

The effects of prolonged exposure to elevated temperatures and elevated CO₂ levels on the growth, yield and dry matter partitioning of field-sown meadow fescue

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Field-sown meadow fescue (*Festuca pratensis*, cv. Kalevi) stands were exposed to elevated temperatures (+3°C) and elevated CO₂ (700 ppm) levels in two experiments conducted in 1992–1993 (experiment 1) and in 1994–1995 (experiment 2). Total aboveground yield was, on average, 38% higher at elevated than at ambient temperatures. At ambient temperatures elevated CO₂ increased the number of tillers by 63% in 1992, 24% in 1993, 90% in 1994 and 14% in 1995. At elevated temperatures, the increase in tiller number in elevated CO₂ was seen only in the first growing seasons after sowing. The total yield in a growing season was about 10% higher in elevated CO₂ in experiment 1. In experiment 2 the yield was more than 20% higher in elevated CO₂ at elevated temperatures, whereas at ambient temperatures the rise in CO₂ level had no effect on the yield; the root biomass, however, increased by more than 30%. In elevated CO₂ at ambient temperatures the root biomass also increased in experiment 1, but at elevated temperatures there was no consistent change. The soluble carbohydrate content of above-ground biomass was 5–48% higher in elevated CO₂ at most of the measuring times during the growing season, but the nitrogen content did not show a clear decrease. The reasons for the lack of a marked increase in biomass in elevated CO₂ despite a 40–60% increase in photosynthesis are discussed.

Key words: carbon dioxide, grass, *Festuca pratensis*, climate change, roots, carbohydrate, nitrogen

Introduction

The mean global atmospheric concentration of carbon dioxide (CO₂) has risen from about 270 ppm in pre-industrial times to almost 360 ppm in 1994 (IPCC 1996). This figure has been projected to increase to between about 485 and 850 ppm by 2100, the exact level depending largely

on future anthropogenic emissions of CO₂ into the atmosphere (Carter 1996). The increased CO₂ concentration is expected to enhance the photosynthetic capacity of C₃ plants, because the net photosynthesis is currently often limited by the less than optimal CO₂ concentration and by photorespiration (see reviews by e.g. Lawlor and Mitchell 1991 and Bowes 1993). Higher photosynthetic rates are expected to lead to an increase

in the dry matter production of C₃ plants, an effect that has already been observed in many experiments (Lawlor and Mitchell 1991, Bowes 1993).

Increases in photosynthesis are seldom translated into equivalent increases in crop yields, however, because of other constraining factors in the environment or genetic factors at plant level, which limit plant growth (Nijs et al. 1989, Lawlor and Mitchell 1991, Ryle et al. 1992, Bowes 1993, Gay and Hauck 1994). Alternatively, the extra photosynthate may be translocated to roots (Nijs et al. 1988, 1989, Bowes, 1993, Luo et al. 1994, Schenk et al. 1995) or extracted to the soil as carbohydrate (Diaz et al. 1993, Zak et al. 1993). A more extensive root system would be beneficial for grass and for cereal crops through the improvement in nutrient and water availability, and also as a carbohydrate storage for regrowth of grass during the first days after cuts (Nijs et al. 1988). Moreover, increased excretion of carbohydrate through roots to the soil might increase the microbial biomass of the soil, thus either improving (Zak et al. 1993) or diminishing nitrogen availability (Diaz et al. 1993), probably depending on the soil type and the chemical composition (the C:N ratio) of the litter being digested by the microbes.

Increases in concentrations of CO₂ along with changes in other atmospheric constituents are also known to affect the global climate. Recent projections for Finland indicate a mean annual warming of between 1.1 and 6.6°C by 2100, with a central estimate of 4.4°C (Carter 1996). Higher growing-season temperatures could be expected to enhance the yield of crops with continuous growth, such as grass, mainly through a lengthening of the growing season. Gains in yield might be especially great in the spring, when the light intensity is high but temperatures are now too low for crop growth.

The aim of the investigation described here was to evaluate, through direct experimentation, the impacts of future climate changes on the growth and yield of a grass crop, meadow fescue (*Festuca pratensis*). Although many experiments have been conducted to study the effects

of CO₂ on individual or several grass plants in pots (e.g. Nijs et al. 1988, 1989, Ryle et al. 1992, Baxter et al. 1994), few investigations have been made of the effects of both CO₂ and temperature on crop stands, especially under the long photoperiod conditions prevailing during the growing season at high latitudes. As the sward was sown directly on the field at normal sward density, the arrangement of the experiments simulated natural conditions closely with respect to canopy structure and intraspecific competition, and there was no pot size limitation for root growth, as may have been the case in many previous experiments (Arp 1991, Thomas and Strain 1991).

Material and methods

The experiments were carried out in southern Finland, Jokioinen (60°49'N, 23°30'E). Meadow fescue (*Festuca pratensis* Hudson) cv. Kalevi was grown according to the following four treatments: a) ambient air temperature and ambient CO₂ concentration; b) increased temperature (3°C above ambient) and ambient CO₂; c) ambient temperature and elevated CO₂ (700 ppm), and d) increased temperature and elevated CO₂. To maintain the experimental temperatures at a constant 3°C higher than the ambient temperatures, a greenhouse (20 m x 30 m) was built over an experimental field (Hakala et al. 1996). The experimental field outside the greenhouse, at ambient temperature, was covered at a height of 3–4 m with the same plastic film that was used in the construction of the greenhouse to achieve radiation conditions comparable to those in the greenhouse and to protect the area from rain. The temperatures in the open field under the film cover were recorded, and the greenhouse temperatures were regulated so that they were constantly 3°C higher than these. The mean temperatures during the day (from 6 a.m. to 6 p.m.) under the cover in the open field were from 1°C lower to 1.5°C higher than those in

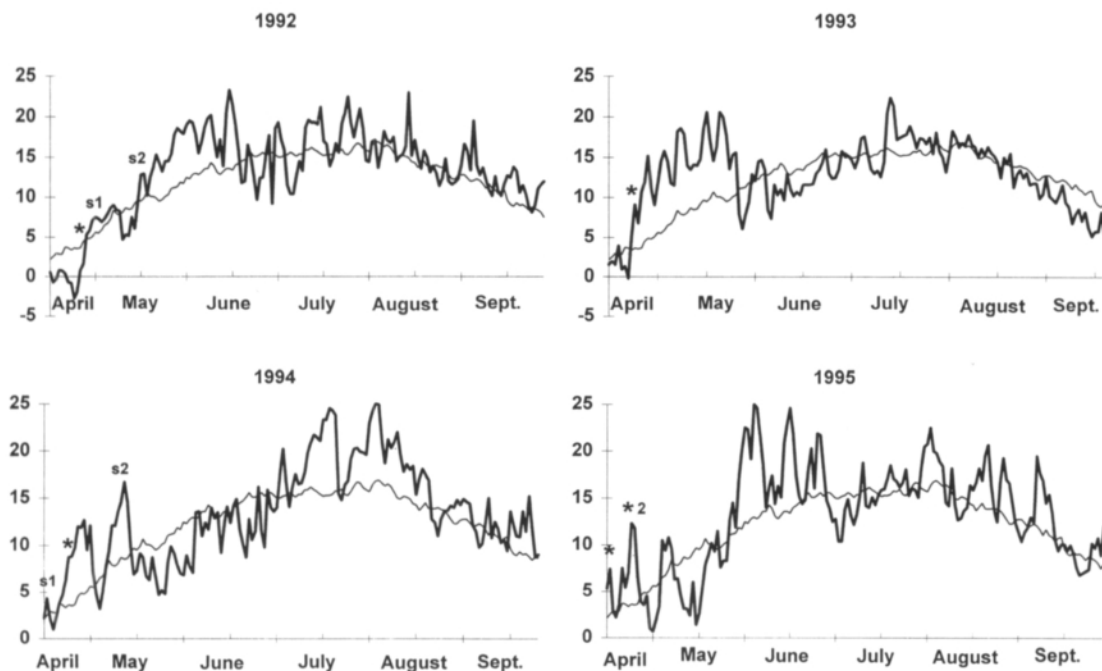


Fig. 1. Mean daily temperatures in the open field (heavy line) during 1992, 1993, 1994 and 1995 and the average temperatures at nearby Jokioinen Observatory during 1961–1990 (light line), for the period 15 April until the last cut of the grass in September (for exact dates of last cuts, see Table 1). The beginning of the thermal growing seasons is marked with * (for exact dates, see Table 1). s1 = sowing in the greenhouse, s2 = sowing in the open field. *2 = beginning of growing season in the open field in 1995. The temperatures inside the greenhouse were 3°C higher than those in the open field (see Hakala et al. 1996 for details).

the adjacent field without a cover (average temperature difference from 1 June to 31 August 0.0°C, standard deviation 0.62°C). The cover over the open field was removed during the winter to allow snow to protect the grass naturally from freezing temperatures. In the greenhouse the grass crop was covered with a light cloth for periods of extreme low temperatures in winter.

The CO₂ experiments were conducted in open-top chambers (OTCs) 3 m in diameter and 2 m high (Hakala et al. 1996). The OTCs were divided into two halves, the southern half being occupied by the meadow fescue stand, and the other half being used for experiments with spring wheat. Two experiments were conducted, each covering two growing seasons: those of the year of sowing and those of the following year, which is considered as the main yield producing sea-

son. Figure 1 shows the temperature regimes of the four growing seasons 1992–1995.

Experiment 1 was conducted on a heavy clay soil. Before the experiments the soil was mixed with 1000 m³/ha of peat containing 35% sand. The peat was limed and fertilized with a peat fertilizer containing 11% nitrogen, 11% phosphorus, 20% potassium, 6.2% sulphur, 1% copper, 0.6% sodium, 0.6% chloride, 0.5% iron, 0.4% manganese, 0.2% zinc, 0.1% molybdenum, 0.1% magnesium and 0.08% boron. The peat-sand mixture was mixed with the clay soil at a depth of 25–30 cm, after 500 kg/ha of a fertilizer containing 20% N, 4% P and 8% K had been added. The soil was treated similarly both in the greenhouse and in the open field. At the end of 1993, when experiment 1 was finished, the clay-peat soil of the experimental site was

Table 1. Beginning of thermal growing season (temperatures permanently over 5 °C) in 1992–1995, sowing density and sowing dates of meadow fescue stands in 1992 and 1994, and cutting dates in 1992–1995.

experiment/gr. season year	I/1st 1992		I/2nd 1993		II/1st 1994		II/2nd 1995				
treatment	amb. T amb. CO ₂ elev. CO ₂	elev. T amb. CO ₂ elev. CO ₂	amb. T amb. CO ₂ elev. CO ₂	elev. T amb. CO ₂ elev. CO ₂	amb. T amb. CO ₂ elev. CO ₂	elev. T amb. CO ₂ elev. CO ₂	amb. T amb. CO ₂ elev. CO ₂	amb. T amb. CO ₂ elev. CO ₂	elev. T amb. CO ₂ elev. CO ₂	elev. T amb. CO ₂ elev. CO ₂	elev. T amb. CO ₂ elev. CO ₂
soil	clay/peat	clay/peat	clay/peat	clay/peat	sandy loam	sandy loam	sandy loam	sandy loam	sandy loam	sandy loam	sandy loam
beginning of thermal growing season	27 April	25 April	22 April	22 April	22 April	19 April	20 April	20 April	15 April	15 April	
sowing density, germinating seeds/m ²	1250	1250			750	750					
sowing	14 May	29 April			9 May	15 April					
1. cut	9 July	15 June	1 June	18 May	29 July	17 June	6 June	6 June	22 May	22 May	
2. cut	14 Aug.	15 July	8 July	24 June	24 Aug.	18 July	12 July	3 July	15 June	16 June	
3. cut	24 Sept.	20 Aug.	16 Aug.	2 Aug.	21 Sept.	15 Aug.	14 Aug.	24 July	3 July	10 July	
4. cut		22 Sept.	15 Sept.	13 Sept.		12 Sept.	20 Sept.	14 Aug.	19 July	27 July	
5. cut								18 Sept.	14 Aug.	6 Sept.	
6. cut									11 Sept.		

replaced with a lighter sandy loam soil brought to the experimental plots from another field in Jokioinen, and the drainage of the soil was improved by placing new drainage pipes under the soil at a depth of about 40 cm. Because nutrient analysis of the soil showed a deficiency in Ca and Mg, the soil was limed with 8000 kg/ha of a fertilizer containing 35% calcium and 3% magnesium. Before sowing began, 500 kg/ha (greenhouse) or 550 kg/ha (open field) of a fertilizer containing 20% N, 6% P and 6% K was added to the soil surface. With the different fertilization rates, the nitrogen levels inside the greenhouse and in the open field were adjusted to about 120 kg N/ha.

The experimental plots were sown directly on the field at 1250 germinating seeds/m² in 1992 (experiment 1) and 750 germinating seeds/m² in 1994 (experiment 2), row width 12.5 cm. Inside the greenhouse, at elevated temperatures, sowing was completed shortly after the thermal

growing season had started, i.e. when the temperature could be expected to stay constantly above 5°C. The sowing dates inside the greenhouse were thus 29 April in 1992 and 14 April in 1994. In the open field there was a delay in sowing, due partly to the later onset of the thermal growing season and partly to the need for the soil to dry sufficiently for sowing. Sowing thus proceeded some 2–3 weeks later in the outside field than in the greenhouse (14 May in 1992 and 9 May in 1994, Table 1).

After emergence, the seedlings were enclosed in OTCs: four in the greenhouse and four in the open field. Two of the four OTCs were maintained at elevated CO₂ levels and the other two at ambient levels, giving two independent replicates per treatment (Hakala et al. 1996). The CO₂ levels in the high-CO₂ OTCs were not elevated during the winter, but the CO₂ treatments of the grass were started in April, as soon as the growing season began. Irrigation was applied using

drip-irrigation in experiment 1 and manually in experiment 2, to ensure that soil moisture levels would not limit growth. Fertilizer was administered both in the open field and in the greenhouse at such a rate that the N level of the soil was 120 kg before sowing and in the spring. Thereafter in the first growing seasons the grass was fertilized with 80 kg N after the first cut and with 60 kg N after the second cut both in the open field and in the greenhouse, and with 60 kg N after the third cut but only in the greenhouse. In the second growing seasons the grass was fertilized with 80 kg N after the first cut and 40 kg N after the second and third cuts both in the open field and in the greenhouse. The fertilizer used contained 20% N, 6% P, 6% K, 5% Ca, 2.1% S, 0.5% Mg, 0.03% B, 0.1% Fe, 0.1% Na and 0.016% Se. Pest and disease control were applied when needed.

In 1992–1994, meadow fescue was cut at approximately monthly intervals (Table 1). During the second growing seasons it was cut for the first time shortly after it began to flower. This occurred in both experiments 2 weeks earlier at elevated temperatures than at ambient temperatures (Table 1). In 1995, following the first cut at the beginning of flowering, the grass was always cut after the leaf area index (LAI) of a stand had reached a value of 5, as measured with an automatic LAI meter (Licor, USA). This resulted in a different number of cuts in each treatment (Table 1). Biomass samples were collected during the cuts from 10 randomly chosen sampling plots in each of the chambers, each sampling plot comprising 15 cm of planted row. For biomass, nitrogen and yield determinations, the samples were oven-dried (2 hours at 100 °C, then overnight at 60 °C). The samples for soluble carbohydrate measurements were freeze-dried and stored at -20 °C before analysis.

Root samples were taken at a depth of 20 cm during the first and second cuts in the first growing season of experiment 1 (1992), and during the last cuts in the other growing seasons (1993–1995). The sample size was 15 cm of row, and both tiller number and root biomass were determined from the samples.

The nitrogen content of the above-ground biomass was determined in 1992 with the Kjeldahl method with a Kjeltac System 1026 Distilling Unit (Tecator AB, Sweden), and with $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ as the catalyst. For details of the procedure, see manual of the Kjeltac System 1026 Distilling Unit. In 1993, the nitrogen levels were not measured because insufficient resources were available for the laborious Kjeldahl procedure. In 1994–1995, the nitrogen content was determined with an automatic nitrogen analyser, LECO FP-428 (LECO corp., USA). For the soluble carbohydrate analysis, the plant samples were first inverted overnight at +50 °C in 0.1 N HCl. They were then filtered, and the filtrate was mixed with ion-exchangers, shaken for one hour and refiltered; 2-ml samples of this filtrate were then used for the analysis of soluble sugars (glucose, fructose, saccharose and fructosans). The analysis was performed photometrically (Schimadzu, Japan, 540 nm), according to the method of Nelson (1944) and Somogyi (1945), but modified in such a manner that after the addition of copper reagent the test tubes were filled with distilled water to 7 ml before the arsenomolybdate reagent was added.

To give an idea of the variation between samples, standard errors of the mean were calculated over all the samples taken from each treatment at each sampling time. The "n" in the tables and figures refers to the total number of samples of both replicates.

Results

Number of tillers and yield

The number of tillers was counted in connection with the first and second cuts in the first growing season of experiment 1 (1992) and in connection with the last cuts in all the other growing seasons (1993–1995). The number of tillers/15 cm of row was 1.7–2.7 times higher (depending on the treatment) in the first grow-

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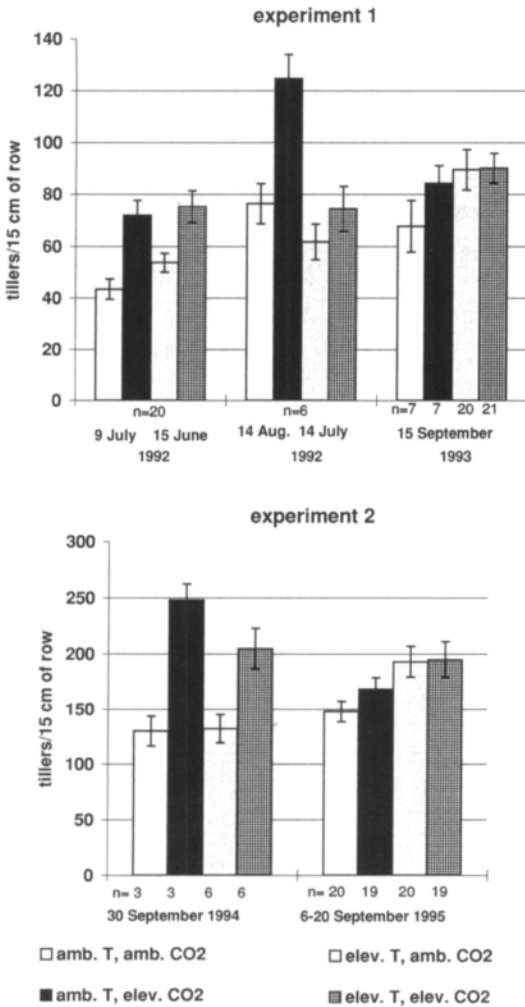


Fig. 2. Tiller number/15 cm of planted row in meadow fescue from the first and second cuts of the first growing season (1992) and the last cut of the second growing season (1993) of experiment 1 (top) and from the last cuts of the two growing seasons of experiment 2 (1994–1995) (bottom). n is the number of 15-cm samples.

ing season and 2.0–2.2 times higher in the second growing season of experiment 2 than in the first and second growing seasons of experiment 1 (Fig. 2). There was no consistent effect of the temperature treatment on the tiller number of meadow fescue, but the increase in CO₂ concentration increased the tiller number by 63% and 90% at ambient temperatures and 20% and 55%

at elevated temperatures during the first growing seasons of experiments 1 and 2, respectively (counted on 14 July–14 August 1992 and 30 September 1994) (Fig. 2). The tiller number also increased in elevated CO₂ during the second growing seasons of experiments 1 and 2 at ambient temperatures (by 24% and 14%, respectively), but no increases were recorded at elevated temperatures (Fig. 2).

The total above-ground yield (cumulative agricultural yield of the growing season, excluding stubble biomass) of meadow fescue was 32% (experiment 1) and 41% (experiment 2) higher at elevated temperatures in ambient CO₂ than at ambient temperatures and ambient CO₂ in the first growing seasons (Fig. 3). During the second growing season of experiment 1, when there were four cuts both inside the greenhouse and in the open field, the yield was 15% higher in the greenhouse in ambient CO₂ than in the open field. As the crop was cut whenever it attained a LAI of 5 during the second growing season of experiment 2, there were six cuts inside the greenhouse in ambient CO₂, and four cuts on the equivalent plots in the open field, and the total above-ground yield of the plots inside the greenhouse was 65% higher than in the open field (Fig. 3).

The total yield in a growing season was about 10% higher in elevated than in ambient CO₂ at both ambient and elevated temperatures in the first growing season of experiment 1. In the second growing season, the total yield was still 10% higher in elevated CO₂ at elevated temperatures, but there was no difference in total cumulative yield at ambient temperatures (Fig. 3). In experiment 2 the yield of meadow fescue was 29% (first growing season) and 22% (second growing season) higher in elevated than in ambient CO₂ at elevated temperatures, but more or less the same in both CO₂ treatments at ambient temperatures (Fig. 3).

In experiment 1, at elevated temperatures, the increase in the total yield in elevated CO₂ was achieved before the first cut, after which CO₂ enrichment had no effect on growth rate (Fig. 3). At ambient temperatures, an increase in yield in

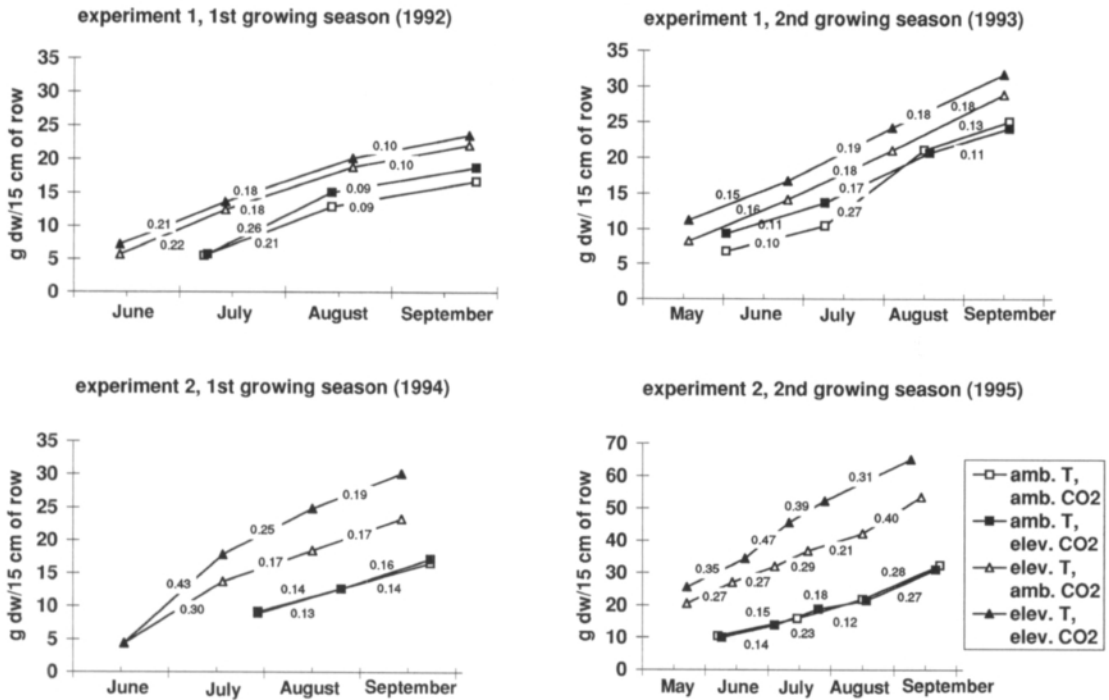


Fig. 3. Cumulative yield (g dry weight of above-ground biomass/15 cm of planted row) during the growing seasons of experiment 1 (1992–1993) and experiment 2 (1994–1995). The numbers on the lines represent the daily growth rate of the grass during the period between cuts. The number of samples (n) was 17–20 in all cuts except at ambient temperatures in 1993, when it was 7, and at ambient temperatures in 1995, when it was 14. The standard error of the mean of the biomass samples at different cuts was in general around or less than 10% of the mean, but in 1993, at ambient temperatures, it averaged 19% of the mean.

elevated CO₂ also occurred early in the growing season, i.e. between the first and the second cuts during the first growing season and before the first cut during the second growing season. During the second growing season, however, the growth rate in ambient CO₂ increased markedly relative to that in elevated CO₂ after the second cut, resulting in an equal total yield in both CO₂ treatments. In experiment 2, at elevated temperatures, the favourable effect of CO₂ enrichment on growth rate was evident until late in the season (August), after which the effect was slight (first growing season) or negative (second growing season). At ambient temperatures the growth rate was more or less the same in both ambient and elevated CO₂ (Fig. 3).

Root biomass

Root biomass was measured both in the open field and in the greenhouse at the end of the 1993–1995 growing seasons, and during the second cut in 1992 (Fig. 4). Root biomass increased markedly towards the end of both experiments. It was approximately the same in ambient CO₂ treatments both at ambient and at elevated temperatures except in the second growing season of experiment 1, when the root dry weight was higher at ambient temperatures (Fig. 4).

At ambient temperatures, the root dry weight was 67% (first growing season) and 38% (second growing season) higher in elevated CO₂ in experiment 1 and over 30% higher in experiment

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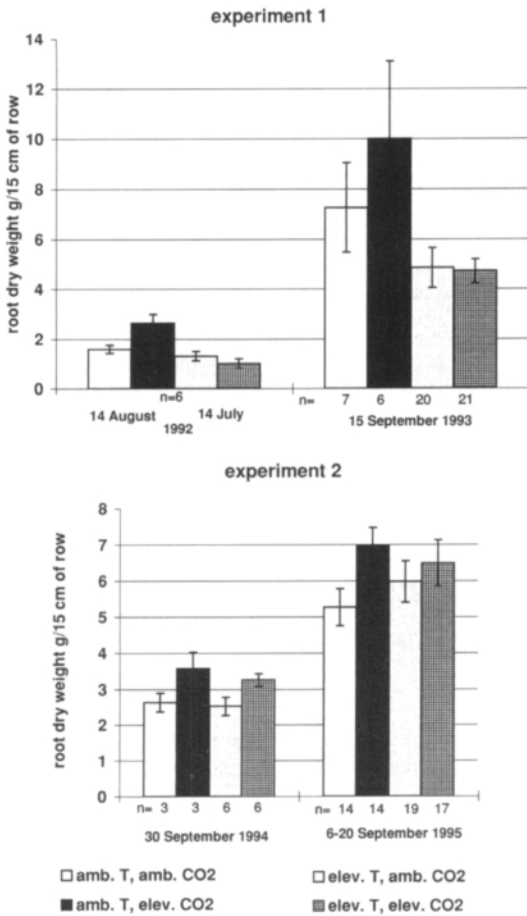


Fig. 4. Root weight/15 cm of planted row in experiment 1 and experiment 2. n is the number of 15-cm samples.

2 (Fig. 4). At elevated temperatures, the rise in CO₂ did not increase root weight in experiment 1; in experiment 2, however, it increased root weight by 29% (first growing season) and 8% (second growing season) (Fig. 4).

Nitrogen content of above-ground biomass

The nitrogen content of meadow fescue above-ground biomass ranged from 2% to 5% of dry

weight, being generally higher in experiment 2 than in experiment 1 (Table 2), possibly because of the different soil types. The nitrogen content was 5–22% higher in elevated CO₂ than in ambient CO₂ in experiment 1 (measured only in the first growing season) at both temperatures. In experiment 2 the nitrogen content of the above-ground biomass of the grass was 2–17% higher in elevated CO₂ than in ambient CO₂ at ambient temperatures, and 3–12% lower at elevated temperatures (Table 2).

Soluble carbohydrate content of shoots and roots

The soluble carbohydrate content of meadow fescue above-ground biomass was 5–48% higher in elevated than in ambient CO₂ most of the measuring times during summer, but there was no effect of elevated CO₂ on the carbohydrate content in the autumn (Table 3). The effect of the elevation of CO₂ levels on the carbohydrate content of the roots was inconsistent: in the first growing season of experiment 2 the carbohydrate content of the roots was lower in elevated CO₂ at both temperatures, but in the second growing season it was the same at ambient temperatures and higher at elevated temperatures in elevated CO₂ (Table 3).

Discussion

The total cumulative agricultural yield of meadow fescue, cv. Kalevi during the growing season was high compared to the long-term average (1988–1995) of the official variety trials of the same cultivar from the same area (Järvi et al. 1996). The yield of the stands at ambient temperatures and ambient CO₂ levels was already 10% higher in the years of sowing (1992 and 1994) than the long-term average for cv. Kalevi achieved in variety trials in the same agricultural area. In the year after sowing, the yield was

Table 2. Nitrogen content (% of dry weight) of meadow fescue above-ground biomass in 1992 (experiment 1, first growing season) and in 1994–1995 (experiment 2). n is the number of 15-cm sampling plots.

date	amb. T, amb. CO ₂	amb. T, elev. CO ₂	date	elev. T, amb. CO ₂	elev. T, elev. CO ₂
experiment 1					
1992			1992		
9 July	1.88 (±0.10) n=20	2.29 (±0.13) n=17	15 June	2.75 (±0.14) n=20	3.31 (±0.09) n=20
14 Aug.	2.68 (±0.10) n=17	2.83 (±0.13) n=15	15 July	2.10 (±0.15) n=16	2.40 (±0.11) n=16
24 Sept.	3.15 (±0.19) n=17	3.34 (±0.14) n=18	20 Aug.	2.67 (±0.08) n=20	3.18 (±0.10) n=20
			22 Sept.	3.65 (±0.14) n=19	4.21 (±0.10) n=22
experiment 2					
1994			1995		
29 July	3.32 (±0.08) n=20	3.38 (±0.10) n=20	17 June	4.47 (±0.10) n=20	4.06 (±0.15) n=20
24 Aug.	4.82 (±0.11) n=20	5.23 (±0.10) n=20	18 July	4.10 (±0.06) n=21	3.97 (±0.08) n=20
21 Sept.	5.06 (±0.10) n=20	5.34 (±0.05) n=17	15 Aug.	4.56 (±0.06) n=20	4.38 (±0.07) n=20
			12 Sept.	4.93 (±0.09) n=20	5.04 (±0.07) n=20
6 June	3.41 (±0.11) n=19	6 June 3.46 (±0.12) n=20	22 May	3.26 (±0.12) n=20	22 May 3.19 (±0.15) n=21
12 July	4.09 (±0.12) n=20	3 July 4.78 (±0.09) n=20	15 June	4.61 (±0.07) n=20	16 June 4.42 (±0.10) n=21
14 Aug.	3.62 (±0.09) n=19	24 July 4.13 (±0.12) n=20	3 July	5.12 (±0.06) n=20	10 July 4.50 (±0.06) n=21
20 Sept.	2.39 (±0.10) n=20	18 Sept. 2.12 (±0.04) n=19	11 Sept.	2.57 (±0.13) n=20	6 Sept. 2.68 (±0.07) n=19

from 63% (in 1993) to 105% (in 1995) higher than the average yield of the grass in the variety trials.

The total above-ground yield of meadow fescue was higher at elevated than at ambient tem-

peratures in all the growing seasons studied. In the first growing seasons, the higher total yields at elevated temperatures were partly due to the longer growing period, since the grass was sown 2–3 weeks earlier in the greenhouse than in the

Table 3. Soluble carbohydrate content (% of dry weight) of meadow fescue above-ground (shoots) and below-ground (roots) biomass in 1992–1995. n is the number of 15-cm sampling plots.

date	amb. T, amb. CO ₂	amb. T, elev. CO ₂	date	elev. T, amb. CO ₂	elev. T, elev. CO ₂
<i>shoots</i>					
experiment 1					
9.7.1992	15.4 (±1.2) n=5	21.2 (±1.7) n=4	15.6.1992	9.9 (±0.6) n=11	11.6 (±1.0) n=10
8.7.1993	8.2 (±1.05) n=3	12.1 (±0.9) n=3	5.8.1993	8.2 (±0.2) n=2	9.4 n=1
15.9.1993	17.9 (±1.1) n=5	16.5 (±1.0) n=3	10.9.1993	13.6 (±1.0) n=10	12.7 (±1.3) n=9
experiment 2					
29.7.1994	10.6 (±1.2) n=2	13.5 (±0.5) n=2	18.7.1994	7.2 (±0.4) n=6	9.5 (±0.4) n=6
25.8.1994	13.6 (±0.1) n=2	12.7 (±1.6) n=2	25.8.1994	11.3 (±0.1) n=2	11.9 (±0.6) n=2
21.9.1994	9.4 (±0.5) n=3	9.1 (±1.1) n=3	12.9.1994	9.3 (±0.2) n=6	9.6 (±0.8) n=6
6.6.1995	5.1 (±0.2) n=6	4.4 (±0.2) n=6	22.5.1995	6.1 (±0.5) n=6	7.8 (±0.8) n=6
<i>roots</i>					
experiment 2					
21.9.1994	11.9 (±0.5) n=3	9.9 (±1.4) n=3	12.9.1994	10.1 (±0.6) n=6	8.7 (±0.6) n=5
20.9.1995	15.0 (±0.5) n=20	15.6 (±0.6) n=19	11.9.1995	5.9 (±0.6) n=20	7.5 (±0.6) n=19

open field, but higher growth rates at elevated temperatures also contributed to the increase in yield, especially in 1994 (Fig. 3). In the second growing season of experiment 1, the yield in the greenhouse was only 15% higher than that in the open field. Because the grass was not cut according to LAI, but at about monthly intervals during the second growing season of experiment 1, the small difference between yields in the open field and inside the greenhouse may have been caused by stronger self-shading and, consequently, a lower growth rate of the grass in the greenhouse. When the crop was cut each time it attained a LAI of 5 (in 1995), the total yield in the greenhouse was about twice that in 1993, and the growth rate between the cuts was clearly higher than in 1993, resulting in 65% higher yields than at ambient temperatures.

Although favourable, the effect of CO₂ on the yield of meadow fescue was less favourable than expected. Earlier investigations and reviews have reported increases in plant biomass of between 20% and 209% at CO₂ levels double those of the ambient level (Lawlor and Mitchell 1991, Bowes 1993). Even though the photosynthetic rate of meadow fescue in the present experiment was 40–60% higher in elevated than in ambient CO₂ at both ambient and elevated temperatures (Heliö et al. 1995), the increase in photosynthesis was not translated into an equal increase in biomass. Similar results have been reported previously with grasses, and the lack of a greater effect of elevated CO₂ on the yield has been attributed to low sink strength due to limited tiller formation capacity (Ryle et al. 1992, Gay and Hauck 1994, Schenk et al. 1995).

After experiment 1, control of CO₂ levels in the CO₂-enriched OTCs was improved; the clay-peat soil was replaced with sandy loam, a soil with good moisture properties, and the drainage of the soil was improved. Moreover, the sowing rate was lowered from 1250 to 750 germinating seeds/m², and cuts were adjusted to take place according to the LAI of the grass (in 1995). These changes were made to promote the effect of CO₂ on the tiller number and yield, as it is known that tiller development and yield are en-

hanced in soils with good nutrient availability, and when the light penetration into the canopy is improved (by lowering the sowing rate and by more frequent cuts) (Williams 1982). The tiller number/sample increased markedly in all treatments after these changes were made, and the effect of elevated CO₂ on the number of tillers was greater in the first growing season of experiment 2 than in the first growing season of experiment 1. However, in the course of experiment 2, just as in experiment 1, the effect of elevated CO₂ on the tiller number declined, being even smaller at the end of experiment 2 than at the end of experiment 1.

Because the tiller number was approximately 2–3 times higher in each treatment during experiment 2 than during experiment 1, there should have been enough room for the tillers to develop. Thus canopy closure cannot explain the lack of effect of elevated CO₂ on the tiller number at elevated temperatures in the second growing season of experiment 1. In the second growing season of experiment 2, in contrast, canopy closure may have been responsible for the decline in the effect of CO₂ on tiller development.

Even when the tiller number was greater in elevated than in ambient CO₂ (Fig. 2), the total yield per cut did not necessarily increase (Fig. 3). The failure to produce higher yields in elevated CO₂, even if the tiller number increases, has been observed with *Phleum pratense* and *Lolium perenne* (Saebo and Mortensen 1995), *Agrostis capillaris*, *Dactylis glomerata* and *Festuca pratensis* (Saebo and Mortensen 1996) and has been attributed to the lower dry weight of individual tillers, due at least partly to reduced plant height. At elevated temperatures, the tiller number was the same in the CO₂ treatments at the end of the second growing seasons in both experiments, even if the yield was higher in elevated CO₂ (Figs 2 and 3). As the tiller number was counted only at the end of the second growing seasons, the gain in biomass may have been due to an increase in the tiller number earlier in the season, as suggested by the increase in the yield in elevated CO₂ that took place early in

the season (before the first cut) in 1993, and by the reduced daily growth rate in elevated CO₂ relative to that in ambient CO₂ late in the season in 1995.

Closure of the plant canopy leads to poorer light penetration and hence lower biomass production than expected on the basis of higher assimilation rates in elevated CO₂ measured at saturating light (Du Cloux et al. 1987, Nijs et al. 1989, Schenk et al. 1995). When the grass was cut during the second growing season of experiment 2 (1995) according to the LAI of the individual replicates, canopy self-shading was reduced and made more or less similar in all treatments. The higher yields both in the open field (29% greater) and in the greenhouse (85% greater) in ambient CO₂ in 1995 than in 1993 (the second growing season of experiment 1) (Fig. 3) may have been partly due to reduced self-shading and better use of light for photosynthesis and growth at canopy level, although the effects of different soil type and different climatic conditions should not be discounted. Nevertheless, even with conditions apparently favouring a positive effect of enriched CO₂ on yield in experiment 2, such an effect was still only observed in the greenhouse.

In cases when the above-ground biomass does not increase in proportion to the increase in photosynthesis, there have been reports of the extra photosynthate being translocated to the roots (Nijs et al. 1988, Luo et al. 1994, Schenk et al. 1995) or to the stubble (Saebo and Mortensen 1995). There was evidence of this occurring here, too, as the root fraction increased in elevated CO₂ even though the elevation of CO₂ had no effect on the above-ground biomass at ambient temperatures in experiment 2 (Figs 3 and 4). As there was no decrease in the nitrogen content in the shoots of meadow fescue at ambient temperatures in either experiment 1 or 2, it is improbable that the root fraction would have increased mainly to make more of the nitrogen and other nutrients available for the plant, as proposed in another study on grass swards (Schenk et al. 1995), but the response seems to be rather a way of translocating extra photosyn-

thate to roots when the above-ground biomass cannot use it efficiently enough (Luo et al. 1994). Even if the yield of the grass did not increase at ambient temperatures in elevated CO₂ in experiment 2, the increase in root biomass could have been beneficial for grass growth during drought or if nutrients had become scarce, and could also have served as a bigger carbohydrate reserve for the grass to help it survive the winter better.

Accumulation of carbohydrate in the leaves and/or an increase in the number of mesophyll cell layers have been interpreted as another sign of the reduced sink strength (Ryle et al. 1992, Bowes 1993, Baxter et al. 1994, Luo et al. 1994) often associated with a decrease in the nitrogen content of the leaves (Campbell et al. 1988, Ryle et al. 1992, Bowes 1993, Luo et al. 1994, Schenk et al. 1995). The decrease in the nitrogen level in the leaves has been explained, at least partly, by dilution of nitrogen with the carbohydrates (Campbell et al. 1988, Luo et al. 1994) or by translocation of the nitrogen from rubisco and photorespiratory enzymes to other proteins more limiting to photosynthesis, or to other parts of the plant to increase the sink strength in elevated CO₂ (Hocking and Meyer 1991, Stitt 1991, Conroy and Hocking 1993). The carbohydrate content of the leaves was not measured separately here, but that of the total above-ground biomass was higher in elevated CO₂ at both ambient and elevated temperatures at most of the measuring times during summer (Table 3).

According to the official variety trials conducted in 1988–1995, the average protein content of the above-ground biomass of meadow fescue cv. Kalevi is 15%, or 2.3% N of dry weight (Järvi et al. 1996). The nitrogen levels in meadow fescue in the present experiments were thus approximately average or slightly above average in 1992, and clearly above average in 1994–1995. Despite the increase in the carbohydrate content of the above-ground biomass in elevated CO₂, the nitrogen content of the above-ground biomass was not reduced in elevated CO₂, except for a slight decrease at elevated temperatures in experiment 2. Rather, there seemed to be an increase in the uptake of nitrogen in ele-

vated CO₂ at ambient temperatures in all the years that nitrogen content was studied, and at elevated temperatures in experiment 1 (in 1992).

It has been noted that the effect of elevated CO₂ on photosynthesis is lower at low light intensity (Gay and Hauck 1994) and may even be reduced relative to that in ambient CO₂ (Nijs et al. 1989). Lowered photosynthesis rates at low light intensities, e.g. inside the grass canopy or on cloudy days, would not have been detected here, because the measurements reported by Heliö et al. (1995) were always performed at saturating light intensity. The measurements were also usually conducted in the morning or early afternoon; thus any late-afternoon decreases in the photosynthetic rate (expected to take place because of sink size limitation and the consequent accumulation of photosynthetic products in the leaves) would not have been detected (Nijs et al. 1989). It is possible that the relatively minor effect of CO₂ on the yield of meadow fescue, especially at ambient temperatures, was partly due to lower photosynthetic activity of meadow fescue in elevated than in ambient CO₂ at non-saturating light intensities and/or during

the late afternoon if both the sink capacity and the capacity of the leaves to store carbohydrate were restricted. The increases in the dry weight of the root fraction at ambient temperatures without any increase in the above-ground biomass also suggests the restricted sink capacity of the above-ground biomass (Luo et al. 1994). Evidence further exists for significantly higher dark respiration rates in elevated CO₂, causing a large part of the CO₂ assimilated during the day to be released during the night (Nijs et al. 1989, Wolfenden and Diggle 1995). This possible mechanism suppressing biomass increases in enriched CO₂ remains to be investigated. Diurnal changes in the photosynthetic activity of meadow fescue in elevated and ambient CO₂ concentrations will also be the subject of future experiments.

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SELOSTUS

Kohotetun lämpötilan ja kohotetun CO₂-pitoisuuden vaikutukset peltoon kylvetyⁿ nurminadan kasvuun, satoon ja kuiva-aineen jakautumiseen

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Peltoon kylvettyä nurminataa (lajike Kalevi) kasvatettiin normaalissa ja kohotetussa (+3 °C) lämpötilassa ja normaalissa ja kohotetussa CO₂-pitoisuudessa kahdessa kahden vuoden mittaisessa kokeessa vuosina 1992–1993 (koe 1) ja 1994–1995 (koe 2). Kasvatus kohotetussa lämpötilassa lisäsi nurminadan kokonaissatoa keskimäärin 38 % normaalissa lämpötilassa kasvatettuun verrattuna. Kohotettu CO₂-pitoisuus lisäsi normaalissa lämpötilassa nurminadan versojen määrää 63 %, 24 %, 90 % ja 14 % vuosina 1992–1995. Kohotetussa lämpötilassa kohotetun CO₂-pitoisuuden vaikutus versomäärään näkyi vain ensimmäisten kasvukausien aikana molemmissa kokeissa. Nurminadan kokonaissato nousi 10 % kohotetussa CO₂-pitoisuudessa kokeessa 1. Kokeessa 2 sadot nou-

sivat CO₂-käsittelyn vaikutuksesta yli 20 % kohotetussa lämpötilassa. Normaalissa lämpötilassa CO₂-käsittelyllä ei ollut vaikutusta nurminadan satoon, mutta juuriston paino lisääntyi yli 30 %. Juuriston paino nousi normaalissa lämpötilassa CO₂-käsittelyssä myös kokeessa 1, mutta kohotetussa lämpötilassa CO₂-käsittelyllä ei ollut selvää vaikutusta juuriston biomassaan. Liukoisen hiilihydraatin määrä nurminadan maanpäällisessä osassa oli useimmilla mittauskerroilla kasvukauden aikana 5–48 % suurempi kohotetussa CO₂:ssa, mutta typen määrä ei laskenut. Syitä siihen, miksi CO₂-käsittely vaikuttaa vain vähän biomassaan, vaikka saman kokeen yhteydessä on aikaisemmin todettu fotosynteesin nousevan 40–60 %, pohditaan.