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Effects of nitrogen on development and growth of the leaves of vegetables. 2. Appearance, expansion growth and life span of leaves of leek plants

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Abstract

Leaf growth and development of leek (*Allium porrum* L.) were examined in three experiments, with different amounts and dates of application of nitrogen as treatments. Rates of leaf appearance, leaf expansion, leaf size and leaf senescence were measured.

The rate of leaf appearance was not affected by N treatments and almost constant across experiments at 0.15 d^{-1}. The rate of leaf expansion and the mature leaf area increased with leaf number, reached a maximum between leaf numbers 11 and 14 and decreased with higher leaf numbers. Both variables increased with more nitrogen. The duration of leaf expansion was more or less constant across leaf numbers and not influenced by nitrogen treatments; the leaf expansion rate was the main factor determining mature leaf area. The rate of leaf senescence was not influenced by N treatments. Differences in total green leaf area per plant were caused by differences in (mature) leaf area of individual leaves and not by the differences in the number of leaves. The specific leaf area of all leaves was more or less constant at 100 $cm^2\ g^{-1}$.

Keywords: Leek, *Allium porrum* L., leaf development, leaf expansion, leaf senescence, nitrogen nutrition

Introduction

Leek is a biennial plant with a vegetative phase in the first year and a reproductive phase in the second year. Leaves are produced in the vegetative phase. The flower stalk usually grows during the second year, although sometimes already during the first year (Dragland, 1972). Development of the flower stalk indicates the end of leaf initiation.

Total leaf area per unit soil area is important for crop production, because it determines how much radiation is intercepted by the crop. For leek, also the number of leaves is relevant, because this number (and the thickness of the leaves) determines the diameter of the shaft, which is a quality characteristic. Leaf area at any time of crop development is determined by several processes and variables, such as the rates

of leaf appearance and leaf expansion, the area of mature leaves and the rate of leaf senescence, all of which are influenced by the availability of nutrients, especially nitrogen. Some data on development and growth of leaves of leek have been reported, but information on effects of nitrogen is scarce. Hay & Brown (1988) analysed development and expansion of leek leaves and concluded that leaf appearance was dependent on temperature. Hay & Kemp (1992) developed a simple model of leaf canopy expansion in leek, based on primordial development. This paper reports on one glasshouse and two field experiments with leek, designed to quantify the effects of nitrogen supply on rate and duration of leaf appearance, expansion and senescence.

Materials and methods

Plant culture – glasshouse

Young, pencil-thick leek plants (cv. Albana), with five leaves, were planted on 1 May 1991 in 20–l pots (four plants per pot), containing sand, free from organic matter. The pots were placed in a glasshouse, set to maintain a day (12 h) temperature of 18 °C and a night temperature of 12 °C. Natural light was supplemented with 400 Watt Philips SON-AGRO-T lamps at a density of 0.7 lamps m^{-2}. The density of the pots was 5.0 m^{-2} during the whole experiment, i.e. 20 plants m^{-2}. Water was administered from the top of the pot until the plants were well established. Subsequently, a 5-cm-high saucer under the pots was filled daily with water to its brim. The pots were covered with polyethylene granules to reduce evaporation and thus the accumulation of salts in the top layer of the soil. Once every three weeks the plants were allowed to absorb all the water from the saucers. Then water was administered from the top once. Subsequently the standard procedure of supplying water via the saucer was resumed (Datema *et al.*, 1986).

Plant culture – field

The two field experiments were conducted on a sandy soil with about 3% organic matter. Plants comparable to those of Experiment 1 were planted at about 10 cm depth in rows, at a row-spacing of 25 cm and a plant distance within the row of 20 cm, i.e. a plant density of 20 plants m^{-2}. Experiment 2 was planted on 12 May 1992 and Experiment 3 on 7 May 1993. Irrigation was applied immediately after planting and later on whenever necessary.

Treatments

Treatments consisted of different amounts and different timing of nitrogen application. Other nutrients were supplied in equal amounts to all treatments. Experiment 1 had four different treatments: N(1.8/2): 1.8 g N per pot, supplied in two equal splits; N(1.8/6): 1.8 g N per pot, in six equal splits; N(5.4/2): 5.4 g N per pot, in two equal

Table 1. Amounts and dates of application of nitrogen in the different treatments of Experiment 1. (DAP = days after planting.)

	Amount of nitrogen (g per pot)			
Time (DAP)	N(1.8/2)	N(1.8/6)	N(5.4/2)	N(5.4/6)
0	0.9	0.3	2.7	0.9
13	–	0.3	–	0.9
27	–	0.3	–	0.9
37	0.9	–	2.7	–
41	–	0.3	–	0.9
55	–	0.3	–	0.9
69	–	0.3	–	0.9
Total	1.8	1.8	5.4	5.4

splits; N(5.4/6): 5.4 g N per pot, in six equal splits (Table 1). The experiment was laid out in a randomized complete block design with five blocks. In the statistical analyses the four treatments were split into two factors: 1. amount of nitrogen and 2. number of applications.

The two field experiments had the same three treatments: N(0): no application of fertilizer nitrogen; N(200/1): 200 kg N per ha, applied shortly after planting; N(200/5): 200 kg N per ha, applied in five equal splits (Table 2). These two experiments were laid out in a split-plot design with nitrogen treatment as main factor and harvest date (see *Destructive sampling*) as split factor. Both experiments had four blocks. In the statistical analyses of each experiment, each harvest was analysed separately.

Determination of leaf characteristics

In Experiment 1 the dynamics of leaf area of individual leaves were derived from frequent measurements of leaf length. From the moment that a new expanding leaf could be distinguished at the apex, i.e. when it was visible in the sheath of the older leaves,

Table 2. Amounts and dates of application of fertilizer nitrogen in two field experiments with leek (Experiments 2 and 3).

		Amount of nitrogen (kg ha^{-1})		
Time (DAP)				
Expt 2	Expt 3	N(0)	N(200/1)	N(200/5)
16	3	0	200	40
37	49	0	0	40
58	60	0	0	40
79	82	0	0	40
94	98	0	0	40
Total		0	200	200

the length of the leaf was recorded, usually at intervals of 2–3 days, until further extension was negligible. The data were collected throughout the growth period on 20 plants per treatment (two plants of two pots per block). A leaf was considered 'appeared' on the date of its first record of leaf length. In Experiment 1 the number of dead leaves was recorded each time leaf lengths were measured. The day of leaf senescence was defined as the day on which more than 90% of the leaf area was yellow.

In Experiment 1 destructive sampling was applied (see *Destructive sampling*) at regular intervals to obtain paired data on leaf length and leaf area (determined with a Li-Cor model 3100 electronic area meter; Li-Cor, Lincoln, Nebraska). These data were fitted to a quadratic regression yielding: leaf area (in cm^2) = $2.579*10^{-4}$ (s.e. $2.237*10^{-6}$) * (leaf length (in mm))^2 ($r^2 = 0.84$; n = 1017). Treatments had no significant effects (LSD-test, $P=0.05$) on this relation. The regression equation was used to calculate leaf areas from routinely measured leaf lengths.

Figure 1 presents typical examples of the time course of leaf expansion. The shape of the curves appears more or less sigmoidal, as normal for leaf growth curves (Dennett et al., 1978). However, the largest part of the leaf area is formed during a phase with practically linear increasing area. Therefore, for each leaf, linear regressions were fitted to the data of leaf area in the linear phase and the expansion rate was characterized by the slope of that regression (= tan α in Figure 1). A variable 'effective duration of expansion' (d; length of line 'a' in Figure 1) can be defined as the maximum area of a leaf (cm^2; length of line 'b' in Figure 1) divided by its expansion rate ($cm^2\ d^{-1}$) (cf. Vos & Biemond, 1992).

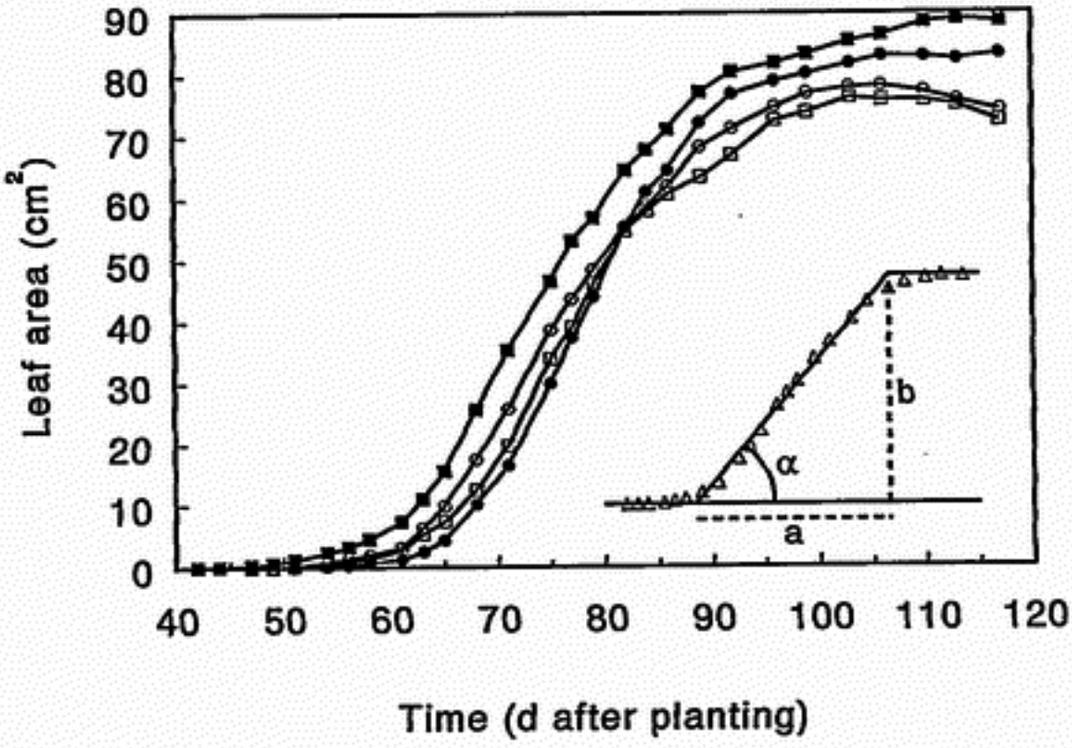

Figure 1. The change over time of the leaf area of leaf 12, Experiment 1. (□) N(1.8/2); (○) N(1.8/6); (■) N(5.4/2); (●) N(5.4/6). The insert at the lower right explains the method of calculation of the rate and duration of leaf expansion. The length of line 'a' represents the duration of leaf expansion (d), the length of line 'b' the mature leaf area (cm^2) and tan α the rate of leaf expansion ($cm^2\ d^{-1}$).

No leaf lengths were measured in the field experiments. Information on leaf growth, however, was derived from data collected during intermediate harvests (see *Destructive sampling*) on leaf appearance, leaf senescence and increase in leaf area with time.

Destructive sampling

Destructive sampling of plants were made several times: in Experiment 1 on six occasions between 26 and 117 DAP (days after planting), in Experiment 2 on six occasions between 35 and 134 DAP and in Experiment 3 on five occasions between 38 and 122 DAP. In Experiment 1 at each sampling date one pot (= four plants) per treatment was used from each block. In Experiments 2 and 3 at each sampling date 1.0 m^2 per treatment was harvested from each block.

Measurements included leaf area, and fresh and dry weights of leaf blades, leaf sheaths and apex. In Experiment 1 each leaf blade and each leaf sheath were sampled separately, while in Experiments 2 and 3 two leaf blades or two leaf sheaths were combined.

Results

Rate of leaf appearance and senescence and number of leaves

Figure 2 shows the dynamics of mean total number of leaves and mean number of

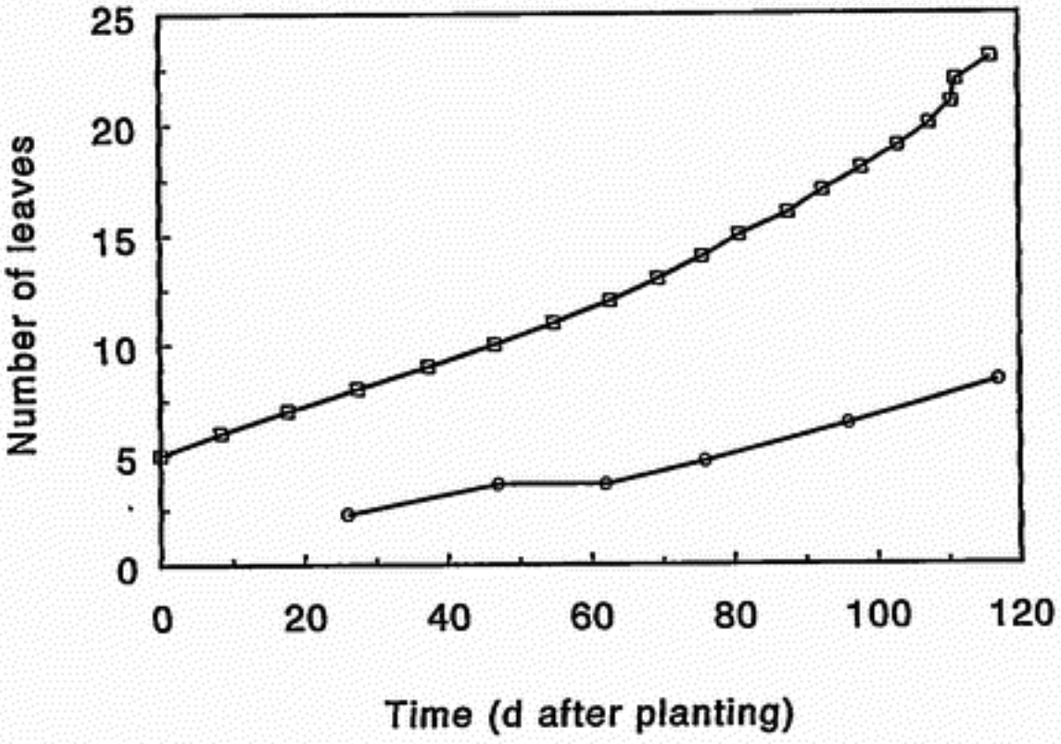

Figure 2. The mean total number of leaves (□) and mean number of dead leaves (○) as a function of time and averaged over nitrogen treatments for Experiment 1.

dead leaves in Experiment 1. They represent averages over all treatments, because treatment effects were generally insignificant (LSD-test, P=0.05). The rate of leaf appearance, which was more or less constant during the first half of the growing period, slowly increased in the second half. The mean rate of leaf appearance over the first 60 days was 0.11 d^{-1}, equivalent to 0.74 leaves per 100 degree days (base temperature 0°C). In Experiments 2 and 3 the rate of leaf appearance was almost constant until 100 DAP and slowly decreased subsequently. The rates of leaf appearance, derived from linear regressions over the whole growing season (Table 3), were not affected by treatment and ranged between 0.14 d^{-1} and 0.16 d^{-1} across experiments.

At planting, usually one or two leaves per plant were dead. In all experiments the increase in the number of dead leaves was nearly linear (Figure 2: Experiment 1). At 62 DAP N(1.8/2) had significantly more dead leaves than N(1.8/6) and N(5.4/2)

Table 3. Leaf appearance rate over the whole growing season; total number of leaves, number of dead leaves and number of green leaves per plant in Experiment 1 at 117 DAP, in Experiment 2 at 134 DAP and in Experiment 3 at 122 DAP.

Leaf appearance rate (d^{-1})					
Experiment 1		Experiment 2		Experiment 3	
N(1.8/2)	0.15	N(0)	0.14	N(0)	0.16
N(1.8/6)	0.16	N(200/1)	0.15	N(200/1)	0.16
N(5.4/2)	0.16	N(200/5)	0.15	N(200/5)	0.16
N(5.4/6)	0.15				
Total number of leaves					
Experiment 1		Experiment 2		Experiment 3	
N(1.8/2)	21	N(0)	23	N(0)	24
N(1.8/6)	23	N(200/1)	24	N(200/1)	24
N(5.4/2)	23	N(200/5)	25	N(200/5)	24
N(5.4/6)	22				
Number of dead leaves					
Experiment 1		Experiment 2		Experiment 3	
N(1.8/2)	8	N(0)	12	N(0)	8
N(1.8/6)	9	N(200/1)	12	N(200/1)	8
N(5.4/2)	8	N(200/5)	13	N(200/5)	8
N(5.4/6)	8				
Number of green leaves					
Experiment 1		Experiment 2		Experiment 3	
N(1.8/2)	13	N(0)	11	N(0)	16
N(1.8/6)	14	N(200/1)	13	N(200/1)	16
N(5.4/2)	15	N(200/5)	12	N(200/5)	16
N(5.4/6)	14				

(Experiment 1); at 76 DAP treatments with two nitrogen applications had significantly more dead leaves than treatments with six applications (LSD-test, $P=0.05$). As death rate was lower than leaf appearance rate, the number of green leaves increased with time in all experiments till the end.

Treatments did not affect final number of leaves, number of dead leaves or number of green leaves per plant in either of the experiments (Table 3). Even the differences among experiments were small: at the end of each experiment dead leaves represented between one-third and half of the total number of leaves.

Rate of leaf expansion and size of mature leaves

The rate of leaf expansion was influenced by leaf number in all experiments. It increased in Experiment 1 (Figure 3) with leaf number, until it reached a maximum value of about 4.2 cm^2 d^{-1} at leaf 11 and decreased again for higher leaf numbers. The curves for leaf expansion rate in Experiments 2 and 3 had similar shapes as in Experiment 1 (data not shown), but the maximum was reached at slightly higher leaf numbers, viz. leaf pair 13+14 (in Experiments 2 and 3 two leaves were combined). The maximum rates were 9.1 and 8.2 cm^2 d^{-1} in Experiment 2 and 3, respectively, i.e. more than twice as high as in Experiment 1. In Experiment 1 the rate of leaf expansion was not affected by nitrogen treatment, while especially in Experiment 3 it was lower for most leaf pairs in N(0), than in N(200/1) and N(200/5).

The curves relating mature leaf area (and final leaf area of not full-grown leaves) to leaf number had similar shapes as the corresponding curves for leaf expansion

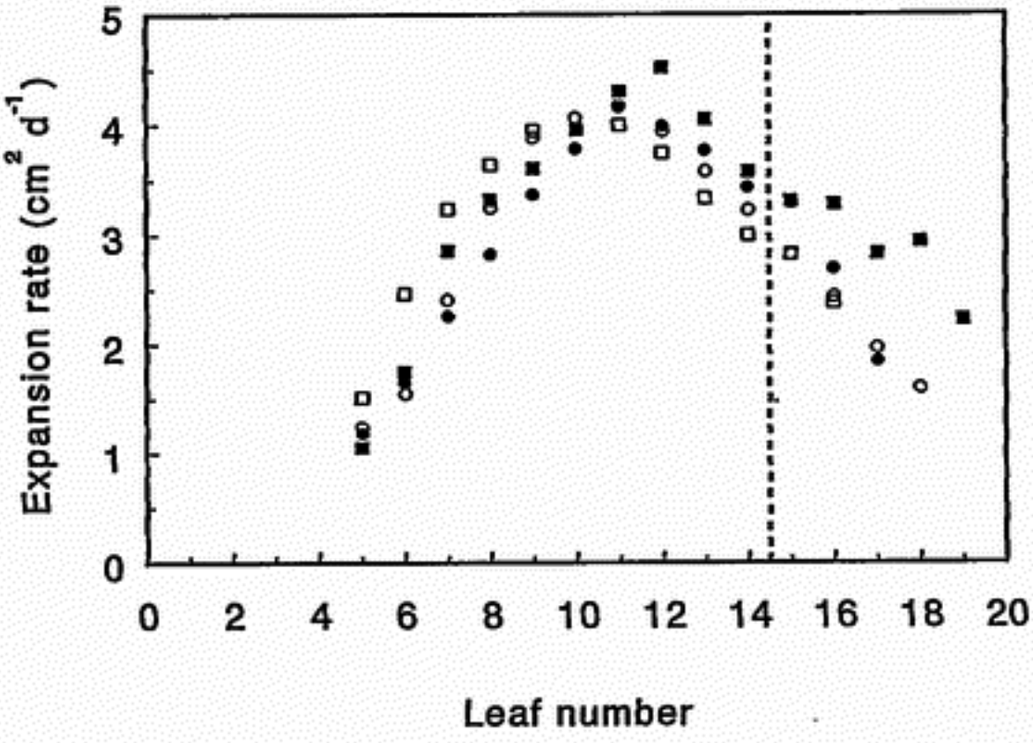

Figure 3. The rate of leaf expansion in relation to leaf number and nitrogen supply for Experiment 1. Data from not full-grown leaves are included. The dotted line is the border between full-grown (left) and not full-grown leaves (right). (□) N(1.8/2); (○) N(1.8/6); (■) N(5.4/2); (●) N(5.4/6).

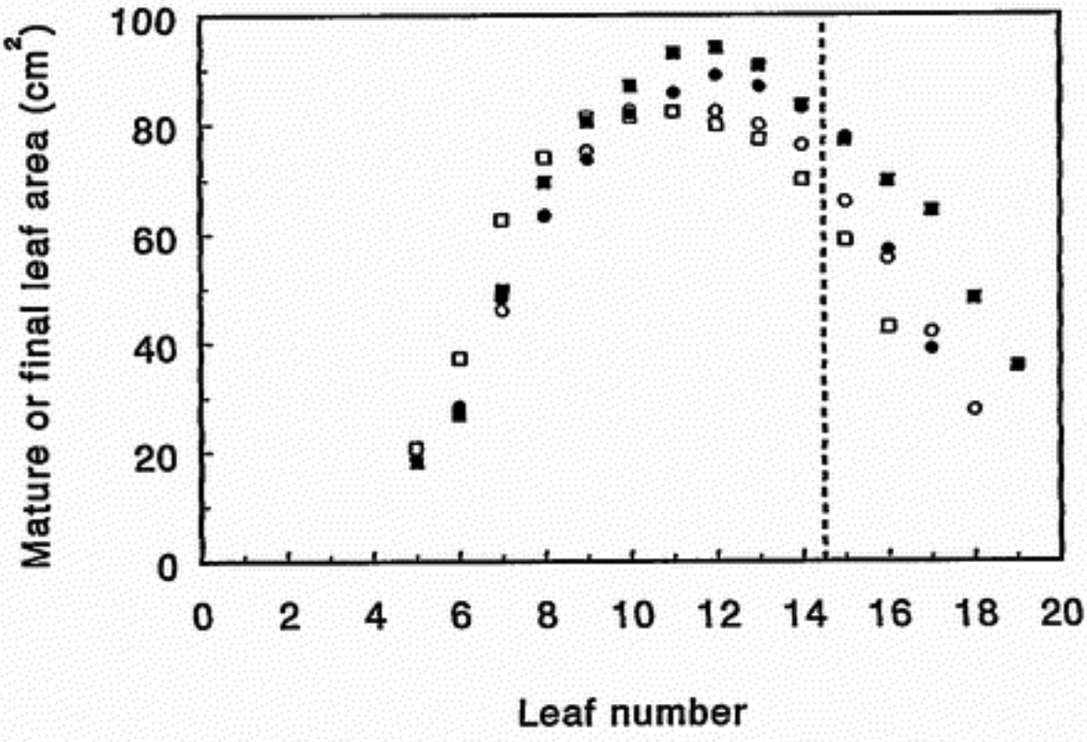

Figure 4. Mature leaf area of full-grown leaves or final leaf area of not full-grown leaves of Experiment 1 in relation to leaf number and nitrogen supply. The dotted line is the border between full-grown (left) and not full-grown leaves (right). (□) N(1.8/2); (○) N(1.8/6); (■) N(5.4/2); (●) N(5.4/6).

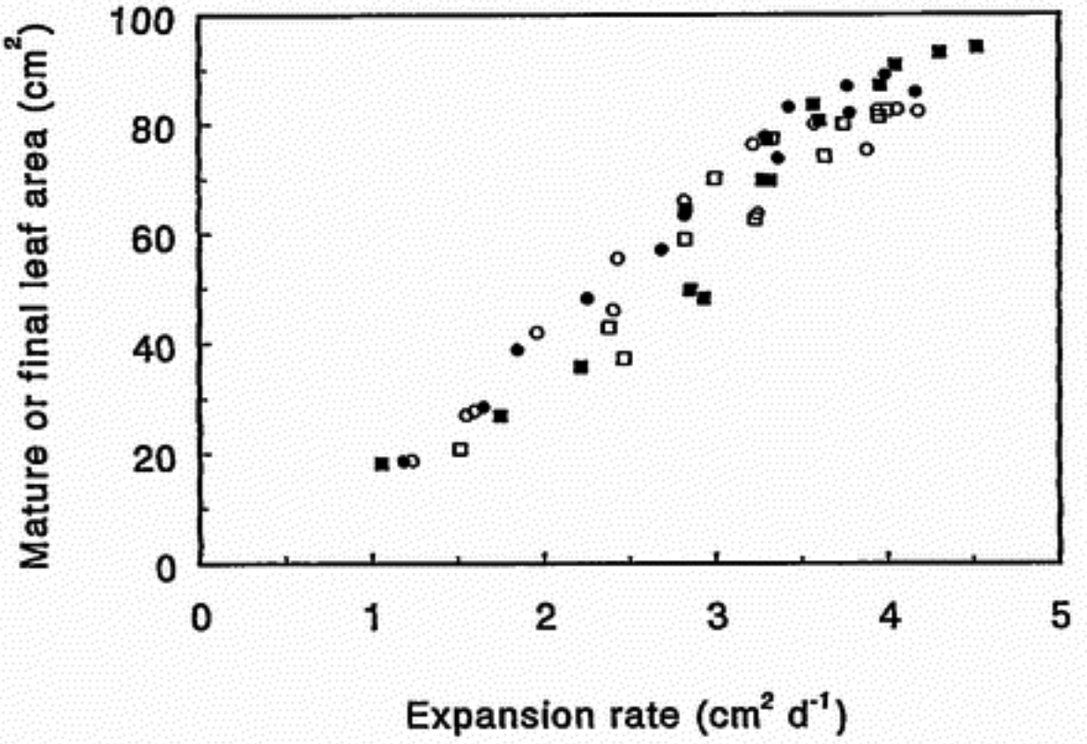

Figure 5. The relation between mature or final leaf area and leaf expansion rate, irrespective of leaf position (Experiment 1). Data from not full-grown leaves are included. (□) N(1.8/2); (○) N(1.8/6); (■) N(5.4/2); (●) N(5.4/6).

rate (Figure 4: Experiment 1). These similarities imply that the leaf expansion rate is the major determinant of mature leaf size. Mature (or final) leaf sizes in Experiment 1 fell on one line when plotted against leaf expansion rate (Figure 5), including the data of not full-grown leaves. This also applies to the data of Experiments 2 and 3, although in those experiments treatment effects on leaf expansion rate and mature leaf size were observed. The largest leaves in Experiments 2 and 3 had a mature area of about 335 (Experiment 2) or 400 cm^2 (Experiment 3), which is much larger than in Experiment 1 (maximum about 95 cm^2). N(0) leaves in Experiments 2 and 3 above leaf number 10 had about half the mature size of N(200/5) leaves.

The effective duration of expansion in Experiment 1 (Figure 6) increased with leaf number from 14 d to 24 d. This variable decreased slowly with leaf number in Experiments 2 and 3 (data not shown). Mean value for Experiment 2 was nearly 40 d and for Experiment 3 nearly 50 d, which is much longer than in Experiment 1. Nitrogen treatments had no effects in any experiment.

Specific leaf area

Specific leaf area (SLA) for all green leaves in Experiment 3 decreased for all treatments from about 116 $cm^2\ g^{-1}$ at 38 DAP to about 103 at 60 DAP and continued to decrease gradually for N(0) plants to reach 91 $cm^2\ g^{-1}$ at 122 DAP (Figure 7). SLA for N(200/1) and N(200/5) fluctuated after 60 DAP until it reached a final value of 102 for N(200/1) and 112 $cm^2\ g^{-1}$ for N(200/5). At 38 DAP N(0) and N(200/1) were

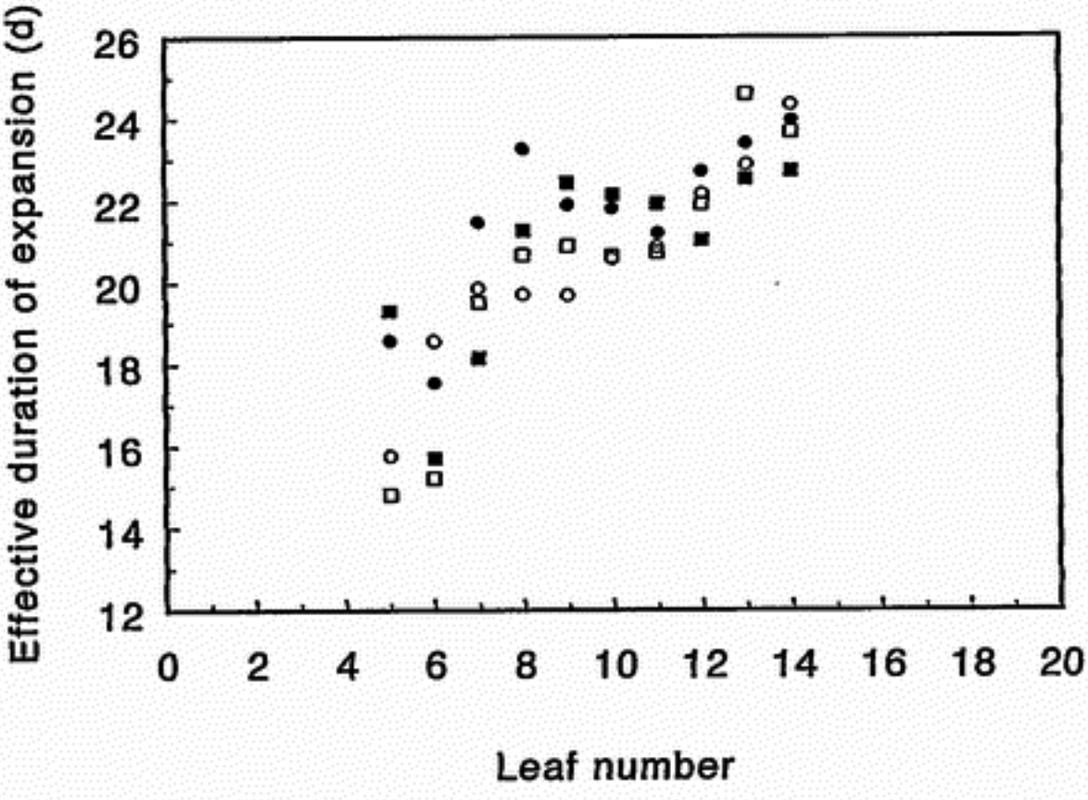

Figure 6. The effective duration of expansion as a function of leaf position and nitrogen treatment (Experiment 1). Data from not full-grown leaves are not included. (□) N(1.8/2); (○) N(1.8/6); (■) N(5.4/2); (●) N(5.4/6).

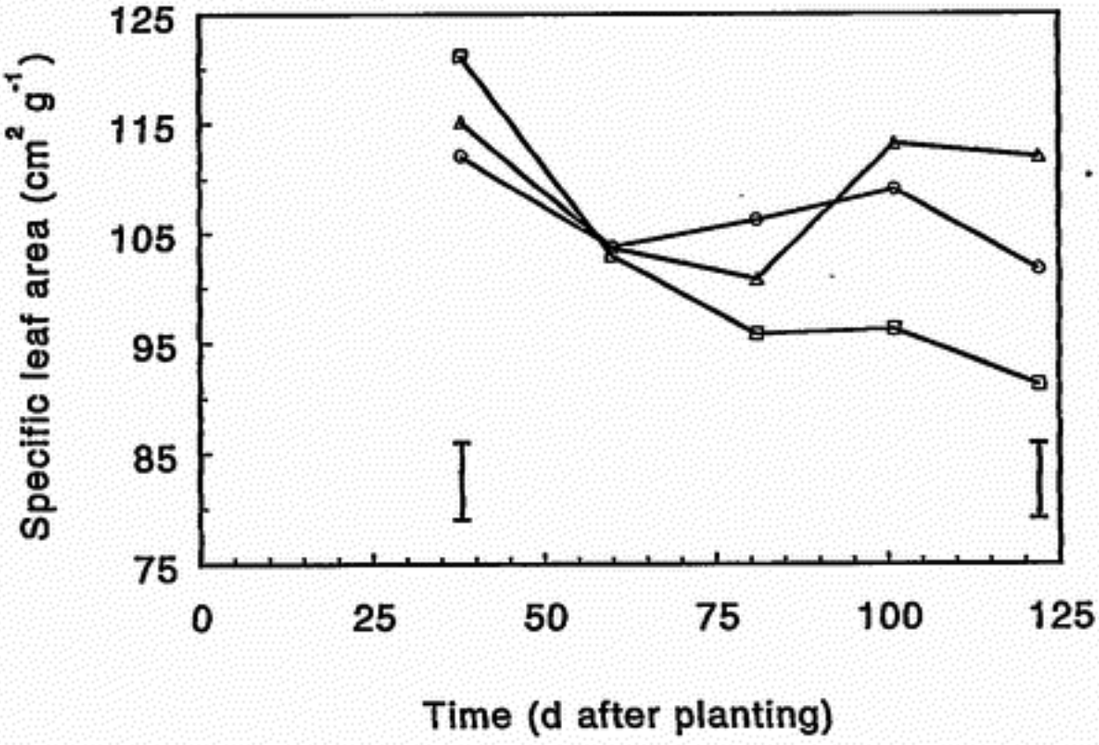

Figure 7. Specific leaf area over all leaves of a plant for Experiment 3 as a function of time and nitrogen treatment. The vertical bars represent LSD values (P=0.05). (□) N(0); (○) N(200/1); (△) N(200/5).

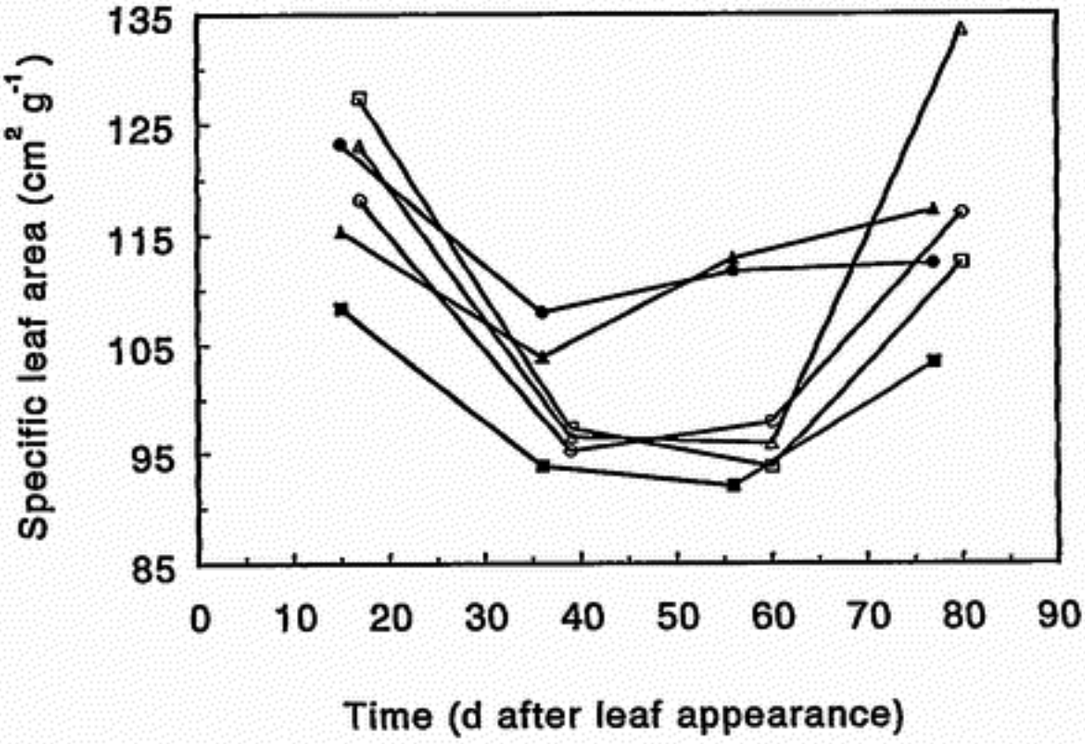

Figure 8. Specific leaf area of leaf pairs 7+8 and 11+12 against days after leaf appearance (Experiment 3). Leaf pair 7+8: (open markers; (□) N(0); (○) N(200/1); (△) N(200/5)); leaf pair 11+12: (closed markers; (■) N(0); (●) N(200/1); (▲) N(200/5)).

significantly different, at 122 DAP all differences between treatments were significant (LSD-test, P=0.05). SLA of individual leaf pairs was as variable as that over all green leaves (Figure 8). Differences between leaf pairs were small and all curves were similar in shape: SLA decreased at the onset of the life of a leaf, then remained constant for some time and increased at the end of the leaf life.

SLA over all green leaves in Experiment 2 rapidly decreased from about 145 cm^2 g^{-1} at 35 DAP to 110 at 56 DAP, but subsequently only slowly until it reached a final value of about 90 cm^2 g^{-1}. It never differed significantly among treatments. SLA in Experiment 1 was hardly influenced by treatments; however, applying nitrogen in two (compared to six) splits resulted in a significantly higher SLA at 47 DAP; 1.8 g N per pot (compared to 5.4) resulted in a significantly (P=0.05) higher SLA at 62 DAP. SLA in this experiment fluctuated between 80 and 100 cm^2 g^{-1}.

Total leaf area

Leaf area index (LAI) in Experiment 2 (Figure 9) increased until 91 DAP and subsequently decreased for N(0) and N(200/5) but not for N(200/1). At most occasions total leaf area for the N(200/1) and N(200/5) treatments was significantly (LSD-test, P=0.05) higher than for the N(0) treatment, but N(200/5) was never higher than N(200/1). LAI in Experiment 1 increased over the whole experimental period until N(1.8/2) and N(1.8/6) reached a final LAI of about 1.2 and N(5.4/2) and N(5.4/6) of about 1.8. LAI was significantly higher (LSD-test, P=0.05) for 5.4 g N at 96 and 117 DAP. LAI in Experiment 3 also increased monotously over the growth period. N(0) reached a final value of 3.16, N(200/1) of 5.24 and N(200/5) of 5.03. LAI in

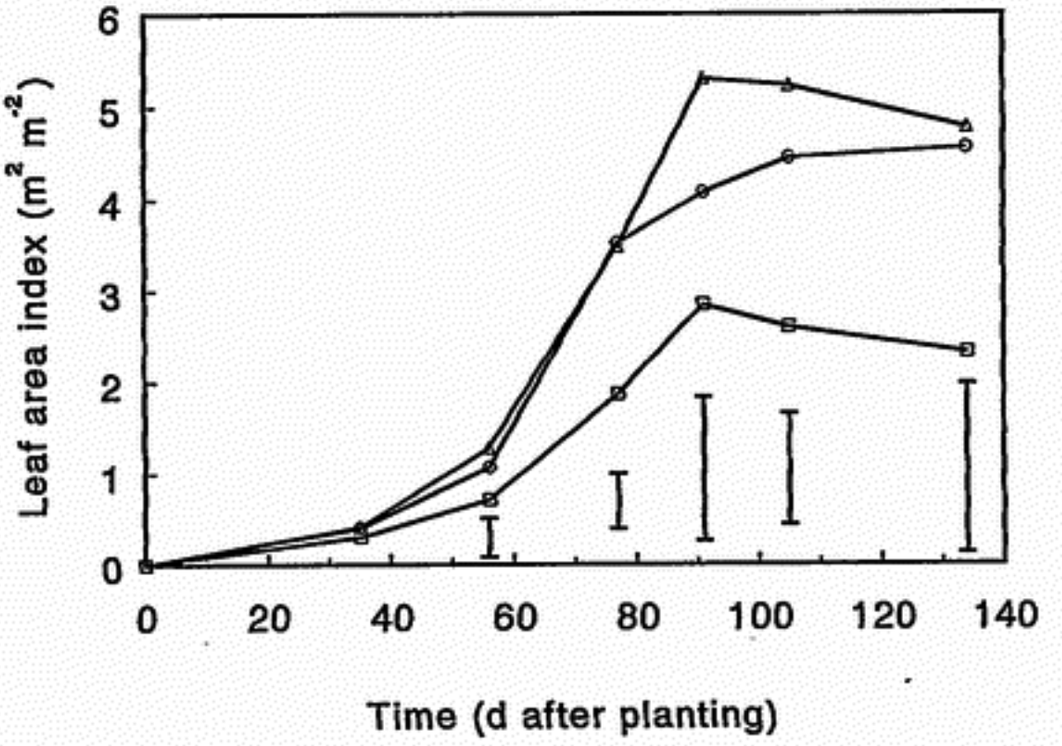

Figure 9. Total leaf area per plant for Experiment 2 as a function of time and nitrogen treatment. The vertical bars represent LSD values (P=0.05). (□) N(0); (○) N(200/1); (△) N(200/5).

Table 4. Length of the period of exponential increase of the LAI (leaf area index) and the relative growth rate of the LAI, calculated over the period from the first harvest until the end of the phase of exponential growth.

Length of period of exponential increase of LAI (d)					
Experiment 1		Experiment 2		Experiment 3	
N(1.8/2)	96	N(0)	91	N(0)	81
N(1.8/6)	96	N(200/1)	77	N(200/1)	101
N(5.4/2)	96	N(200/5)	91	N(200/5)	101
N(5.4/6)	96				
Relative growth rate of LAI (d^{-1})					
Experiment 1		Experiment 2		Experiment 3	
N(1.8/2)	0.0297	N(0)	0.0395	N(0)	0.0353
N(1.8/6)	0.0334	N(200/1)	0.0514	N(200/1)	0.0449
N(5.4/2)	0.0406	N(200/5)	0.0452	N(200/5)	0.0411
N(5.4/6)	0.0390				

N(0) was significantly (LSD-test, P=0.05) lower than in N(200/1) and N(200/5) at 101 and 122 DAP.

LAI increased exponentially during a large part of the growing period (Table 4). RGR during this period was calculated from the first harvest until the end of the phase of exponential growth. The largest difference in length of the exponential phase across treatments and experiments, was that between N(200/1) in Experiment 2 and N(200/1) and N(200/5) in Experiment 3 and amounted to 24 d. The largest difference in RGR of the LAI was that between N(1.8/2) in Experiment 1 and N(200/1) in Experiment 2 and amounted to 0.0216 d^{-1}.

Discussion

Total green leaf area per plant is the integrated value of the number of green leaves and the size of each leaf. The number of green leaves is the resultant of the rate of leaf appearance and the life span of leaves. The size of each leaf is determined by the rate and duration of leaf expansion. Total leaf area is influenced by treatment effects on any of these components.

The rate of leaf appearance was not affected by amount and timing of nitrogen fertilization. Hay & Brown (1988) and Hay & Kemp (1992) found a linear relation between accumulated temperature and leaf appearance rate. However, the results of Experiment 1 show an increase in leaf appearance rate at the end of the experiment, although the temperature was constant. The rate of leaf appearance over the first 60 days (0.74 leaves per 100 degree days) was in accordance with the results of Hay & Brown (1988) and Hay & Kemp (1992), who found values of 0.76 and 0.74 leaves

per 100 degree days, respectively. Mean temperature was lower at the end of Experiments 2 and 3, which resulted in a lower leaf appearance rate. Muchow (1988) found for maize and sorghum (also monocotyledons, but determinate plants) positive effects of nitrogen supply on rate of leaf appearance, but not on the final number of leaves. In experiments with sugar beet (a dicotyledonous plant), Terry (1970) found positive effects of nitrogen supply on the rate of leaf appearance.

Leaf expansion rates and mature leaf sizes in Experiment 1 were not affected by N treatment. This is surprising, because nitrogen effects on these variables are often found, i.e. by Muchow (1988) for maize and sorghum. In Experiments 2 and 3 the amount of nitrogen influenced both variables positively. Nitrogen enhances mature leaf size by increasing the rate of leaf expansion and not its duration, as observed by Terry (1970) and Milford & Riley (1980) for sugar beet and Radin & Boyer (1982) for sunflower. Hay & Brown (1988) found a constant rate of leaf extension for leek leaves, independent of leaf number, which is not in agreement with the present results. Hay & Brown concluded that leaf length increased with increasing leaf number, because the number of leaves per plant, which were expanding at the same time, increased progressively. The number of expanding leaves per plant increased, because the duration of the linear phase of leaf expansion increased with increasing leaf number.

As a result of the nearly constant rate of leaf appearance and constant, but lower, rate of leaf senescence, the number of green leaves per plant increased linearly, confirming results for leek from Hay & Kemp (1992).

The change in SLA with time was mainly due to changes in SLA of individual leaves. The differences in SLA among leaf numbers were relatively small, compared to the changes in time. More nitrogen and/or more applications of nitrogen affected SLA positively.

Although leaf characteristics such as rate of leaf appearance, rate of leaf expansion and duration of expansion were almost equal for all treatments in Experiment 1, there was a large difference in final LAI between treatments with 1.8 and 5.4 g N per pot, as a result of small differences in the mature area of mainly higher leaf numbers. In Experiments 2 and 3 the differences in LAI among the treatments resulted mainly from differences in the area of mature leaves. The differences in final LAI between Experiment 1 on the one hand and Experiments 2 and 3 on the other also mainly resulted from the differences in the area of mature leaves. The differences in mature leaf area, however, cannot be explained. Differences in mature area per leaf within an experiment were always the result of differences in the amount of nitrogen and not of the timing of nitrogen fertilization.

Leek has, compared to other crops, a relatively low growth rate at the start of the growing season, which appears e.g. from Figure 9: in Experiment 2 an LAI of three was reached in about 70 days, while a crop as potato reaches this LAI under Dutch circumstances 30–40 days after emergence (Van der Zaag, 1984). A low growth rate implies a small demand for nitrogen. Therefore it was expected that leek would benefit from split nitrogen fertilization, as with this treatment nitrogen was applied when the growth rate (and the demand for nitrogen) was higher. However, splitting (N(200/5) treatments in Experiments 2 and 3) had insignificant effects.

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