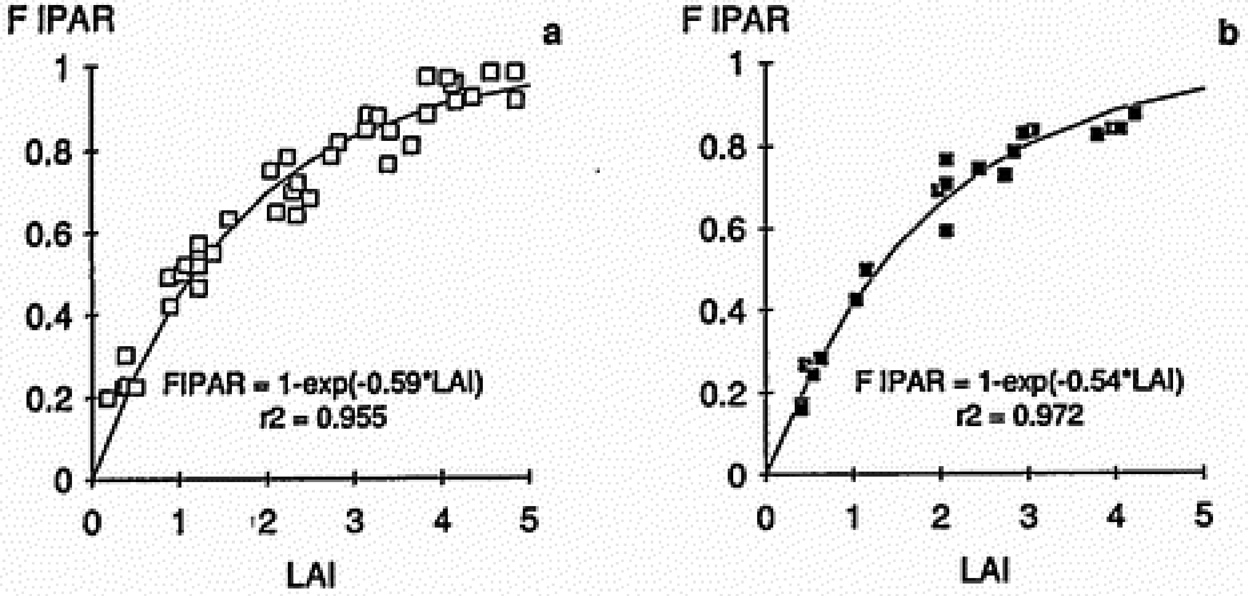

Figure 7. The relationship between leaf area index (LAI) and the fraction of incoming photosyntheticly active radiation (FIPAR) intercepted by the crop canopy of Brussels sprouts (a) and leeks (b). The same observations as presented in Figure 6 are included and the equation of the best fitting line is given.

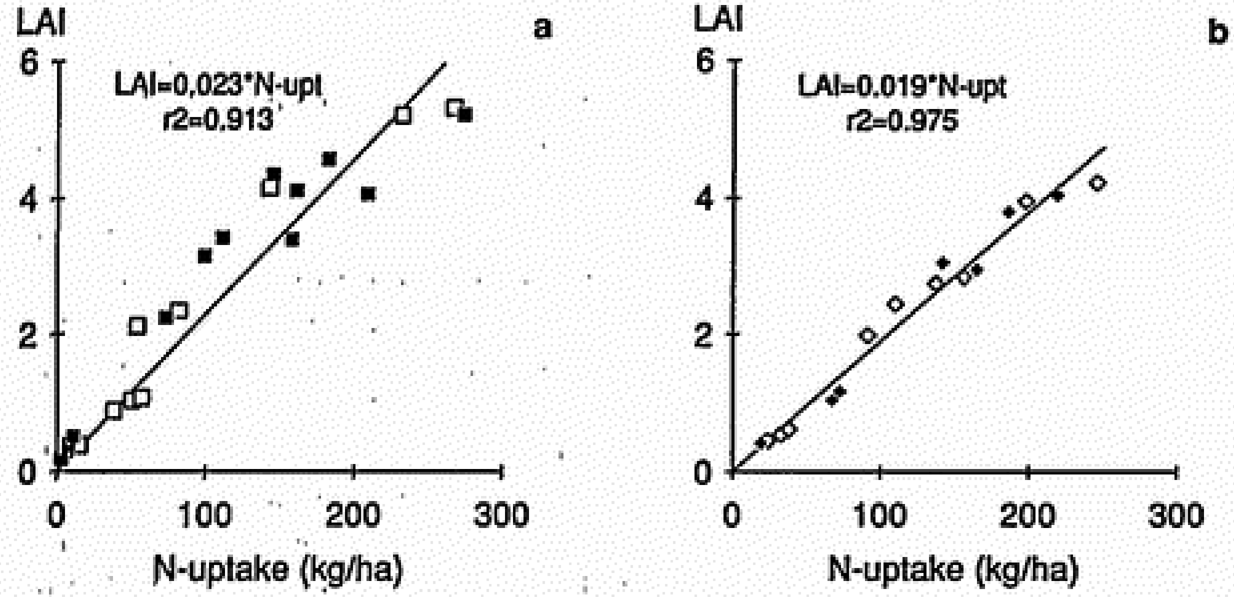

Figure 8. Relationship between nitrogen uptake and leaf area index (LAI) for Brussels sprouts (a) and leeks (b) in 1991 (□) and 1992 (■). Only data points, referring to harvest dates, up to maximum LAI were included of all fertilizer rates (applied before transplanting). The best fitting linear regression line is drawn and the equation of this relationship is given.

perimental years and all N-rates, the total dry matter production increased linearly with the total intercepted radiation during crop growth (Figure 9). There were no significant (P<0.001) effects of experimental year, crop or N application rate on the slope of the relationship. So, for all treatments one linear regression was calculated. The slope of the line, representing the radiation use efficiency (RUE), was 2.3 g/MJ.

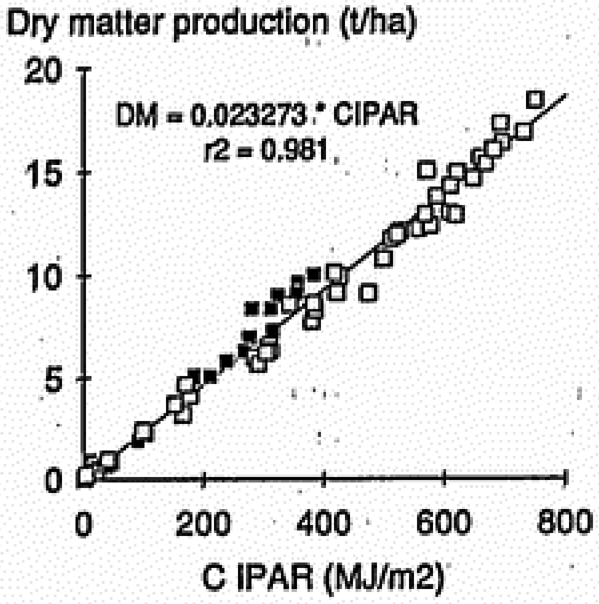

Figure 9. Relationship between cumulative interception of photosynthetically active radiation (CIPAR) and dry matter production of Brussels sprouts (□) and leeks (■). Data points for all fertilizer levels, applied before transplanting, of the 1991 and 1992 experiment were included. The best fitting linear regression line is drawn and the equation is given.

Discussion

Brussels sprouts and leeks differed mainly in the effect of nitrogen application rate on dry matter production and nitrogen uptake (Figures 1 and 2). In Brussels sprouts application of nitrogen fertilizer had a strong positive effect on dry matter production, while in leeks nitrogen fertilization hardly stimulated dry matter production. For leeks the amount of nitrogen obtained from mineralisation of organic matter in the soil was almost (1991) or fully (1992) sufficient to achieve maximum dry matter production. The relative growth rate of Brussels sprouts is twice as high as in leeks, due to a twofold higher leaf area ratio (Booij *et al.*, 1993). This means that the daily nitrogen demand in Brussels sprouts develops much faster than in leeks and that also the nitrogen requirement to support dry matter production is higher. This causes a much faster depletion of the nitrogen from the soil by Brussels sprouts and therefore a stronger reaction on nitrogen supply. When all nitrogen is applied at transplanting and the crop uptake rate is low (leeks), the nitrate pool in the soil is maintained for a long period. This enhances the risk of losses during the growing period in slow growing crops and results in low 'apparent fertilizer recoveries' (Table 2).

The relationship between dry matter production and nitrogen uptake is determined by the nitrogen fertilizer application rate and the crop growth stage. At a high nitrogen fertilizer rate at the start of crop growth, nitrogen uptake increased relatively stronger than did dry matter production, while towards the end of crop growth dry matter production increased relatively stronger than nitrogen uptake (Figure 3). At the lowest nitrogen fertilizer rate there was hardly an effect of growth stage so that dry matter production and nitrogen uptake increased relatively at the same rate during crop growth (Figure 3). Similar relationships were shown by Simán (1974) for wheat. During early crop growth the nitrate reserves in the soil are high due to the application of nitrogen fertilizer before transplanting and the crop can take up nitrogen in excess ('luxury consumption', Justes *et al.* (1994)). This 'luxury consumption' is not restricted to early growth, it also occurred when nitrogen was applied during the latest part of the growing period, when the nitrate pool in the soil was depleted and growth was restricted due low irradiation (Figure 5). The nitrogen pool within the plant consists of nitrate and organic nitrogen and allows the plant to continue growth for some time, when nitrogen is withheld after ample nitrogen supply (Burns, 1994), depending on the size of the pool. However, this results in a lower growth rate (Burns, 1994). During this phase the nitrogen concentration decreases, the nitrogen 'dilutes' (Justes *et al.*, 1994). Greenwood & Barnes (1978) stated that the lower nitrogen concentration in the plant with increasing crop weight is due to a change in plant composition (more cell wall and less cytoplasm). Our results show that after a late nitrogen application the nitrogen dilution could partly be prevented (Figure 5). We showed, and so did Simán (1974), that the decreasing tissue nitrogen concentration is also due to a decreasing nitrogen availability during crop growth. The 'luxury consumption' on one hand and the 'dilution' of nitrogen on the other hand justify the use of curves for the relationship between dry matter production and nitrogen uptake with an asymptote. During the period of 'luxury consumption' radiation interception is limiting, while during dilution nitrogen availability is limiting the rate of dry matter production. Lemaire *et al.* (1985) and Justes *et al.* (1994) used an allometric function to describe the relationship between N-uptake and dry matter production during crop growth. This function does not approach a maximum value, but their range of dry matter production was much smaller (up to 6 tons ha^{-1}) than ours and the phase of complete nitrogen depletion probably was not reached in their experiments.

The interaction between growth stage and nitrogen availability on the relationship between nitrogen uptake and dry matter production makes it difficult to define the demand of the crop (Figure 3). A dry matter production in Brussels sprouts of 9 t ha^{-1} can be reached without nitrogen fertilizer as well as with a fertilizer application rate of 300 kg N ha^{-1} (Figure 3a). In the first situation approximately 120 kg N ha^{-1} was taken up and in the second situation 350 kg N ha^{-1}. However, in the last situation the 9 t ha^{-1} was reached much earlier. The daily nitrogen demand should be defined as the required nitrogen to be taken up to support a set growth rate. Or, how much N needs to be taken up to obtain a set dry matter yield at a set time. Despite the necessary extrapolation to determine near maximum dry matter yield at a set time, there was a fairly good linear relationship between near maximum dry matter yield and the nitrogen uptake required to achieve this yield during crop growth (Figure 4). Our results for Brussels sprouts and leeks suggest that to obtain near maximum dry matter yield at any time during crop growth, a minimum tissue nitrogen concentration of 2.8–3.1% should be maintained. Accepting a lower nitrogen percentage may result in a similar dry matter yield, but to be reached later in the season (Figure 4). Greenwood *et al.* (1990) proposed a universal relation between nitrogen percentage and maximum dry matter yield. Our near maximum dry matter yield for Brussels sprouts deviated far from this relation, but for leeks there was a better agreement. Also Justes *et al.* (1994) studied the relationship for different crops and found a universal relationship to be unlikely. Our results showed a constant nitrogen percentage during crop growth to obtain near maximum dry matter yield (Figure 4), while Greenwood *et al.* (1990) and Justes *et al.* (1994) assumed a decreasing nitrogen percentage needed to obtain maximum dry matter yield with increasing crop weight. Most of the data presented by these authors are restricted to dry matter yields lower than 8 t ha^{-1}. The strongest nitrogen dilution occurred in the range 1.5–4 t ha^{-1}. Especially within this range we had hardly data (Figure 3), so we are not able to establish accurately the relationship between N-uptake and dry matter production at lower dry matter yields. To establish the relationship between minimum nitrogen uptake needed to support maximum dry matter production, it is essential to obtain maximum dry matter production. Especially at higher dry matter yields Greenwood *et al.* (1990) and Justes *et al.* (1994) did not reach maximum dry matter yield (See Figure 3 in Justes *et al.* (1994)). In such cases nitrogen dilution is due to shortage of available nitrogen (Figure 5). In conclusion, the linear relationship is likely to holds for higher dry matter yields, while the non-linear relationship holds for lower dry matter yields (< 4 t ha^{-1}).

A large part of the nitrogen is recovered in the leaves (Greenwood, 1990) and most of the nitrogen within the leaves is in enzymes involved in photosynthesis (Evans, 1989; Sinclair & Horie, 1989). So a close relationship between nitrogen uptake and

LAI is not surprising (Figure 8) and in agreement with the results found in wheat by Van Keulen & Stol (1991). Because nitrogen application and the experimental year hardly affected the relationship (Figure 8), the LAI can be used as an estimate for N-uptake during the early growth phase. It can be used only for the period until maximum LAI is reached, because henceforward LAI decreases due to leaf shedding, while total N taken up by the crop remains constant or slightly increases (if N recovered in shed leaves is included). As LAI closely correlated with radiation interception (Figure 7) and as this relation was neither affected by N-application nor by the experimental year, nitrogen uptake can be estimated by measuring radiation interception until all incoming radiation is intercepted by the canopy.

For all crops there is a linear relationship between cumulative radiation interception and cumulative dry matter production (Monteith, 1977) and the slope of the line represents the radiation use efficiency (RUE). The RUE depends on the composition of the dry matter and on growth factors (Gosse *et al.*, 1986; Kiniry *et al.*, 1989). As Brussels sprouts and leeks consist mainly of leaves or leaflike structures having a similar composition of the dry matter, the RUE is likely to be the same, as we found. RUE depends also on the nitrogen supply (Hammer & Wright; 1994, Sinclair & Horie, 1989). RUE increases with an increase of nitrogen content per unit leaf area (g N per m^2 of leaves), until a maximum RUE is reached at a nitrogen content per unit leaf area of $1.2 - 2$ g m^{-2} (Sinclair & Horie, 1989). In our experiments the nitrogen application rate did not affect the RUE (Figure 9), because the nitrogen content per unit leaf area was always higher than 2 (g N m^{-2}) of both crops in the unfertilized plots during the whole growing period (data not shown).

Acknowledgements

We want to thank dr A.P. Everaarts (PAGV) and dr A.J. Haverkort (AB-DLO) for their comments on the manuscript.

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