



Shoot and root production in mixed grass ley under daily fertilization and irrigation: validating the N productivity concept under field conditions

Katharina H. E. Meurer · Martin A. Bolinder · Olof Andrén · Ann-Charlotte Hansson · Roger Pettersson · Thomas Kätterer

Received: 5 June 2018 / Accepted: 10 June 2019 / Published online: 18 June 2019
© The Author(s) 2019

Abstract The literature suggests a linear relationship between the N supply and relative growth rate (RGR) of plants. Our objective was to evaluate this concept for a typical mixed grass-ley in Sweden under field conditions, subjected to various combinations of irrigation and N fertilization, and to assess belowground C and N allocation patterns. For that purpose, we measured aboveground biomass 30 times through two consecutive years. Environmental variables, such as soil temperature and radiation, were continuously monitored and soil mineral N concentrations were measured to 0.9 m depth at 10 occasions. During the

second year, belowground biomass to 1 m depth was measured. The unfertilized and non-irrigated control treatment showed the lowest aboveground production. In this experiment, both fertilization and irrigation had significant effects on production. Growth dynamics for all growth periods and treatments was reflected by a logistic function ($R^2 = 0.98$). RGR significantly increased with N concentration in aboveground plant tissues ($R^2 = 0.81$), validating the nitrogen productivity concept for a forage crop under field conditions. Living root biomass ($247\text{--}330\text{ g m}^{-2}$) was mainly (83–92%) located in the upper 0.30 m under all treatments. Generally, the shoot-to-root ratios (0.58–2.67) and N concentrations in living roots increased with irrigation and N fertilization. Soil profiles of mineral N gave no clear indications of environmental risks. Supplementary materials provide the detailed dataset useful for crop growth modelling purposes.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10705-019-10006-3>) contains supplementary material, which is available to authorized users.

K. H. E. Meurer (✉) · M. A. Bolinder · T. Kätterer
Department of Ecology, Swedish University of Agricultural Sciences (SLU), Box 7044, 750 07 Uppsala, Sweden
e-mail: katharina.meurer@slu.se

O. Andrén
Oandren, Björklundavägen 3, 756 46 Uppsala, Sweden

A.-C. Hansson
Planeringsavdelningen, SLU, Box 7044, 750 07 Uppsala, Sweden

R. Pettersson
Utbildningsavdelningen, SLU, Box 7044, 750 07 Uppsala, Sweden

Keywords Grass ley · Steady-state nutrition · Nitrogen productivity · Growth rate · Shoot-to-root ratio

Introduction

Ley is the major crop in Scandinavian agriculture. In Swedish agro-ecosystems, leys are commonly grown for forage and grazing in rotation with cereals, oilseed

crops and root crops, and cover almost half the cultivated area (Statistics Sweden 2016). Most of these leys are mixtures of grasses and legumes, with timothy (*Phleum pratense* L.) and meadow fescue (*Festuca pratensis* L.) being the dominant grasses (Huss-Danell et al. 2007). Cultivation of grass leys as forage crops usually demands fertilization for acceptable productivity. Under favorable growing conditions, nitrogen (N) is taken up rapidly, while periods of poor ley growth can result in considerable losses of N down to the groundwater in the form of nitrate (NO_3^-) (Bergström and Johnsson 1988). These N losses to the environment can be reduced by increasing the precision in fertilization through consideration of the dynamic nutrient demand of the crop plants (Andrén et al. 1996; Murphy et al. 2007).

According to the concept of relative addition rate, developed to identify optimal nutrition conditions for plant growth (Ingestad and Lund 1979, 1986), the amount of nutrients supplied to the plant per unit time has to be related to the amount of nutrients in current biomass and the nutrient requirement for forming new plant tissues. In accordance with nutrient availability in the plant-soil system. Hence, matching nutrient addition to plant uptake demand ensures maximum plant growth under the given climate conditions. During the early exponential growth phase of plant biomass, nutrients must be supplied at a corresponding exponentially increasing rate (Ingestad and Lund 1979). Optimal growth conditions are achieved under steady-state nutrition, in which nutrients are repeatedly added to the plant so that the relative nutrient uptake rate and the relative plant growth rate are identical (Ingestad and Lund 1986; Ingestad and Ågren 1988). This concept has been applied in laboratory studies investigating plant development under demand-driven nutrient addition and under steady-state nutrition (e.g., Ingestad 1988; Smolders and Merckx 1992; De Pinheiro Henriques and Marcelis 2000; Glimskär 2000; Rytter et al. 2003). It has been shown that dry matter partitioning in the plant (S:R, shoot-to-root ratio) is strongly affected by the nutrient status, particularly the N status. Under nutrient-limited conditions, plants tend to compensate for low nutrient availability with lower growth and nutrient allocation to shoots and a correspondingly higher proportion of root growth (e.g., Clement et al. 1979; Wilson 1988; Jarvis and MacDuff 1989). Consequently, there is a direct link between dry

matter partitioning and relative resource limitation (Glimskär and Ericsson 1999).

Field experiments with steady-state fertilization have mainly been performed with trees (see review by Zabek and Prescott 2007), and little information for grass and forage crops is available from field experiments. Compared with other plants, grasses have considerably long roots and greater root biomass which is a strong advantage in the competition for soil N (e.g., Jumpponen et al. 2002; Franzluebbers et al. 2014). Higher N mass per unit area in grass roots compared with leaves and stems is often reported (e.g., Huss-Danell et al. 2007). Furthermore, a sound knowledge about the S:R ratio and root depth distribution is crucial for estimating carbon (C) inputs to the soil from the more frequently measured aboveground biomass production. Temporary grassland has the potential to obtain biogeochemical characteristics that are close to continuous grassland and introduction of temporary grasslands can be assumed to increase C concentrations in arable soil (e.g., Crème et al. 2018). Due to the strong impact of root input on soil organic matter and, consequently, soil carbon balance (e.g. Franzluebbers et al. 2014), measurements of root biomass and its distribution with depth are essential for calibrating soil carbon models (Kätterer et al. 2011; Menichetti et al. 2015). Several assessments have been made, but root samplings are usually concentrated to the topsoil (e.g., Bolinder et al. 1997; Izaurrealde et al. 2001) and depths below 0.25 m are often not considered (Fan et al. 2016).

The objective of this study was to test the hypothesis that the linear relationship between N supply and relative growth rate applies for ley under field conditions. The data used in this analysis were obtained in a field experiment in central Sweden in which a grass ley was subjected to optimal and suboptimal conditions in terms of water and nutrient supply. The experiment was part of an integrated project examining soil properties, litter decomposition, belowground biomass, and nitrogen dynamics of several crops (Andrén et al. 1996). A series of field experiments were conducted, involving daily irrigation and fertilization of arable crops in Sweden including grain crops, i.e., winter wheat (Andrén et al. 1993; Kätterer and Andrén 1995, 1996; Kätterer et al. 1993, 1997) and barley (Hansson et al. 1992), as well as reed canarygrass (Kätterer et al. 1998; Kätterer and Andrén 1999). In this paper, we present results for

aboveground biomass, growth dynamics, and N allocation, measured by frequent sampling over a two-year period. It also includes belowground biomass distribution from a sampling to 1 m depth in the second year, separated into living roots, stem bases, and macroscopic soil litter.

The dataset also provides a good basis for calibration or validation of plant growth models. This was beyond the scope of our study but interested readers have access to detailed data in the supplementary materials.

Materials and methods

Site description and treatments

This field experiment was carried out at Ultuna (59°48'N, 17°38'E), about 5 km south of Uppsala, in Central Sweden. The climate is cold temperate and subhumid, with mean annual temperature of 6.2 °C (1981–2010). Mean annual precipitation is 557 mm, with a maximum in late summer and a minimum in late winter. The soil is a Fluventic Eutrochrept and the topsoil (0–0.30 m) contains 53% clay, 36% silt and 5% sand. The total C content is 2.8%, total N content is 0.28%, and the pH (H₂O) is 7.4 (Andrén et al. 1990).

Prior to the start of the experiment in autumn 1989, the field was under bare fallow for three years and then cropped with spring barley (not fertilized) in 1988 and winter wheat (not fertilized) in 1989. After harvesting the winter wheat and removing the straw, the field was plowed, harrowed and rolled in early September. On 19 September 1989, a mixture of perennial rye grass (*Lolium perenne*), timothy (*Phleum pratense*), meadow fescue (*Festuca pratensis*), and smooth-stalked meadow grass (*Poa pratensis*), was sown in rows (0.125 m spacing between rows) at a rate of 7, 8, 8, and 4 kg ha⁻¹, respectively.

In May 1990, five treatments were established in a randomized factorial design with four blocks, giving 20 plots. The plots were 8 m × 11 m, separated by 2.5 m-wide untreated areas. Although the field had high PK status (Andrén et al. 1990; Kätterer et al. 1993), all treatments received 105 kg ha⁻¹ P, 240 kg ha⁻¹ K, and micro-nutrients to eliminate possible limitations of all elements except for N. The five treatments were: Control (C₀) without fertilizer and irrigation; no irrigation but fertilization with solid

Ca(NO₃)₂ in a split dose (C₁); and three irrigated treatments (I₁, IF₁ and IF₂) with different fertilization regimes (Table 1). Treatment I₁ received N in solid form, as in C₁, while IF₁ received the same amount as liquid mixed into the daily irrigation water. In IF₂, fertilizer was applied as in IF₁, but at a 50% higher dose in 1991 (Figure S1). Irrigation was adjusted daily, to keep the topsoil close to field capacity. The water was distributed through a drip-tube system with one tube per plant row (0.125 m). Total amount of water applied was 219 mm in 1990 and 374 mm in 1991.

Abiotic measurements

Weather data were obtained from the Ultuna weather station on the University campus (59°49'N, 17°39'E). Interception of photosynthetically active radiation (PAR) was calculated from measurements of photosynthetic photon flux density above the crop and at the soil surface in treatment IF₂ (LI-190SA sensors, LICOR, Lincoln, NE 68504, USA).

Soil temperature was monitored at 0.10 m depth in each plot from April to November at two-hour intervals. Both PAR and temperature measurements were monitored using a Campbell CR 10 logger (Campbell, Logan, UT, USA).

Soil mineral nitrogen concentrations were measured four times in 1990 and six times in 1991. Four samples per plot were taken from the 0–0.30, 0.30–0.60, and 0.60–0.90 m layers and bulked into one sample per treatment and depth layer for analysis. Soil samples were extracted with 250 mL 2 M KCl and the concentrations of ammonium (NH₄⁺) and nitrate (NO₃⁻) were measured using an auto-analyzer. The values were converted into g N m⁻².

Aboveground biomass

Aboveground biomass was sampled 30 times between May 1990 and November 1991. The whole field was harvested two times during 1990 and five times during 1991 using a harvester with header and collector. To estimate the exported biomass, i.e., the aboveground biomass that was removed from the field with harvest, the crop was cut in each plot in two randomly chosen circular areas (0.25 m²) shortly before and after the whole-field harvest. At all other dates between the whole-field harvests only one circular area per plot

Table 1 Treatments included in the experimental study in 1990 and 1991

	Treatment	Irrigation	Fertilizer		
			Amount (g N m ⁻²)	Date	Application
	C ₀	None	None	None	None
	C ₁	None	12	16 May 1990	Split dose as solid Ca(NO ₃) ₂
			8	27 July 1990	
			10	4 May 1991	
			10	10 June 1991	
			7	11 July 1991	
Daily water supply in treatments I ₁ , IF ₁ , and IF ₂ was through a drip-tube irrigation system			5	8 August 1991	
^a Daily dose applied according to a logistic function including the assumed nutrient demand of the crop (Ingestad and Lund 1986)	I ₁	Daily	See C ₁	See C ₁	Split dose as solid Ca(NO ₃) ₂
	IF ₁	Daily	20	1990	Daily doses in irrigation water ^a
			32	1991	
	IF ₂	Daily	20	1990	Daily doses in irrigation water ^a
			48	1991	

was sampled. The mass remaining in the field after whole-field harvest consisted of both stubble and harvest debris. The biomass was not quantified before establishing the treatments in May 1990.

All samples were dried at 70 °C and weighed. The biomass samples were then milled in a high-speed mill and analyzed for total nitrogen (N) concentration using a NA 1500 Elemental Analyzer (Carlo Erba Strumentazione, Milano, Italy).

At each sampling date during 1991, 10 shoots per plot, adjacent to the biomass sampling area, were cut at the ground following a randomized sampling protocol. In the laboratory shoots were sorted into leaves (leaf blades only) and stems (including ears and leaf sheaths encircling the stems). The green areas of leaves and stems were then separated with scissors and measured separately with a surface area meter (model no. 3320; Li-Cor Inc., Lincoln, NE, USA), including one side of each green leaf lamina and the projected areas of the other green plant parts. The specific leaf area (SLA) (m² g⁻¹) was calculated from the area/mass relationships of the shoot fractions and the total dry mass per unit area.

Calculating growth rate and nitrogen productivity

For each growth period (between the harvests) and experimental plot, the specific growth rate (μ ; DM DM⁻¹ T_{sum}⁻¹) was estimated by fitting a logistic function to the measured aboveground dry mass (Thornley and Johnson 1990):

$$DM = \frac{DM_0 DM_{max}}{DM_0 + (DM_{max} - DM_0)e^{-\mu T_{sum}}} \quad (1)$$

where T_{sum} is the accumulated sum of daily mean air temperatures above 5 °C, DM is the measured aboveground dry mass (g m⁻²), DM₀ is the aboveground dry mass remaining after each harvest (g DM m⁻² at t = 0), and DM_{max} is the maximum dry mass that was assumed to be achievable under ambient conditions. In this study, DM_{max} was set to 700 g m⁻² for all treatments and growth periods, which was close to the highest biomass value measured in one replicate in IF₂ on 5 August 1991.

Since sampling of aboveground biomass started in July 1990, the absolute growth rate μ of the first growth period was calculated by solving Eq. 1 for measured DM at harvest and setting DM₀ to 50 g m⁻² for all treatments. Daily average air temperatures were obtained from the Ultuna climate station at the University campus.

According to the logistic growth function, the actual relative growth rate (RGR), expressed as a function of mass (Paine et al. 2012), decreases linearly with DM:

$$RGR = \frac{dDM}{dT_{sum}} \frac{1}{DM} = \mu \left(1 - \frac{DM}{DM_{max}} \right) \quad (2)$$

Following the nitrogen productivity (P_N) concept introduced by Ågren (1985), the growth rate is related to the amount of N present in the plant (c_N). Basically, this concept describes the amount of biomass produced per amount of nitrogen in the plant per unit time.

As not all the N in the plant is active in growth, a minimum concentration $c_{N,min}$ is assumed, below which the relative growth rate is zero (Ågren and Bosatta 1998). Under the assumption that P_N is constant, both parameters P_N and $c_{N,min}$ can be estimated from the linear relation to RGR:

$$RGR = P_N(c_N - c_{N,min}) \quad (3)$$

To test the relationship between nitrogen concentration in the aboveground biomass and RGR, the unirrigated treatments (C_0 and C_1) were excluded because they also depend on water and not only on nitrogen.

Belowground biomass

Belowground biomass was sampled at the end of summer 1991, when it was assumed to be at its maximum (Bolinder et al. 2002). On 11 September 1991, two soil core samples (0.07 m diameter) were taken in each plot after clipping the crop at the soil surface, following the technique described by Welbank et al. (1974) and modified by Hansson (1987). One soil core was taken within rows to 0.50 m depth and one between rows to 1 m depth. Each core was divided into three or five vertical sections, respectively, i.e., 0–0.10, 0.10–0.30, 0.30–0.50, 0.50–0.70, and 0.70–1 m. Belowground biomass to 0.5 m depth was calculated by averaging the samples from within row and between row locations. According to previous studies in the same field showing insignificant effects of row location on root biomass below 0.5 m depth (Kätterer et al. 1993), we assumed that the samples taken at 0.5–1 m depth were representative for the whole field plot.

Samples were stored in plastic bags at $-20\text{ }^\circ\text{C}$ before further treatment. The soil was removed from the cores using a washing machine devised by Smucker et al. (1982). This process, through which some N might get lost, was chosen because of the heavy clay soil of the experimental site. Macro-organic material (MOM) was caught on sieves with a 0.5 mm mesh size and manually sorted into living roots (LR), belowground stem bases (SB), and soil litter (SL). The latter included harvest residues, weed seeds, dead roots, and stem bases from previous years.

All samples were dried at $70\text{ }^\circ\text{C}$ for 2 days and weighed. Dried subsamples from the soil cores were

pooled to one sample for each fraction and treatment before milling. The nitrogen concentration was then measured (NA 1500 Element Analyzer; Carlo Erba Strumentazione, Milan, Italy) and the ash content was determined by combustion for 6 h at $550\text{ }^\circ\text{C}$.

The shoot-to-root ratio for each treatment was calculated by dividing the average aboveground biomass exported throughout 1991 by the root biomass sampled on 11 September 1991. This calculation was done in two ways and the root biomass was either considered to include solely the living roots or both living roots and stem bases.

Statistical analyses

Statistical analyses were performed using the R software (i386 3.3.1, R Core Team 2016) and the *openxlsx* package (Walker 2017) and the *ddply* function (*plyr* package, Wickham 2011) were used for data processing. Equation 1 was fitted to aboveground biomass data by non-linear least-squares estimation using the *nlsLM* function from the *minpack.lm* package (Elzhov et al. 2016). The effect of the treatment on specific leaf area, above- and belowground biomass and N contents, exported biomass and nitrogen, estimated growth rates and shoot-to-root ratios was tested using nonlinear mixed-effects models. The *lme* function from the *nlme* package (Pinheiro et al. 2017) was used with “block” as random effect. The models were fitted by maximizing the log-likelihood (method = “ML”). Differences between means were assessed by the Tukey test using the *glht* function from the *multcomp* package (Hothorn et al. 2008). Results were regarded significant at $p < 0.05$. Graphics were created using the *ggplot2* (Wickham 2009) and *cowplot* packages (Wilke 2017).

Results

Abiotic conditions

Precipitation was higher than average (557 mm) during both 1990 (648 mm) and 1991 (602 mm) with particularly high rainfall during the summer months (Table S1). Winter and spring temperatures were higher in 1990 than in 1991 and in both years above the long-term average. PAR was higher during spring 1990 than spring 1991 (Figure S2). During the second

half of the year monthly mean temperatures and PAR were lower in 1990 than in 1991. Maximum mean values for PAR over 10-day periods were just beyond $40 \text{ mol m}^{-2} \text{ day}^{-1}$, which corresponds to about $9 \text{ MJ m}^{-2} \text{ day}^{-1}$ (McCartney 1978).

Daily mean soil temperature did not vary greatly between the plots and differences were only visible during the summer months, when irrigated plots were somewhat cooler (Figure S3).

Growth dynamics

In both years, average aboveground dry mass was lowest in the unfertilized and non-irrigated control (C_0) and highest in the irrigated and higher fertilized treatment (IF_2) (Table S2). However, no significant differences were found between I_1 , IF_1 and IF_2 in either 1990 or 1991. For individual sampling dates, differences between fertilized and unfertilized treatments were significant mostly during the summer months (Table S2).

The logistic function reflected growth dynamics for all growth periods and treatments (Fig. 1). Good agreement between observed and estimated aboveground dry mass was achieved, as is evident by $R^2 = 0.98$ ($n = 50$) and a good fit along the 1:1 line ($y = 1.02x - 7.02$) (Figure S4). However, the negative intercept of the linear function indicated lower model validity when production rates were very low.

On average, the estimated RGR ($\text{g DM g DM}^{-1} \text{ day}^{-1}$) was lowest for the unfertilized control treatment C_0 and highest for the fertilized but not irrigated C_1 treatment (Table 2). However, the latter did not differ significantly from the irrigated + fertilized IF_1 and IF_2 treatments and the irrigated I_1 treatment. The effect of fertilization was significant during only two growth periods (2 and 7) when RGR for C_0 was significantly lower than for the other treatments. The I_1 treatment did not differ significantly from the equally fertilized but unirrigated C_1 treatment, except for the first summer period (2). Similarly, the positive effect of daily fertilization with irrigation water (IF_1) compared to split application of N fertilizer (C_1) was significant during the same period (2). The higher N dose in IF_2 resulted in higher growth rates compared with IF_1 in the four warmer growth periods (2, 4, 5 and 6). On average, fertilization rather than irrigation had an impact on plant growth and RGR differed significantly only between fertilized and unfertilized treatments. The estimated growth rate μ as a function of temperature sum and growing days for individual treatments and growth periods, upon which the calculation of RGR is based, are presented in Table S3.

Averaged over the individual growth periods, daily RGR increased significantly with N concentration in plant biomass ($R^2 = 0.81$, $n = 21$; Fig. 2). The negative intercept (-0.004 day^{-1}) reflects the fact that a minimum N concentration ($c_{N,\min}$) was required for

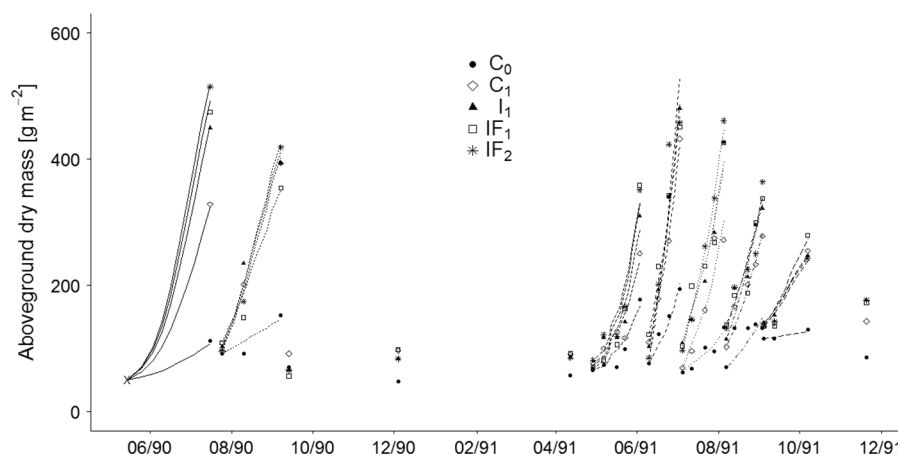


Fig. 1 Measured aboveground dry mass for individual treatments and growth periods and corresponding logistic functions (see Eq. 1). Aboveground biomass on 15 May 1990 (DM_0) was not measured, but was set to 50 g m^{-2} for all treatments

(marked as “X”). Freestanding symbols are measurements that were not associated with a growth period. See Table 1 for treatment explanation

Table 2 Treatment-specific relative growth rates (RGR) ($\times 10^{-3}$) estimated for the seven growth periods during 1990–1991, related to the sum of the daily air temperature (T_{sum}^{-1}) and number of days with daily average temperatures $\geq 5\text{ }^\circ\text{C}$ (day^{-1})

Growth period	Timeframe	C ₀	C ₁	I ₁	IF ₁	IF ₂
[g DM g DM ⁻¹ T _{sum} ⁻¹] ($\times 10^{-3}$)						
1	15 May–16 Jul 1990	0.86 (0.42) a	1.46 (0.12) b	1.34 (0.23) ab	1.23 (0.42) ab	1.14 (0.22) ab
2	25 Jul–07 Sep 1990	0.59 (0.46) a	1.37 (0.16) b	1.11 (0.12) b	1.12 (0.39) b	1.23 (0.11) b
3	29 Apr–03 Jun 1991	3.30 (1.37) a	3.67 (1.24) a	4.14 (0.38) a	3.96 (0.14) a	3.76 (0.96) a
4	10 Jun–03 Jul 1991	2.79 (0.49) a	2.62 (0.61) a	2.58 (1.15) a	2.54 (0.21) a	3.49 (0.42) a
5	05 Jul–05 Aug 1991	1.18 (22.2) a	2.12 (0.39) b	1.26 (0.28) a	1.37 (0.15) ab	1.40 (0.91) ab
6	07 Aug–03 Sep 1991	1.60 (0.65) a	1.81 (0.27) a	1.88 (0.60) a	1.53 (0.51) a	1.56 (0.33) a
7	04 Sep–07 Oct 1991	0.29 (0.45) a	1.59 (0.23) b	1.58 (0.28) b	1.83 (0.31) b	1.54 (0.61) b
Average		1.52 (1.23) a	2.01 (0.92) b	1.98 (1.12) b	1.94 (1.00) b	2.02 (1.17) b
[g DM g DM ⁻¹ day ⁻¹] ($\times 10^{-3}$)						
1	15 May–16 Jul 1990	11.3 (5.45) a	19.2 (1.52) a	17.6 (2.98) a	16.2 (5.58) a	15.1 (2.84) a
2	25 Jul–07 Sep 1990	9.31 (7.11) a	21.4 (2.36) b	17.4 (2.10) ab	17.6 (5.97) ab	19.4 (1.75) b
3	29 Apr–03 Jun 1991	28.3 (10.4) a	31.6 (9.47) a	35.7 (3.39) a	34.0 (1.23) a	32.2 (7.10) a
4	10 Jun–03 Jul 1991	37.4 (6.61) a	34.8 (8.19) a	34.4 (15.4) a	33.8 (2.84) a	46.3 (5.61) a
5	05 Jul–05 Aug 1991	21.2 (3.96) a	38.0 (7.01) a	22.5 (4.99) a	24.5 (2.67) a	25.0 (16.2) a
6	07 Aug–03 Sep 1991	25.4 (10.3) a	28.7 (4.23) a	29.7 (9.46) a	24.3 (8.05) a	24.8 (5.22) a
7	04 Sep–07 Oct 1991	27.3 (4.36) a	15.3 (2.24) b	15.2 (2.72) b	17.6 (2.98) b	14.8 (5.88) b
Average		19.4 (13.3) a	27.0 (9.72) b	24.6 (10.4) b	24.0 (8.23) b	25.4 (12.6) b

Daily values were calculated according to Eqs. 1 and 2 and using day instead of T_{sum} . Values are presented as means and standard deviation is given in parentheses. Different letters after values within rows indicate significant differences between treatments ($p < 0.05$). See Table 1 for treatment explanation

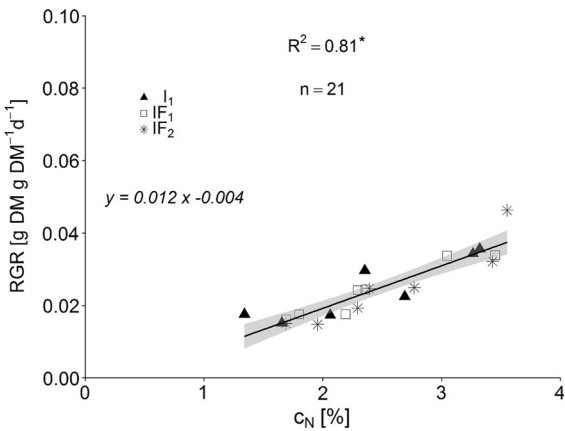


Fig. 2 Linear relationship between nitrogen concentration in the aboveground biomass c_N (%) and relative growth rate (RGR) [$\text{g DM g DM}^{-1} \text{ day}^{-1}$] ($RGR = 0.012(c_N - 0.33)$). The grey shaded area represents the 95% confidence interval. $*p < 0.05$. See Table 1 for treatment explanation

plant growth. The estimated value for N productivity (P_N) derived from this linear relationship was $0.12 \text{ g DM (mg N)}^{-1} \text{ day}^{-1}$.

Specific leaf area (SLA) was higher in the irrigated than in the unirrigated treatments during 1991, except for one sampling in September when the average leaf area under IF₂ was lower than under C₁ (Table S4). Leaf development pattern over time was similar for all treatments and leaf area was lowest in May and highest in mid-June (Figure S5a). Differences between the treatments mainly occurred during the summer months and in early autumn. For stems, differences between treatments were less obvious than for leaves. However, except for one sampling date in May 1991, stem area in treatments C₀ and C₁ was always lower than in treatments I₁, IF₁, and IF₂ (Table S4). No seasonal variation in stem development was observed (Figure S5b).

Exported biomass

For all treatments, exported biomass and nitrogen were highest during summer 1991 (03 July 1991) and lowest at the last harvest in September 1991 (Table 3).

Table 3 Exported dry mass (g m^{-2}) and exported amount of nitrogen (g m^{-2}) during 1990 and 1991

Sampling date ^a	C ₀	C ₁	I ₁	IF ₁	IF ₂
	Dry mass (g m^{-2})				
16 Jul 1990	20 (60) a	233 (140) b	346 (106) bc	365 (109) bc	417 (110) c
07 Sep 1990	82 (56) a	301 (101) b	327 (184) b	298 (159) b	354 (123) b
Total 1990	102 a	534 b	673 bc	663 bc	771 c
03 Jun 1991	101 (46) a	141 (27) a	207 (69) b	236 (52) b	266 (54) b
03 Jul 1991	132 (27) a	363 (40) b	371 (148) b	347 (76) b	361 (57) b
05 Aug 1991	64 (14) a	169 (71) a	312 (103) b	288 (67) b	329 (122) b
03 Sep 1991	18 (37) a	139 (93) b	182 (80) b	202 (81) b	229 (63) b
Total 1991	314 a	811 b	1072 c	1073 c	1184 c
Total	416 a	1346 b	1745 c	1737 c	1956 c
	Nitrogen (g m^{-2})				
16 Jul 1990	0.13 (0.78) a	4.28 (2.64) b	4.54 (1.41) b	6.24 (1.84) bc	7.22 (1.84) c
07 Sep 1990	1.57 (0.92) a	6.50 (2.05) b	7.71 (4.08) b	7.46 (3.79) b	8.44 (2.83) b
Total 1990	1.70 a	10.78 b	12.25 bc	13.70 bc	15.66 c
03 Jun 1991	1.88 (0.79) a	4.33 (0.86) b	6.57 (2.15) c	8.22 (1.63) cd	10.28 (2.11) d
03 Jul 1991	2.05 (0.41) a	9.17 (1.01) b	9.75 (3.25) b	9.70 (2.00) b	9.77 (1.22) b
05 Aug 1991	1.12 (0.24) a	5.19 (1.88) b	7.56 (2.39) b	7.91 (1.35) b	10.79 (3.72) c
03 Sep 1991	0.58 (0.59) a	4.18 (2.17) b	4.70 (1.61) c	6.06 (2.05) bc	7.03 (1.62) c
Total 1991	5.62 a	22.87 b	28.58 bc	31.89 cd	37.88 d
Total	7.33 a	33.65 b	40.83 bc	45.59 cd	53.54 d

Values are averaged over four blocks and standard deviation is given in parentheses. Different letters after values within rows indicate significant differences between treatments ($p < 0.05$). See Table 1 for treatment explanation

^aExported dry mass and nitrogen was not calculated for the seventh growth period (04 Sep–07 Oct 1991), since the biomass of the last harvest (07 Oct 1991) remained in the field

Biomass exports from the unfertilized control (C₀) were significantly lower than those from the irrigated and fertilized treatments (Table 3). As expected, the highest values were observed in IF₂, but except for the first harvest date (16 July 1990) IF₂ did not differ significantly from I₁ and IF₁, which received less fertilizer N in 1991. However, compared with the control treatment, daily irrigation combined with fertilizer supply led to 4.2-fold (IF₁) and 4.7-fold (IF₂) higher total yield. Considering the individual years, the influence was stronger in 1990 (6.5-fold and 7.6-fold for IF₁ and IF₂, respectively) compared with 1991 (3.4-fold and 3.8-fold, respectively). The pure effect of irrigation, obtained by comparing C₁ and I₁ with the same fertilization regime, was comparatively low but still resulted in 1.26-fold and 1.32-fold higher biomass in 1990 and 1991, respectively.

Nitrogen concentration in dry biomass was on average lowest in C₀ and highest in IF₂ (Table S2). Compared with the control (C₀), the amount of N exported with biomass (Table 3) for C₁ and I₁ was 6.3-fold and 7.2-fold higher, respectively, in 1990 and 4.1-fold and 5.1-fold higher, respectively, in 1991. Export of N was highest for the daily liquid N fertilization treatments, IF₁ and IF₂, where it was 8.2-fold and 9.2-

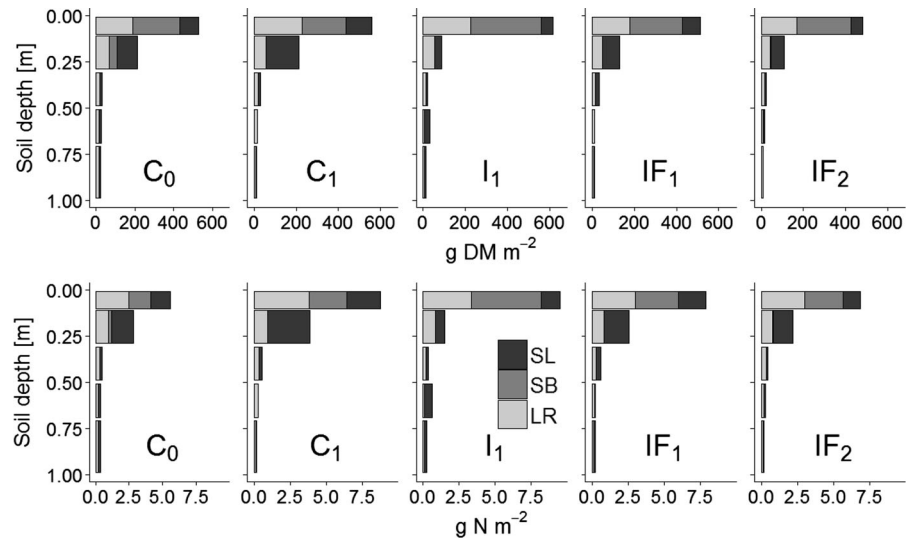
fold higher, respectively, than in C₀ in 1990 and 5.7-fold and 6.7-fold higher, respectively, in 1991.

Belowground biomass

Living root biomass (LR) differed significantly between the five treatments (Table S5). Highest values were found in C₁ ($330 \pm 34 \text{ g m}^{-2}$) and lowest values in IF₂ ($247 \pm 32 \text{ g m}^{-2}$) (Fig. 3). Irrespective of treatment, the majority (83–92%) of the MOM was found within the top 0.30 m of the soil. No stem bases (SB) were found below this depth in treatments C₀, C₁ and IF₂, while in I₁ and IF₁, SB occurrence was limited to the 0–0.10 m soil layer. Similarly to MOM, total soil litter (SL) was highest in the non-irrigated treatments, while the lowest value was found in the I₁ treatment. Significant differences between treatments in SL were only found for the second soil layer (0.10–0.30 m). The total belowground biomass (i.e., LR + SB + SL) did not differ significantly between treatments.

Nitrogen concentrations in LR, SB and SL were lowest in C₀ (1.01, 0.96, and 0.58%, respectively) (Table S6). The highest N concentrations in LR were recorded in IF₁ and IF₂ (1.30%), while SB and SL

Fig. 3 Treatment-specific depth distribution of belowground biomass (top row) and nitrogen (N) mass (bottom row) separated into soil litter (SL), stem-bases (SB) and living roots (LR). Note that the thickness of the bars differs according to the thickness of the sampled depths, so the bars are not a true image of the depth distribution per unit volume. See Table 1 for treatment explanation



showed the highest concentrations in the I_1 treatment (1.52 and 1.11%, respectively).

The main belowground N mass was found within the top 0.10 (LR and SB) and 0.30 m (SL), respectively, and this was independent of the treatment (Fig. 3, Table S5). However, the total amount of N in belowground biomass (i.e., LR + SB + SL) was highest under C_1 (13.70 g m^{-2}) and lowest under C_0 (9.62 g m^{-2}) and these differences were significant. Nitrogen mass did not differ considerably between the irrigated treatments and was 12.27 in I_1 , 11.50 in IF_1 , and 10.05 g m^{-2} in IF_2 . Here, none of the differences in N mass were significant.

Soil mineral nitrogen

Ammonium and nitrate contents in the soil varied strongly between treatments and sampling depths (Table S7). Although a clear response to fertilizer N addition in the topsoil (0–0.30 m) and transport to deeper layers under the irrigated treatments was not found in the first year, in the second year N_{\min} contents in 0.30–0.60 and 0.60–0.90 m depth usually were higher under irrigated treatments than under the non-irrigated but fertilized treatment C_1 . However, considering the entire experimental period until the last harvest (05 September 1991), changes in soil mineral N contents in the whole profile were negative under all treatments. Highest and lowest reductions were found under IF_1 (4.63 g N m^{-2}) and IF_2 (1.28 g N m^{-2}),

respectively. Reductions were 3.76, 2.63 and 2.28 g N m^{-2} under C_0 , C_1 , and I_1 , respectively.

Discussion

Growth and nutrient dynamics

The average aboveground dry mass was highest in treatment IF_2 and lowest in C_0 , but for the individual sampling dates differences were not always significant (Table S2). Besides differences in management, the dynamics in plant growth are also driven by weather conditions (e.g., air temperature and precipitation) and dynamic soil parameters, e.g., soil temperature. Average air temperature was slightly lower in the beginning of the second year of growing (April–June 1991) and higher towards the end (July–October 1991) (Table 1). The monthly distribution of precipitation was different in the two years and total rainfall over the growing season (April–September) was higher in 1991 (409 mm) than in 1990 (346 mm).

Using linear regression, a significant relation between average aboveground biomass and cumulative precipitation was found for all but the control treatment C_0 . No relation was found between the average aboveground biomass and soil temperature for any of the treatments ($p > 0.05$).

Considering the six harvest events throughout 1990 and 1991, exported biomass was mostly highest in July

and lower when harvested later during the season (Table 3). Exceptions are C_0 and C_1 , where, in 1990, exported biomass was higher in September than in July.

The biomass exported during 1991 in C_1 (in total 812 g m^{-2}), which is the treatment closest to conventional agricultural practice in Sweden, was similar to aboveground net primary production measured in more frequently cut public lawns in central Sweden (933 g m^{-2} ; Poeplau et al. 2016). It was also similar to ryegrass yields reported for southern Sweden (four cuts per year; Wallgren et al. 1995) and to yields of lucerne (*Medicago sativa*) in central Sweden after three years of cultivation (980 g m^{-2} ; Pettersson et al. 1986). However, reported 10-year mean farm yields (1982–1991) for temporary grass leys (two cuts per year) in Uppsala County and Sweden overall are lower, i.e., 698 and 675 g m^{-2} , respectively (SCB 2017).

In a study by Pettersson et al. (1986), total amount of nitrogen exported in lucerne biomass (*Medicago sativa*) was 12 g m^{-2} in the first year and 20 g m^{-2} in the second, which is similar to our findings for C_1 and I_1 , respectively (Table 3). Higher yields, i.e., 22.8 (first year) and 25.3 g N m^{-2} (second year) have been reported by Hansson and Pettersson (1989) for perennial grass ley (*Festuca pratensis*) based on two cuts per year.

Over the two-year experiment, irrigation on the experimental site increased total yield by approximately 30% (26% in 1990 and 32% in 1991) and the amount of N exported by 21% (14% in 1990 and 25% in 1991; comparison C_1 and I_1 ; Table 3). In both cases the increase was significant in both years of the cultivation. Similar to that, fertilization (comparison C_0 and C_1) had a significant impact on both yield and exported N and lead to threefold higher yield (fivefold in 1990 and threefold in 1991) and fivefold higher exported N (sixfold in 1990 and fourfold in 1991). As expected, the higher N fertilizer dose in IF_2 resulted in higher yield (13%) and, consequently, more export of N (17%) compared with IF_1 . However, exported biomass did not differ significantly between I_1 , IF_1 and IF_2 . Exported N mass increased significantly with irrigation and fertilization. Similar to that, in a previous study reported by Kätterer et al. (1998) for reed canary grass at the same site, N exported at crop harvest increased with fertilization and irrigation and was highest in the irrigated treatment high highest

fertilization. However, treatment differences in that study were not significant.

Besides the different number of sampling occasions in the two years, yields were on average lower in 1990 compared to 1991. This can be attributed to the fact that the plants had to establish during the first year, which resulted in lower aboveground biomass production and, consequently, lower growth rates compared to 1991. However, treatment effects on exported biomass were mostly visible in significantly lower values for the unirrigated treatments C_0 and (on two occasions) C_1 (Table 3). It was only for the first growth period (15 May–16 July 1990) that significant yield differences were found for most of the treatments. For the irrigated treatments, yields under IF_2 were significantly higher than under I_1 and IF_1 , which did not differ from each other. Similar to that, the absence of irrigation in combination with fertilization (C_1) resulted in significantly lower yields. These results show that both fertilization and irrigation had a positive effect on the juvenile plant development. This clear difference is not visible for the following growth periods.

Generally, the logistic function adequately described the observed development of aboveground biomass (Figs. 1 and S5). However, our data derived from a cool temperate field experiment and, in contrast to studies performed in the greenhouse under controlled conditions, air temperature was a main driver of crop growth. Consequently, the maximum relative growth rate (RGR_{\max}) was 0.05 day^{-1} (IF_2 treatment during growth season 4; Table 2). This is lower than values (obtained under controlled laboratory conditions that were more favorable for plant growth) reported previously for *Lolium perenne* (0.19 day^{-1} , Grime and Hunt 1975; 0.21 day^{-1} , Poorter and Remkes 1990) and *Phleum pratense* (0.23 day^{-1} , Poorter and Remkes 1990). Similarly, RGR_{\max} values reported for forbs and grasses that occur in semi-natural grasslands in Sweden are also higher and range from 0.10 to 0.28 day^{-1} (Glimskär and Ericsson 1999).

The underlying assumptions in the approaches used for calculating μ and P_N are rather simple, where the linear relationship between RGR and plant N concentration also assumes that the N concentration of each plant component is constant. Earlier studies supporting this latter relationship have been performed under controlled conditions, mainly on different woody

species (e.g., Ingestad and Lund 1979; Ingestad 1979; Ericsson 1981; Ågren 1985), but also on forbs and grasses (Glimskär and Ericsson 1999; Ericsson et al. 2012). Laboratory conditions obviously do not reflect field conditions. Lemaire and Gastal (1997) showed that for several crops, a hyperbolic formulation is adequate for describing the decline in crop N concentration with time and increased dry mass. Based on the field data obtained in the present study, we found a strong correlation ($p < 0.001$) between RGR and plant N for irrigated treatments, when averaged over the individual growth periods and treatments (Fig. 2). This supports the hypothesized positive effect of increased N supply and, consequently, N uptake on plant growth.

Above a specific optimal N concentration (saturation), plant uptake is no longer equal to the N addition rate and growth rates do not increase further. We found no decreasing trend here, suggesting that the optimal N concentration was not reached within our experiment. Even in the highly fertilized and daily irrigated IF₂ treatment, growth rates increased with increasing N concentration.

The effect of low N supply in limiting growth was visible in leaf development (Table S4). The specific area of leaves was always significantly lower under C₀, except at the first sampling date (7 May). This also applies to the stems, but here, no differences between the treatments were additionally found at the fifth (10 June) and seventh (25 June) sampling occasion. This is in line with laboratory results by McDonald et al. (1992) and Glimskär and Ericsson (1999) showing that N-limiting conditions lead to reduced SLA.

Belowground biomass and biomass partitioning

Total biomass of living roots (LR; 0–1 m) recorded in this study ranged from 247 for IF₂ to 330 g m⁻² for the C₁ treatment (Table S5). This is lower than that estimated by Hansson and Andrén (1986) for *Festuca pratensis* 2 years after establishment, albeit on a lighter soil (approximately 590 g m⁻²). However, our results clearly show higher allocation of resources to roots under N limitation. Based on a similar experimental setup at the same site for canary grass (*Phalaris arundinacea*), Kätterer and Andrén (1999) also reported higher root biomass in C₁ than in the IF₂ treatment after 2 years (359 and 248 g m⁻², respectively). They attributed this response to the heavy

fertilization and irrigation which is in agreement with a function describing how increased N availability affects carbohydrate reserves, prioritizing shoots over roots (Schlossberg and Karnok 2001).

In the present study, shoot-to-root (S:R) ratio was lowest in the C₀ treatment and increased with intensity of irrigation and fertilization (Table 4). This increase in the relative proportion of shoots has been observed not only in forage crops (Leyshon 1991), but also in small-grain cereals (Welbank et al. 1974) and maize (Eghball and Maranville 1993). A similar trend has been reported by Schlossberg and Karnok (2001) for grass turf, with a S:R ratio of 0.40 and 0.77 for the lowest and highest N application rate, respectively. Generally, the S:R ratio in the present study were within the range of values (i.e., 1.6 ± 1.2) reported in the review by Bolinder et al. (2007) for forage crops in North America. Other studies in Northern Europe report similar values, e.g., the S:R ratio estimated for *Lolium multiflorum* (roots to 0.60 m depth) in Finland was 4.1 (Pietola and Alakukku 2005). In another Finnish study on *Phleum pratense* (roots to 0.60 m depth), Ilola et al. (1988) calculated a S:R ratio of 1.9 and 3.2 for rainfed and irrigated treatments, respectively.

There are also other factors controlling the S:R ratio. For instance, it is well known that root biomass tends to increase with age in perennial forage crops (Weaver and Zink 1946; Troughton 1957), resulting in decreasing S:R ratios (e.g., Bolinder et al. 2002). In the present study, the S:R ratio was calculated from a root sampling late in the second year of production, while the shoot biomass was the total exported dry mass in that year (sum of all harvests in 1991). Furthermore, differences in estimated root biomass and S:R ratio may arise due to the methodology used to collect roots, such as inclusion and correction for undecomposed roots and organic material (e.g., Walley et al. 1996). Another critical issue is the distinction between roots and stem bases, something that is, unfortunately, not always explicitly described in all studies. For example, as shown in our study, although both plant fractions were limited to the upper soil layers, the total biomass of SB was similar to that of LR biomass down to 1 m (Table S5). Consequently, estimated S:R ratio values including SB (Table 4) were much lower and varied significantly between the treatments from 0.58 in C₀ to 2.67 in IF₂.

Table 4 Treatment-specific shoot-to-root ratios (S:R) calculated excluding (R) and including stem bases (RS)

	C ₀	C ₁	I ₁	IF ₁	IF ₂
R	1.03 (0.30) a	2.47 (0.44) b	3.60 (0.89) c	4.10 (0.47) cd	4.83 (0.73) d
RS	0.58 (0.25) a	1.52 (0.25) ab	1.87 (0.91) bc	2.15 (0.25) bc	2.67 (1.05) c

Values are averaged over four blocks and standard deviation is given in parentheses. Different letters after values within rows indicate significant differences between treatments ($p < 0.05$). See Table 1 for treatment explanation

The continuous water supply provided in the irrigated treatments was expected to increase the transport of N, mainly NO_3^- , to deeper layers compared with the unirrigated treatments, but this was not clearly supported by our mineral measurements (Table S7). A mass balance including the N inputs (fertilizer, N deposition) and outputs (exported N mass, N stored belowground) and considering the changes in soil N_{\min} revealed that losses of mineral N occurred under C₀ (16.61 g N m⁻²) and IF₁ (5.1 g N m⁻²). In contrast to that, an increase in N was found for C₁ (8.09 g N m⁻²) and IF₂ (6.83 g N m⁻²) and almost no changes were found under I₁ (0.005 g N m⁻²). The different pathways of the mineral N reduction, such as denitrification, leaching, volatilization and surface runoff, were not investigated in this study.

Conclusions

This study demonstrated the significant impact of nutrient availability and nutrition status on growth and dry mass partitioning of a grass ley. The linear relationship found between RGR and plant N concentration validates the nitrogen productivity concept for a forage crop under field conditions, at least in a cold temperate climate of Sweden. However, the low relative growth rates found in this study also emphasize the importance of external influences other than fertilization, which are not captured under laboratory conditions. Our findings highlight the value of demand-driven fertilization and irrigation as a tool to control plant growth and leaf development, making a better use of these resources while minimizing nutrient losses to the environment. This is supporting the simple and less complex application of this concept used in practice (e.g., split fertilization and irrigation in drought periods), which are likely to become more

common, especially environmental reasons and with changing climate. The results on S:R ratios, which is an important parameter for estimating belowground C inputs in soil organic carbon models, are contributing to a better assessment of the C sequestration potential for leys. Furthermore, the comprehensive and detailed dataset derived from this study is valuable for calibration and/or validation of crop growth and ecosystem models.

Acknowledgements Financial support for conducting the field trial was received from the Swedish Council for Forestry and Agricultural Research. Our work with data analysis and writing was supported by the Swedish Farmers' Foundation for Agricultural Research (Grant No. O-15-23-552).

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

- Ågren GI (1985) Theory for growth of plants derived from the nitrogen productivity concept. *Physiol Plant* 64:17–28
- Ågren GI, Bosatta E (1998) Theoretical ecosystem ecology. Understanding element cycles. Cambridge University Press, Cambridge, p 234
- Andrén O, Rajkai K, Rajkai Véghe K (1990) Spatial variation of soil physical and chemical properties in an arable field with high clay content. Swedish University of Agricultural Sciences, Uppsala, Dept Ecol Environ Res, Rep 40
- Andrén O, Rajkai K, Kätterer T (1993) Water and temperature dynamics in a clay soil under winter wheat: influence on straw decomposition and N immobilization. *Biol Fertil Soils* 15:1–8
- Andrén O, Kätterer T, Pettersson R, Flink M, Hansson A-C (1996) Nitrogen dynamics of crop and soil subjected to different water and nitrogen inputs, including daily irrigation and steady-state fertilization—measurements and modelling. *Plant Soil* 181:13–17

- Bergström L, Johnsson H (1988) Simulated nitrogen dynamics and nitrate leaching in a perennial grass ley. *Plant Soil* 105:273–281
- Bolinder MA, Angers DA, Dubuc JP (1997) Estimating shoot to root ratios and annual carbon inputs in soils for cereal crops. *Agric Ecosyst Environ* 63:61–66
- Bolinder MA, Angers DA, Bélanger G, Michaud R, Laverdière MR (2002) Root biomass and shoot to root ratios of perennial forage crops in eastern Canada. *Can J Plant Sci* 82:731–737
- Bolinder MA, Janzen HH, Gregorich EG, Angers DA, VandenBygaart AJ (2007) An approach for estimating net primary productivity and annual carbon inputs to soil for common agricultural crops in Canada. *Agric Ecosyst Environ* 118:29–42. <https://doi.org/10.1016/j.agee.2006.05.013>
- Clement CR, Jones LHP, Hopper MJ (1979) Uptake of nitrogen from flowing nutrient solution: effect of terminated and intermittent nitrate supplies. In: Hewitt EJ, Cutting CV (eds) *Nitrogen assimilation of plants*. Academic Press Inc., London, pp 123–133
- Crème A, Rumpel C, Le Roux X, Romian A, Lan T, Chabbi A (2018) Ley grassland under temperate climate had a legacy effect on soil organic matter quantity, biogeochemical signature and microbial activities. *Soil Biol Biochem* 122:203–210. <https://doi.org/10.1016/j.soilbio.2018.04.018>
- De Pinheiro Henriques AR, Marcelis LFM (2000) Regulation of growth at steady-state nitrogen nutrition in lettuce (*Lactuca sativa* L.): interactive effects of nitrogen and irradiance. *Ann Bot* 86:1073–1080. <https://doi.org/10.1006/anbo.2000.1268>
- Eghball B, Maranville JW (1993) Root development and nitrogen influx of corn genotypes grown under combined drought and nitrogen stress. *Agron J* 85:147–152
- Elzhov TV, Mullen KM, Spiess A-N, Bolker B (2016) minpack.lm: R interface to the levelberg-marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds. R package version 1.2-1. <https://CRAN.R-project.org/package=minpack.lm>
- Ericsson T (1981) Effects of varied nitrogen stress on growth and nutrition in three *Salix* clones. *Physiol Plant* 51:423–429
- Ericsson T, Blombäck K, Neumann A (2012) Demand-driven fertilization. Part I: Nitrogen productivity in four high-maintenance turf grass species. *Acta Agric Scand B: Soil Plant Sci* 62(1):113–121. <https://doi.org/10.1080/09064710.2012.682735>
- Fan J, McConkey B, Wang H, Janzen H (2016) Root distribution by depth for temperate agricultural crops. *Field Crops Research* 168:68–74. <https://doi.org/10.1016/j.fcr.2016.02.013>
- Franzluebbers AJ, Sawchik J, Taboada MA (2014) Agronomic and environmental impacts of pasture-crop rotations in temperate North and South America. *Agric Ecosyst Environ* 190:18–26. <https://doi.org/10.1016/j.agee.2013.09.017>
- Glimskär A (2000) Estimates of root system topology of five plant species grown at steady-state nutrition. *Plant Soil* 227:249–256
- Glimskär A, Ericsson T (1999) Relative nitrogen limitation at steady-state nutrition as a determinant of plasticity in five grassland plant species. *Ann Bot* 84:413–420
- Grime JP, Hunt R (1975) Relative growth-rate: its range and adaptive significance in a local flora. *J Ecol* 63(2):393–422. <https://doi.org/10.2307/2258728>
- Hansson A-C (1987) Roots of arable crops: production, growth dynamics and nitrogen content. Swedish University of Agricultural Sciences, Uppsala, Dept Ecol Environ Res, Rep 28
- Hansson A-C, Andrén O (1986) Below-ground plant production in a perennial grass ley (*Festuca pratensis* Huds.) assessed with different methods. *J Appl Ecol* 23(2):657–666
- Hansson A-C, Pettersson R (1989) Uptake and above- and below-ground allocation of soil mineral-n and fertilizer-¹⁵N in a perennial grass ley (*Festuca pratensis*). *J Appl Ecol* 26(1):259–271
- Hansson A-C, Steen E, Andrén O (1992) Root growth of daily irrigated and fertilized barley investigated with ingrowth cores, soil cores and minirhizotrons. *Swedish J Agric Res* 22:141–152
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50(3):346–363
- Huss-Danell K, Chaia E, Carlsson G (2007) N₂ fixation and nitrogen allocation to above and below ground plant parts in red clover-grasslands. *Plant Soil* 299:215–226. <https://doi.org/10.1007/s11104-007-9376-4>
- Ilola A, Elomaa E, Pulli S (1988) Testing a Danish growth model for barley, turnip rape and timothy in Finnish conditions. *J Agric Sci Finland* 60:631–660
- Ingestad T (1979) Nitrogen stress in birch seedlings. II N, K, P, Ca, and Mg nutrition. *Physiol Plant* 45:149–157
- Ingestad T (1988) A fertilization model based on the concepts of nutrient flux density and nutrient productivity. *Scand J For Res* 3:157–173
- Ingestad T, Ågren GI (1988) Nutrient uptake and allocation at steady-state nutrition. *Physiol Plant* 72:450–459
- Ingestad T, Lund A-B (1979) Nitrogen stress in birch seedlings. I. Growth technique and growth. *Physiol Plant* 45:137–148
- Ingestad T, Lund A-B (1986) Theory and techniques for steady state mineral nutrition and growth of plants. *Scand J For Res* 1:439–453
- Izaurrealde RC, McGill WB, Robertson JA, Juma NG, Thurston JJ (2001) Carbon balance of the breton classical plots over half a century. *Soil Sci Soc Am J* 65:431–441
- Jarvis SC, MacDuff JH (1989) Nitrate nutrition of grasses from steady-state supplies in flowing solution culture following nitrate deprivation and/or defoliation: I. Recovery of uptake and growth and their interactions. *J Exp Bot* 40(218):965–975
- Jumpponen A, Högberg P, Huss-Danell K, Mulder CPH (2002) Interspecific and spatial differences in nitrogen uptake in monocultures and two-species mixtures in north European grasslands. *Funct Ecol* 16:454–461
- Kätterer T, Andrén O (1995) Measurements and simulations of heat and water balance components in a clay soil cropped with winter wheat under drought stress or daily irrigation and fertilization. *Irrig Sci* 16:65–73
- Kätterer T, Andrén O (1996) Measured and simulated nitrogen dynamics in winter wheat and a clay soil subjected to

- drought stress or daily irrigation and fertilization. *Fertil Res* 44:51–63
- Kätterer T, Andrén O (1999) Growth dynamics of reed canarygrass (*Phalaris arundinacea* L.) and its allocation of biomass and nitrogen below ground in a field receiving daily irrigation and fertilization. *Nutri Cycl Agroecosyst* 54:21–29
- Kätterer T, Hansson A-C, Andrén O (1993) Wheat root biomass and nitrogen dynamics—effects of daily irrigation and fertilization. *Plant Soil* 151:21–30
- Kätterer T, Eckersten H, Andrén O, Pettersson R (1997) Winter wheat biomass and nitrogen dynamics under different fertilizer and water regimes: application of a crop growth model. *Ecol Model* 102:301–314
- Kätterer T, Andrén O, Pettersson R (1998) Growth and nitrogen dynamics of reed canarygrass (*Phalaris arundinacea* L.) subjected to daily fertilisation and irrigation in the field. *Field Crops Research* 55:153–164
- Kätterer T, Bolinder MA, Andrén O, Kirchmann H, Menichetti L (2011) Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment. *Agric Ecosyst Environ* 141:184–192. <https://doi.org/10.1016/j.agee.2011.02.029>
- Lemaire G, Gastal F (1997) N uptake and distribution in plant canopies. In: Lemaire G (ed) *Diagnosis of the nitrogen status in crops*. Springer-Verlag, Berlin Heidelberg, pp 2–43
- Leyshon AJ (1991) Effect of rate of nitrogen fertilizer on the above- and below-ground biomass of irrigated bromegrass in southwest Saskatchewan. *Can J Plant Sci* 71:1057–1067
- McCarty HA (1978) Spectral distribution of solar radiation: II. Global and diffuse. *Q J R Meteorol Soc* 104:911–926
- McDonald AJS, Lohammer T, Ingestadt T (1992) Net assimilation rate and shoot area development in birch (*Betula pendula* Roth.) at different steady-state values of nutrition and photon flux density. *Trees* 6:1–6
- Menichetti L, Ekblad A, Kätterer T (2015) Contribution of roots and amendments to soil carbon accumulation within the soil profile in a long-term field experiment in Sweden. *Agric Ecosyst Environ* 200:79–87. <https://doi.org/10.1016/j.agee.2014.11.003>
- Murphy DV, Stockdale EA, Poulton PR, Willison TW, Goulding KWT (2007) Seasonal dynamics of carbon and nitrogen pools and fluxes under continuous arable and ley-arable rotations in a temperate environment. *Eur J Soil Sci* 58:1410–1424
- Paine CET, Marthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA (2012) How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods Ecol Evol* 3:245–256. <https://doi.org/10.1111/j.2041-210X.2011.00155.x>
- Pettersson R, Hansson A-C, Andrén O, Steen E (1986) Above- and below-ground production and nitrogen uptake in lucerne (*Medicago sativa*). *Swedish J Agric Res* 16:167–177
- Pietola L, Alakukku L (2005) Root growth dynamics and biomass input by Nordic annual field crops. *Agric Ecosyst Environ* 108:135–144. <https://doi.org/10.1016/j.agee.2005.01.009>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) nlme: linear and nonlinear mixed effects models. R package version 3.1-131. <https://CRAN.R-project.org/package=nlme>
- Poeplau C, Marstorp H, Thored K, Kätterer T (2016) Effect of grassland cutting frequency on soil carbon storage—a case study on public lawns in three Swedish cities. *Soil* 2:175–184. <https://doi.org/10.5194/soil-2-175-2016>
- Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83:553–559
- Rytter L, Ericsson T, Rytter R-M (2003) Effects of demand-driven fertilization on nutrient use, root: plant ratio and field performance of *Betula pendula* and *Picea abies*. *Scand J For Res* 18:401–415. <https://doi.org/10.1080/02827580310001931>
- Schlossberg MJ, Karnok KJ (2001) Root and shoot performance of three creeping bentgrass cultivars as affected by nitrogen fertility. *J Plant Nutr* 24(3):535–548
- Smolders E, Merckx R (1992) Growth and shoot: root partitioning of spinach plants as affected by nitrogen supply. *Plant Cell Environ* 5:795–807
- Smucker AJM, McBurney SL, Srivastava AK (1982) Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. *Agron J* 74:500–503. <https://doi.org/10.2134/agronj1982.00021962007400030023x>
- Statistics Sweden (2016) Improvements in agri-environmental and grassland statistics in Sweden. Final report. <https://ec.europa.eu/eurostat/web/agri-environmental-indicators/projects>
- Statistiska Centralbyrån (SCB) (2017) Yield per hectare and total production in regions/country for different crops. Yearly data 1965–2017. http://www.statistikdatabasen.scb.se/pxweb/en/ssd/START_JO_JO0601/SkordarL/?rxid=4b1ad056-4bcf-4797-a080-23cabefe4f1a, 21.06.2017
- Thornley JHM, Johnson RL (1990) *Plant and crop modelling. A mathematical approach to plant and crop physiology*. Oxford Science Publications, Oxford
- Troughton A (1957) The underground organs of herbage grasses. Bulletin no. 44. Commonwealth Bureau of Pastures and Field Crops. Hurlay, UK
- Walker A (2017) openxlsx: Read, Write and Edit XLSX Files. R package version 4.0.17. <https://CRAN.R-project.org/package=openxlsx>
- Walley FL, Tomm GO, Matus A, Slinkard AE, van Kessel C (1996) Allocation and cycling of nitrogen in an alfalfa-bromegrass sward. *Agron J* 88:834–843
- Wallgren B, Nilsson-Linde N, Svanäng K, Halling M, Magnét B (1995) Vallväxter och grönfoderväxter. Sveriges Lantbruksuniversitet, Uppsala, Speciella skrifter 61
- Weaver JE, Zink E (1946) Annual increase of underground materials in three range grasses. *Ecology* 27:115–127
- Welbank PJ, Taylor PJ, Williams ED (1974) Root growth of cereal crops. rothamsted experimental station report, 1973. Part 2:26–66
- Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer, New York. <http://ggplot2.org>

- Wickham H (2011) The split-apply-combine strategy for data analysis. *J Stat Softw* 40(1):1–29
- Wilke CO (2017) cowplot: streamlined plot theme and plot annotations for ‘ggplot2’. R package version 0.8.0. <https://CRAN.R-project.org/package=cowplot>
- Wilson JB (1988) A review of evidence on the control of shoot: root ratio, relation to models. *Ann Bot* 61(4):433–449
- Zabek LM, Prescott CE (2007) Steady-state nutrition of hybrid poplar grown from un-rooted cuttings-. *New For* 34:13–23. <https://doi.org/10.1007/s11056-006-9033-4>

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.