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Changes in forage quality of an upland permanent grassland under climate change including a summer extreme drought combined with a heat wave

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Abstract. An experiment was conducted to predict the response of an upland permanent grassland to future climate change including a summer extreme event. Treatments combined current and future atmospheric CO_2 concentrations (380 and 520 ppm, respectively) with or without an extreme event consisting of a two-week heat wave (+6°C) associated with severe drought during the three summer months, followed by a recovery period in autumn. During the experiment, air temperature was regulated 2°C above the current temperature for all four treatments. Forage quality was measured four times: once in spring the year before the extreme climatic event, twice in spring just before the extreme event, and once in autumn when plants have been rehydrated after the event. Elevated CO_2 resulted in a decrease in plant nitrogen (N) and cell wall contents (NDF), while the extreme event increased N and decreased NDF. Changes in plant chemical composition impacted rumen fermentation as the extreme event consistently increased *in vitro* dry matter digestibility. Extreme climatic events may thus be most likely to modify plant tissue chemistry and improve forage quality than changes in atmospheric CO_2 concentration.

Keywords. Climate change – Grassland – Forage quality – *In vitro* rumen fermentation.

Changements de la qualité fourragère d'une prairie permanente de moyenne montagne sous l'effet du changement climatique incluant une sécheresse estivale extrême combinée à une canicule

Résumé. *Une expérimentation a été conduite pour évaluer la réponse d'une prairie permanente de moyenne montagne au changement climatique avec ou sans évènement extrême. Quatre traitements ont été appliqués : deux niveaux de concentrations de CO_2 atmosphérique (actuelle et future, soit 380 et 520 ppm, respectivement) avec ou sans un évènement extrême estival consistant en une vague de chaleur de deux semaines (+ 6°C) associée à une sécheresse sévère de trois mois, suivie d'une période de récupération en automne. Pour tous les traitements, la température était régulée 2°C au-dessus de la température actuelle. La qualité du fourrage a été mesurée quatre fois : une fois au printemps l'année précédant l'évènement extrême, deux fois au printemps juste avant l'évènement, et une fois en automne après réhydratation des plantes. L'augmentation de la concentration en CO_2 atmosphérique a diminué la teneur en azote et en constituants pariétaux (NDF) des plantes, tandis que l'évènement extrême augmentait la teneur en azote du couvert et diminuait sa teneur en NDF. Ces modifications de composition chimique ont impacté les fermentations ruminales* in vitro *avec une augmentation de la digestibilité de la matière sèche en réponse à l'évènement extrême. Ces résultats suggèrent que les évènements extrêmes pourraient avoir plus d'effet que la concentration de CO_2 atmosphérique sur la valeur des fourrages.*

Mots-clés. *Changement climatique – Prairie – Qualité fourragère – Fermentation ruminale* in vitro.

I – Introduction

There is increasing evidence that climate change due to human activities is expected to result in warmer temperatures, elevated atmospheric CO_2, changes of rainfall patterns, and increased frequency of extreme climatic events (Seneviratne *et al*., 2012). The botanical and ecophysiological changes in plants in response to climate change can affect the chemical composition of forages and their digestive use by domestic herbivores.

The objective of this study was to measure changes in forage chemical composition and *in vitro* rumen fermentation parameters when an upland grassland was exposed to elevated atmospheric CO_2 concentration combined with a summer extreme event in semi-controlled conditions.

II – Materials and methods

In May 2010, monoliths of a permanent grassland were extracted from a site located at Saint Genès-Champanelle in the upland area of central France (45°43'N, 03°01'E, 800 m a.s.l.) and transferred into the Ecotron (Montferrier-sur-Lez, 43°40'N, 03°52'E, 90 m a.s.l., France), a large infrastructure dedicated to the simulation of climatic changes. Twelve macrocosms were allocated to four treatments: current and 2050-atmospheric CO_2 concentrations, 380 and 520 ppm, respectively, combined with an extreme event consisting of a two-week heat wave (+6°C) associated with a severe drought during the three summer months of 2011 (including two weeks of water withheld). After the extreme event, plants were rehydrated to assess their recovery in autumn. In all treatments, air temperature of the macrocosms was regulated 2°C above the current temperature of the upland site.

Samples were collected four times to assess the forage quality: once in May 2010, just before monoliths entered into the macrocosms, in April 2011 and June 2011 just before the extreme event, and once in November 2011 when plants have been rehydrated after the event. Representative samples of plants were taken in each macrocosm, and subsamples were either oven-dried at 60°C for 72h or freeze dried. Nitrogen (N), Neutral Detergent Fiber (NDF), total water-soluble carbohydrates (WSC), as well as glucose, sucrose, fructose and fructans of forage were analysed. To assess the digestive use of forage by ruminants, an *in vitro* rumen fermentation assay was carried out. Freeze-dried plants were ground to pass through a 1 mm sieve and incubated in anaerobic conditions at 39°C during 24h in culture bottles containing 40 mL of buffered rumen juice from sheep (Niderkorn *et al*., 2011). At the end of the incubation period, acidification (dpH), total gas production and composition including methane (CH_4), *in vitro* dry matter digestibility (IVDMD) and concentration of volatile fatty acids (VFA) were measured. Values were adjusted by subtracting at each collection point the values from blanks without plant substrate.

Data were submitted to analysis of variance using the mixed procedure of the SAS software package (version 9, SAS Institute Inc., Cary, NC, USA) with CO_2, extreme event and sampling date as fixed effects, and the macrocosm considered as random effect. Data from the first sampling date in May 2010 were used as a covariate, and the first order autoregressive covariate structure was used for the repeated term. All non-significant interactions were removed from the model.

III – Results and discussion

Increasing atmospheric CO_2 concentration decreased forage N content by 13% ($P<0.001$) and its NDF content by 3% ($P<0.05$) (Tables 1 and 2). The change in availability of N under elevated CO_2 has been well documented (Reich *et al.*, 2006; Wang *et al*., 2012). The reduction of plant cell wall content was consistent with results obtained by Picon-Cochard *et al.* (2004) when an upland community was subjected to an atmospheric CO_2 enrichment owing to the Mini-FACE system. However, the amplitude of CO_2 effect on NDF content remained generally small (Dumont *et al.*, 2014). This could explain that no impact of elevated CO_2 was observed on the extent of *in vitro* rumen fermentation, excepted for acidification which increased (P<0.05), likely due to a lower ammonia production in response to the lower N content (Tables 3 and 4). Contrary to expectation, we did not observe any increase in WSC content induced by elevated CO_2 (Wang *et al.*, 2012). However, air warming may reduce carbohydrate content, thus counterbalancing positive effect of elevated CO_2 on WSC (Casella and Soussana, 1997). In addition, WSC may be subjected to particularly high variability due to time of harvest, speed of sample conditioning, and analytical methods in the different studies (Dumont *et al.*, 2014).

Table 1. Chemical composition (g/kg dry matter) of forage community subjected to two CO_2 concentrations (380 and 520 ppm) with or without extreme event

	Sampling 2 (April)		Sampling 3 (June)		Sampling 4 (November)				SEM
					Control		Extreme		
CO_2 (ppm)	380	520	380	520	380	520	380	520	
N	23.1	20.5	18.2	16.6	17.7	14.4	27.6	21.6	0.83
NDF	515	514	586	569	550	546	533	490	11.7
WSC	263	236	187	192	147	194	166	195	21.3
Glucose	19.8	17.4	20.3	16.9	10.1	7.7	11.1	10.7	1.76
Sucrose	39.7	40.1	29.4	30.5	17.7	20.1	24.0	27.4	3.34
Fructose	21.7	18.5	20.6	17.9	12.8	12.6	15.4	16.6	1.91
Fructans	182	160	117	127	105	155	117	139	17.9

N: nitrogen, NDF: neutral detergent fiber, WSC: water-soluble carbohydrates, SEM: standard error of the mean.

Table 2. Effect of fixed effects on chemical composition parameters of forage community subjected to two CO_2 concentrations (380 and 520 ppm) with or without extreme event

Effect	CO_2 effect	Ext effect	Sampling effect	CO_2 × ext effect	CO_2 × sampling effect	Ext × sampling effect	CO_2 × ext × sampling effect
N	*** (380>520)	*** (E>C)	*** (2,4>3)	NS	NS	***	NS
NDF	* (380>520)	* (C>E)	*** (3>2,4)	NS	NS	NS	NS
WSC	NS	NS	*** (2>3,4)	NS	NS	NS	NS
Glucose	* (380>520)	NS	*** (2,3>4)	NS	NS	NS	NS
Sucrose	NS	NS	*** (2>3>4)	NS	NS	NS	NS
Fructose	NS	NS	*** (2,3>4)	NS	NS	NS	NS
Fructans	NS	NS	*** (2>3,4)	NS	NS	NS	NS

N: nitrogen, NDF: neutral detergent fiber, WSC: water-soluble carbohydrates, E or ext: extreme, C: control.
* P<0.05, ** P<0.01, *** P<0.001, NS : non significant.

The application of the extreme event in summer resulted in an increase in forage N content by 35% (P<0.001) and a decrease in NDF content by 7% (P<0.05) for sampling date 4 (Tables 1 and 2). Consistently, it led to an increase in IVDMD by 8% (P<0.05) (Tables 3 and 4) as plants contained more digestible tissues. In terms of herbivore nutrition, more digestible plants have a better energetic value.

Table 3. *In vitro* rumen fermentation parameters of forage community subjected to two CO_2 concentrations (380 and 520 ppm) with or without extreme event

	Sampling 2 (April)		Sampling 3 (June)		Sampling 4 (November)				SEM
					Control		Extreme		
CO_2 (ppm)	380	520	380	520	380	520	380	520	
N	23.1	20.5	18.2	16.6	17.7	14.4	27.6	21.6	0.83
NAcidification (dpH)	0.91	0.95	0.83	0.84	0.70	0.77	0.66	0.72	0.023
IVDMD (%)	60.3	58.3	52.7	51.5	51.7	51.5	54.0	57.9	1.07
Total VFA (mmol/g DM)	122	126	114	113	108	111	110	116	3.0
C2:C3 (mol/mol)	2.70	2.79	2.82	2.89	2.96	2.91	2.83	2.76	0.052
Total gas (mmol/g DM)	7.12	7.10	6.48	6.37	6.11	6.06	6.29	6.47	0.159
CH_4	1.26	1.25	1.12	1.10	1.08	1.06	1.14	1.12	0.030
CO_2	5.87	5.82	5.32	5.27	5.04	5.02	5.16	5.35	0.120
$CO_{2:}CH_4$ (mol/mol)	4.66	4.67	4.79	4.82	4.69	4.74	4.54	4.80	0.083

IVDMD: *in vitro* dry matter digestibility, VFA: volatile fatty acids, C2: acetate, C3: propionate.

Table 4. Effect of fixed effects on *in vitro* rumen fermentation parameters of forage community subjected to two CO_2 concentrations (380 and 520 ppm) with or without extreme event

Effect	CO_2 effect	Ext effect	Sampling effect	CO_2 × ext effect	CO_2 × sampling effect	Ext × sampling effect	CO_2 × ext × sampling effect
Acidification	* (520>380)	NS	*** (2>3>4)	NS	NS	NS	NS
IVDMD	NS	* (E>C)	*** (2>3,4)	NS	*	*	NS
Total VFA	NS	NS	*** (2>3,4)	NS	NS	NS	NS
C2:C3	NS	NS	** (4,3>2)	NS	NS	**	NS
Total gas	NS	NS	** (2>3,4)	NS	NS	NS	NS
CH_4	NS	NS	*** (2>3,4)	NS	NS	NS	NS
CO_2	NS	NS	*** (2>3,4)	NS	NS	NS	NS
$CO_{2:}CH_4$	NS	NS	NS	NS	NS	NS	NS

IVDMD: *in vitro* dry matter digestibility, VFA: volatile fatty acids, C2: acetate, C3: propionate, E or ext: extreme, C: control. *: P<0.05, **: P<0.01, ***: P<0.001, NS: non-significant.

Strong effects of sampling date were detected on all parameters of both chemical composition and *in vitro* rumen fermentation, except for the CO_2:CH_4 ratio in fermentation gas. Overall, forages harvested in April were richer in rapidly fermentable substrates than forages harvested in June and November, which can be explained by changes in plant phenological stage.

IV – Conclusions

Our results suggest that forage quality of an upland grassland may be impacted by future climate change in different ways. While elevated CO_2 combined with warming decreased both N and fiber contents in plants without leading to an effect on forage digestibility, extreme summer drought increased plant content in digestible tissues after their recovery. Extreme climatic events may thus be most likely to modify plant tissue chemistry and improve forage quality than changes in atmospheric CO_2 concentration.

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