

Seasonal Variation in the Capacity for Plant Trait Measures to Predict Grassland Carbon and Water Fluxes

Georg Everwand,^{1,2*} Ellen L. Fry,³ Till Eggers,^{4,5} and Pete Manning^{2,6}

¹Department of Crop Sciences, Agroecology, Georg-August-University Göttingen, Grisebachstrasse 6, 37077 Göttingen, Germany; ²NERC Centre for Population Biology, Imperial College of Science and Technology, Silwood Park, Ascot SL5 7PY, UK; ³Department of Life Sciences, Imperial College of Science and Technology, Silwood Park, Ascot SL5 7PY, UK; ⁴Present address: BASF SE, Global Research Crop Protection, Data Management and Biometrics, 67117 Limburgerhof, Germany; ⁵Experimental Ecology Group, Department for Biology and Chemistry, University of Osnabrück, Barbarastr. 13, 49069 Osnabrück, Germany; ⁶Institute for Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

ABSTRACT

There is a need for accurate predictions of ecosystem carbon (C) and water fluxes in field conditions. Previous research has shown that ecosystem properties can be predicted from community abundance-weighted means (CWM) of plant functional traits and measures of trait variability within a community (FDvar). The capacity for traits to predict carbon (C) and water fluxes, and the seasonal dependency of these trait-function relationships has not been fully explored. Here we measured daytime C and water fluxes over four seasons in grasslands of a range of successional ages in southern England. In a model selection procedure, we related these fluxes to environmental covariates and plant biomass measures before adding CWM and FDvar plant trait measures that were scaled up from measures of individual plants grown in greenhouse conditions. Models describing fluxes in periods of low biological activity contained few predictors, which were usually abiotic factors. In more biologically active peri-

ods, models contained more predictors, including plant trait measures. Field-based plant biomass measures were generally better predictors of fluxes than CWM and FDvar traits. However, when these measures were used in combination traits accounted for additional variation. Where traits were significant predictors their identity often reflected seasonal vegetation dynamics. These results suggest that database derived trait measures can improve the prediction of ecosystem C and water fluxes. Controlled studies and those involving more detailed flux measurements are required to validate and explore these findings, a worthwhile effort given the potential for using simple vegetation measures to help predict landscape-scale fluxes.

Key words: biodiversity; biomass; climate; community weighted mean; ecosystem services; evapotranspiration; Functional diversity; photosynthesis.

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*Corresponding author; e-mail: georg.everwand@agr.uni-goettingen.de

INTRODUCTION

There is increasing interest in predicting ecosystem functions (for example, carbon (C) and water fluxes) and quantifying the contribution of biodiversity to these in both natural and semi-natural ecosystems (Diaz and others 2007; Schumacher and Roscher 2009; Sapjanskas and Loreau 2010;

Lavorel and others 2011; Verheijen and others 2013). Unfortunately, direct measurements of ecosystem function often require specialist techniques and equipment, making them time consuming and costly (Sala and others 2000). Therefore, some authors have suggested that functional traits could be substituted for direct measurements of function (Garnier and others 2004). This could be advantageous because plant community composition is simple to quantify (for example, in quadrat surveys) and strongly influences ecosystem functioning (for example, by controlling photosynthesis, respiration and decomposition) (Diaz and others 2007).

To date, the most widely used approach to link traits to ecosystem function is to first select plant traits that are closely linked with the ecosystem processes of interest (effects traits, *sensu* Lavorel and Garnier 2002). Next, trait values are assigned to each species in a community and a weighted average is calculated using species abundances as weights. This is known as a “community weighted mean” (CWM) (Garnier and others 2004; Diaz and others 2007). CWMs are based upon the principle that a species’ contribution to ecosystem function is proportional to its biomass, a concept known as the biomass ratio hypothesis (Grime 1998). An additional component of plant community composition that may influence ecosystem function is the functional diversity and variation of traits, one measure of which is FDvar (Mason and others 2003), a constrained value that describes the proportion of variation of a single trait within a community. It is calculated as the variance in traits, weighted by species abundances. The support for such a measure as a predictor of fluxes comes from numerous experimental studies. These have demonstrated that complementary resource use by plant species in diverse mixtures results in higher primary productivity (Hector and others 1999; Cardinale and others 2006; Cardinale and others 2007). It was also shown that functional trait diversity within a community, such as in plant height, leaf structure or root to shoot ratio, may increase community light use efficiency (Vojtech and others 2008). The diversity of plant functional trait values has also explained the greater C fluxes of more species communities in experimental mesocosms (Milcu and others 2014). However, the importance of this relationship in natural field conditions, in which other environmental drivers of ecosystem function vary strongly, remains in question.

Most studies that have attempted to link species or functional trait diversity to function in natural conditions have found the relationship to be weak or absent (Diaz and others 2007; Grace and others

2007; Schumacher and Roscher 2009; Laughlin 2011). In contrast, CWMs tend to be reasonable predictors of function in observational studies. When combined with abiotic predictors CWMs can account for up to approximately 70% of the variation in ecosystem properties, such as biomass production (Lavorel and others 2011), nitrogen availability (Diaz and others 2007), soil bacterial biomass (de Vries and others 2012) and soil C stocks (Garnier and others 2004). To date these studies have focussed on integrated or snapshot measures of ecosystem properties. The capacity of functional markers to explain gas and water fluxes from ecosystems has received less attention, despite indications that the traits and diversity of plant communities can affect ecosystem CO₂ and water fluxes (Craine and others 2001a, b; Johnson and others 2008; Kunert and others 2012; Michel and others 2012; Verheijen and others 2013). Although previous empirical studies have suggested that functional trait measures could improve our capacity to predict fluxes, these typically relate time series C-flux data from a single flux tower to changes in few traits across time (Hui and others 2003; Ma and others 2011). The capacity of trait variation to explain fluxes across wider ranges of environmental conditions is unknown.

Several other questions must first be addressed if traits are to be used to predict fluxes: which traits are the best predictors of which fluxes, and are the identity of the best predictor traits consistent over time? It is likely for example that different traits explain different physiological processes, for example, photosynthetic efficiency traits will control CO₂ uptake and others, like leaf tissue chemistry, will control decomposition rates (De Deyn and others 2008). Because growth, respiration and decomposition vary in their relative importance across the year, then the identity of trait–flux relationships may also vary seasonally (Eviner and others 2006). However, a strong correlation between tissue physiology and chemistry may mean that some traits, for example, specific leaf area (SLA), predict fluxes in both growth and decomposition periods (Wright and others 2004). Another important consideration is whether trait measures make significant improvements to model predictions; how useful are trait measures compared to measures of standing plant biomass and abiotic drivers, such as soil moisture, temperature and light availability, and can they explain additional variation on top of these factors?

In this study, we aimed to address these questions, with a particular focus on investigating the seasonal dependency of trait–function relationships

in grassland ecosystems. As a principal goal of the study was to assess whether database and other ex-situ trait measures are of practical use in predicting ecosystem function, glasshouse-derived species trait measures were used to generate CWM and FDvar values rather than in situ field-derived measures. The latter are more likely to accurately represent field trait expression but are not practical in ecosystem survey and monitoring (Mokany and Ash 2008; Cordlandwehr and others 2013). We conducted this investigation by setting up fixed sampling rings on grasslands of varying successional age in which we measured plant species composition, environmental covariates and C and water fluxes. Composition measurements were combined with measures of functional trait measures to generate CWM and FDvar metrics and these were used alongside the environmental covariate data to build statistical models describing fluxes.

MATERIALS AND METHODS

Study Sites

The study was conducted in the successional mesotrophic grasslands of Silwood Park, Berkshire, in south east England (lat. 51.406371, long. -0.648648). The five selected sites were flat, within 1 km of each other (Appendix A in Electronic Supplementary Material) and were all based upon a nutrient poor and weakly acidic sandy loam soil based upon Tertiary sandstone, the Bagshot beds. These soils have a low phosphorus sorption capacity (Manning and others 2006) and nutrient concentrations are typically 1.6–3.6 mg dissolved inorganic N kg⁻¹ and 2–4 mg extractable P kg⁻¹ (see Table S1, Milcu and others 2011; Fry and others 2013 for details). Community composition varied greatly between the sites and seasons with successional age being the likely dominant cause of these differences. Two sites were recently ploughed in December 2008. The other three sites were in later successional states (approximately 20, 75 and 165 months since ploughing) but all lacked woody plants. Communities can be summarised as forming a successional gradient from the OV10 type of the UK National Vegetation Classification (Rodwell 1992) after disturbance to various variants of the MG6, U1 and MG1 types later in succession (see Crawley 2005 for a detailed ecology of the site). In some areas herbivores, particularly rabbits (*Oryctolagus cuniculus*) and roe deer (*Capreolus capreolus*) graze and browse and due to this and recent ploughing some sites had a low standing biomass

(Figure 1). Vegetation of the five sampling areas is described in further detail in Tables S2, S3 and S4 and Appendix A in Electronic Supplementary Material. A full list of the 66 species found in the study can be found in Table S3.

Plot Layout and Flux Measurements

Within each of the five sites, six 1 m² plots were established. In each we installed two fixed rings of 200 mm diameter PVC pipe, each 200 mm from the centre of the plot along a diagonal axis. The PVC ring was buried 50 mm belowground and protruded 50 mm aboveground to provide a collar for an air-tight seal when taking passive measurements in a closed system connected to a CIRAS 2 Infrared Gas Analyzer (IRGA) (PP Systems, Hitchin, UK).

Rings were buried in December 2008, 4 months prior to the start of the measurements to minimise soil disturbance effects and to allow roots time to recover. This combination of five sites with six plots within each, and two rings in each plot gave a total of 30 replicates for plot level measures and 60 for ring level measures. From each ring single measures of net ecosystem CO₂ exchange (NEE), evapotranspiration and ecosystem respiration were taken in four different time periods: 19th March–1st April 2009 (early spring, hereafter March), 29th May–4th June 2009 (an active growth period, hereafter June), 3rd–6th August shortly after peak biomass (hereafter August) and the 3–6th November 2009 (the autumn senescence phase, hereafter November). Measurements were taken between 11:30 and 13:30 GMT over 3–10 days, in dry conditions when cloud cover was intermediate in density and unbroken. When measuring NEE, the net balance between photosynthetic uptake and soil and plant respiration, the measurement chamber was placed on the ring for 4 min and the flux was determined from the change in CO₂ concentration. To measure total ecosystem respiration, we covered the chamber with an aluminium-coated sheet to exclude light and prevent heat absorbance (Kolari and others 2006) and another 4 min measurement was taken. Gross photosynthesis was estimated as total ecosystem respiration subtracted from NEE. Several abiotic covariates were also recorded during each CO₂ flux measurement (Wagner and others 2009): six measures of photosynthetic active radiation (PAR) (400–700 nm) were taken using a PAR metre (Skye Instruments, Llandrindod Wells, Wales); soil moisture measures

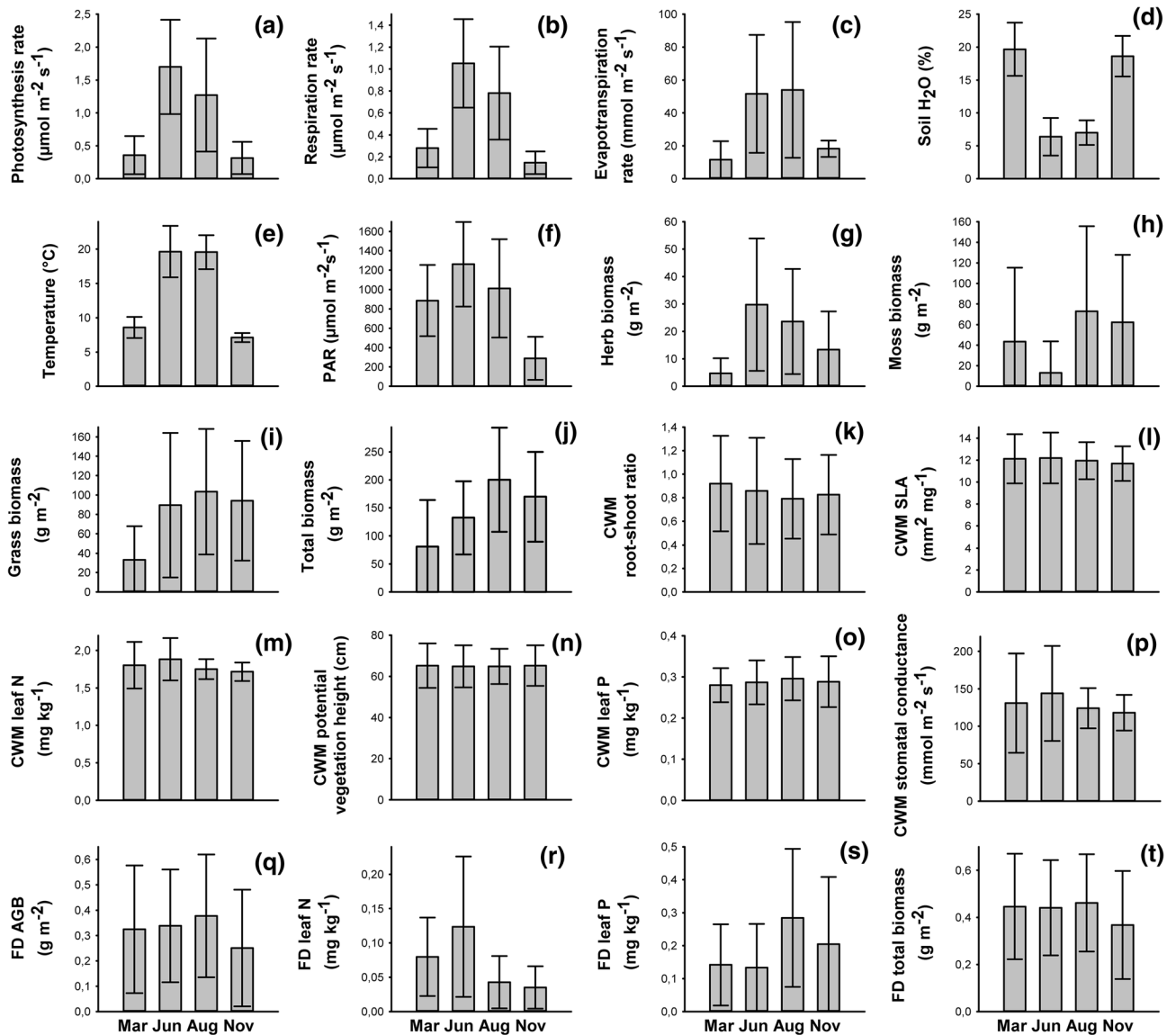


Figure 1. **A–C** Ecosystem fluxes; **D–F** Environmental measures; **G–J** Vegetation measures; **K–P** Community weighed means; **Q–T** Functional diversity data. Data used in model fitting, showing seasonal changes as bar graphs with SD. **A–C** are the response variables of the three fluxes, **D–F** are covariates measured simultaneously to the flux measures, **G–I** are estimates of the plant biomass of major functional groups, **J–O** are community weighted means (CWM) of plant traits, **P–S** are estimates of the diversity of trait values (FDvar). All bars show the mean \pm standard deviation of all measurements for each of the four sampling periods.

were taken using a Theta probe (Delta-T Devices Ltd, Cambridge, UK); and for soil temperature, a Checktemp Soil Thermometer (Hanna HI Instruments, Michigan, USA) was used. For these moisture and temperature measures, three measurements were taken around the ring and averaged. In each ring, the percentage cover of all higher plant species was recorded in the week after flux measures were taken. Mosses were not recorded to species level. For more details on flux measurement see Appendix B in Electronic Supplementary Material.

Cover–Biomass Calibration and Plant Traits

To predict plant biomass non-destructively, we measured plant cover and biomass in plots adjacent to the study plots and used these to build calibration models that predict aboveground biomass from our cover measures. Separate models were constructed for grasses, mosses and herbs as they differed strongly in their biomass per unit cover (for details see Appendix B and Table S5 in Electronic Supplementary Material).

For trait measures, 65 species of the local flora were germinated on seedling compost (John Innes no. 1) in $19 \pm 1^\circ\text{C}$ glasshouses with 8/16-h photoperiod. Then, in January 2008, five individuals of each species with a height of approximately 3 cm were transferred into a single tube each (60 cm deep, 12 cm diameter). Seed was sourced commercially, but of local origin (Herbiseed, Twyford, England). The tubes contained soil from a grassland within our study area and were covered with mesh at the bottom. See Table S1’s mature grassland column and the control conditions of the mid-successional site of Milcu and others (2011) for soil properties. Plants were then grown in conditions described above and watered when required. These conditions were representative in photoperiod and temperature to the field sampling periods of June and August (16 h, 20°C Figure 1E) but much warmer than in the March and November periods. Trait measures may therefore be more representative for the summer sampling periods. After 90 days, or at flowering for short-lived species, we took flux measures on the plants and harvested them. For flux measures, we used a Ciras-1 IRGA (PP Systems, Hitchin, UK), with an Integrated cuvette air supply unit and standardised light emitting diode, to measure the photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$), transpiration ($\text{mmol m}^{-2} \text{s}^{-1}$) and stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) of a healthy leaf, on each plant. Measurements were taken between 10:00 and 15:00 h in full sunlight.

After flux measures were taken, plant height was measured and plants were harvested. We measured photosynthetic surface area (PSA) of all above-ground plant organs using a scanner and the Leaf Area program (Version 1.3., University of Sheffield). After drying for 48 h at 60°C , we measured aboveground biomass (AGB) (g) and belowground

biomass (BGB) (g), the latter obtained by washing roots over a 1-mm sieve. Root–shoot ratio was calculated from AGB and BGB. We calculated specific leaf area by dividing PSA by AGB. This method can be viewed as specific plant area and was used as many of the species were sprawling herbs with very small leaves and green stems. Relative growth rate ($\text{g g}^{-1} \text{d}^{-1}$) was calculated from total biomass of 2-week-old seedlings and that at harvest. Aboveground biomass C, N and P (all in mg kg^{-1}) and C/N ratio were measured according to standard procedures (ball milling, Kjeldahl digestion and colorimetric analysis). This entire process was repeated in January 2009 with a new set of five plants of each species and with soil taken from the same site. This resulted in ten measures for each trait, for each species, which was then averaged to give a species value. A full list of species and their trait values is given in Tables S3a–f.

Species trait data were used to determine CWM trait values for each ring, with the weights being the proportion of estimated biomass for each species within the community (For formula, see Appendix B in Electronic Supplementary Material). Functional diversity of trait values, represented by functional divergence (FDvar) (Mason and others 2003), was also calculated for each plot (for formula, see Appendix B in Electronic Supplementary Material). Only higher plants were used to calculate CWM and FDvar values. These calculations were performed using the R package F-diversity (Casanoves and others 2010).

Statistical Analysis

Statistical models describing fluxes were generated with a modified version of the procedure of Diaz

Table 1. Ecosystem Respiration Models for All Four Measurement Periods

	Variable	R_M^2	ΔAIC	n	Parameter value	SE	df	P
Mar. 09	Intercept	0.20		59	0.103	0.055	28	
	CWM root–shoot ratio		4.06		0.192	0.055	29	0.0117
June 09	Intercept	0.29		60	0.678	0.162	27	
	Herb biomass (g m^{-2})		11.34		0.009	0.002	27	0.0003
	Grass biomass (g m^{-2})		5.00		0.003	0.001	27	0.0082
	FDvar plant-N (mg N kg^{-1})		2.00		−1.070	0.537	27	0.0460
Aug. 09	Intercept	0.16		60	0.225	0.069	28	
	Grass biomass (g m^{-2})		10.17		0.003	0.001	28	0.0005
	FDvar potential above ground biomass (g)		9.11		0.646	0.161	28	0.0009
Nov. 09	Intercept	0.13		58	−0.024	0.064	27	
	CWM plant-P (mg N kg^{-1})		4.40		0.591	0.216	27	0.0114

Order of variables reflects their order of addition in the hierarchy of controls modelling process. R_M^2 = proportion of variance explained by fixed factors, ΔAIC = change in AIC upon deletion from the model, P = significance of each term established using a likelihood ratio deletion test.

Table 2. Photosynthesis Rate Models for All Four Measurement Periods

	Variable	R_M^2	ΔAIC	n	Parameter value	SE	df	P
Mar. 09	Intercept	0.37		59	0.210	0.070	26	
	Grass biomass (g m ⁻²)		18.74		0.006	0.001	26	<0.0001
	FDvar plant-P (mg P kg ⁻¹)		6.78		0.283	0.372	26	0.0046
	Grass biomass × FDvar plant-P		4.79		-0.021	0.008	26	0.0091
June 09	Intercept	0.42		60	0.998	0.793	25	
	Soil water (%)		4.58		0.320	0.113	25	0.0091
	(Soil water) ²		5.40		-0.016	0.006	25	0.0104
	Grass biomass (g m ⁻²)		7.14		0.004	0.001	25	0.0025
	Herb biomass (g m ⁻²)		22.94		0.021	0.004	25	<0.0001
	CWM plant-N (mg N kg ⁻¹)		4.14		-0.816	0.338	25	0.0133
	Intercept	0.62		60	18.068	3.740	22	
Aug. 09	Soil H ₂ O (g g ⁻¹)		14.61		-0.204	0.051	22	0.0001
	Soil temperature (°C)		29.32		-1.528	0.326	22	<0.0001
	(Soil temperature) ²		31.94		0.033	0.007	22	<0.0001
	Herb biomass (g m ⁻²)		16.39		0.016	0.003	22	<0.0001
	Grass biomass (g m ⁻²)		35.49		0.008	0.001	22	<0.0001
	CWM stomatal conductance (mol ⁻¹ m ² s ⁻¹)		5.8		0.003	0.001	22	0.0052
	FDvar potential total biomass (g)		15.39		-1.828	0.805	22	<0.0001
	FDvar potential total biomass × soil water		3.37		0.364	0.114	22	0.0204
	Intercept	0.37		58	-0.678	0.569	24	
Nov. 09	PAR (μmol m ⁻² s ⁻¹)		15.35		0.0049	0.0019	24	0.0001
	Soil temperature (°C)		3.43		0.115	0.080	24	0.0244
	PAR × soil temperature		3.25		-0.0006	0.0003	24	0.022

Order of variables reflects their order of addition in the hierarchy of controls modelling process.

R_M^2 = proportion of variance explained by fixed factors, ΔAIC = change in AIC upon deletion from the model, P = significance of each term established using a likelihood ratio deletion test.

Table 3. Evapotranspiration Rate Models for All Four Measurement Periods

	Variable	R_M^2	ΔAIC	n	Parameter Value	SE	df	P
Mar. 09	Intercept	0.25		59	5.22	4.11	26	
	PAR (μmolm ⁻² s ⁻¹)		38.36		0.014	0.002	26	<0.0001
	Moss biomass (g m ⁻²)		3.55		0.018	0.015	26	0.0185
	CWM potential height (cm)		1.74		-0.118	0.054	26	0.0529
June 09	Intercept	0.64		60	-21.71	36.507	26	
	PAR (μmolm ⁻² s ⁻¹)		12.71		0.034	0.009	26	0.0001
	Soil water (%)		15.40		4.856	1.117	26	<0.0001
	Soil temperature (°C)		3.95		-2.709	1.109	26	0.0148
	CWM specific leaf area (mm mg ⁻¹)		7.89		4.319	1.329	26	0.0016
Aug. 09	Intercept	0.19		60	-937.348	243.148	26	
	Soil temperature (°C)		10.08		93.545	23.046	26	0.0009
	(Soil temperature) ²		10.76		-2.093	0.536	26	0.0004
	Grass biomass (g m ⁻²)		8.25		0.349	0.108	26	0.0014
	CWM potential total biomass (g)		6.88		-4.313	1.447	26	0.0029
Nov. 09	Intercept	0.80		55	35.89	14.69	21	
	Soil water (%)		48.74		-1.268	0.711	21	<0.0001
	CWM relative growth rate (g g ⁻¹ d ⁻¹)		25.27		-346.54	147.31	21	<0.0001
	FDvar root to shoot ratio		3.33		2.725	1.208	21	0.0208
	CWM relative growth rate × soil water		7.28		21.64	3.032	21	0.0023

Order of variables reflects their order of addition in the hierarchy of controls modelling process.

R_M^2 = proportion of variance explained by fixed factors, ΔAIC = change in AIC upon deletion from the model, P = significance of each term established using a likelihood ratio deletion test.

and others (2007). This procedure adds terms according to a hypothetical hierarchy of controls, starting with abiotic drivers of function before adding terms describing species composition and trait distribution. In all cases, mixed-effects models were fitted using maximum likelihood with the lme function of R version 2.11.1 (R-Development-Core-Team 2010) and a ring-within-site random effects structure. Separate models were fitted for each time period and function totalling 12 models (Tables 1, 2, 3). An exponential variance term was included if it significantly improved model likelihood (August respiration and photosynthesis, and March and November evapotranspiration).

The first set of variables added were abiotic factors: photosynthetic active radiation (PAR), soil water content (%), temperature (°C) and age of the plot (no. of month since ploughed). These variables and all possible interactions between them were removed systematically if found to be non-significant (at $P < 0.05$) in a likelihood ratio deletion test (LRT) (Pinheiro and Bates 2000; Crawley 2007). Once abiotic terms were selected we tested for nonlinear effects by adding polynomial terms for each and removing them if non-significant. The second set of terms represented biomass effects. We compared the likelihood of models containing terms for: the predicted biomass of mosses, herbs and grasses, the predicted biomass of vascular plants and mosses and total predicted biomass. Again, nonlinear effects were estimated by adding polynomial terms and removing these if not significant. After this we added first-order interactions between retained biomass variables and abiotic terms and removed these sequentially if non-significant, starting with the least significant. The third stage estimated plant functional trait effects. Given strong correlation between many traits, we placed the CWM for each trait in the model singly and then substituted with another, noting the significance when it was removed. The most significant trait CWM was retained. This process was repeated for FDvar measures in the fourth stage. The traits used were CWMs and FDvars of: photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance ($\text{mmol}^{-1} \text{m}^2 \text{s}^{-1}$), plant height (cm), aboveground biomass (g m^{-2}), total plant biomass (g m^{-2}), root–shoot ratio, plant C, N and P content (mg kg^{-1}), C to N ratio and specific leaf area ($\text{mm}^2 \text{mg}^{-1}$). The final stage sought interactions between the retained abiotic and trait variables. Initially, all possible first-order interactions were fitted. These were then removed sequentially, as before, until only significant parameters remained. Once this final model was reached the significance of each term

was assessed with a LRT. When assessing the significance of main effects any interactions containing the term were also removed. Sometimes it was found that terms that were significant earlier in the modelling process were no longer significant and these terms were removed. For each of the final models marginal R^2 (R_M^2), a measure of fit for the fixed effects of a mixed model was calculated using the method of Nakagawa and Schielzeth (2013). AIC change on deletion from the final model (ΔAIC) was also noted to assess the relative importance of each predictor.

RESULTS

Ecosystem Respiration

Respiration models had a low fit (R_M^2 0.13–0.29), and the most important descriptors were biomass terms (Table 1). Ecosystem respiration in the inactive late winter period (March Figure 1B) was best explained by CWM root–shoot ratio, with higher respiration under communities of plants with a high root allocation. In contrast, the model for June respiration, a period that was warm (Figure 1E), contained terms for grass and herb biomass, both of which had a positive relationship with respiration (Table 1). The model also contained a marginally significant negative term for the FDvar of leaf N content; communities with diverse leaf N concentrations respired less. The model for August respiration, a period with intermediate fluxes (Figure 1B), was similar to June in that grass biomass positively affected respiration. There was also a strong positive relationship with FDvar potential biomass; communities containing plants with a wide range of potential sizes respired more (Table 1). In November, only the CWM of leaf P content showed a significant relationship with respiration. This relationship was positive in that communities producing P-rich tissues respired more (Table 1). No abiotic variables were retained in the respiration models.

Photosynthesis

Models describing photosynthesis had a reasonable fit ($R_M^2 = 0.37$ – 0.62). The most important variables were biomass, abiotic influences (that is, PAR, soil water and temperature) and plant biomass, but trait measures were also important in periods of high activity (Table 2). The model for photosynthesis in March, when fluxes were very low (Figure 1A), shows that fluxes were positively associated with grass biomass (which accounted for 72% (± 4 SE) of AGB) and FDvar of leaf P content.

There was also a negative interaction between these two variables; in plots with high grass biomass the relationship between the FDvar of leaf P and photosynthesis was negative (Table 2). The model for June photosynthesis, when C uptake was much higher (Figure 1A) had a positive relationship with grass biomass, but also a positive effect of herb biomass, which was now far more abundant ($36\% \text{ of AGB} \pm 4 \text{ SE}$) and which had a stronger per unit biomass effect than grasses. A significant effect of soil moisture was also observed. This was quadratic, with photosynthesis peaking at a soil water content of 11%. Finally, there was a weak negative relationship with CWM leaf N. Photosynthesis was slightly lower in communities containing N-rich leaves. The model for August photosynthesis, when fluxes were still relatively high (Figure 1A) and community biomass was at its highest ($200 \text{ g m}^{-2} \pm 12.00 \text{ SE}$), was complex and contained many highly significant descriptors. Two of these were soil water, which had a negative relationship, and soil temperature, which had a quadratic relationship, with photosynthesis declining to near zero between 16 and 22°C and remaining there at higher temperatures. As in June, photosynthesis in August was positively associated with herb and grass biomass, but grasses had stronger, and herbs weaker, per unit biomass effects compared to the June model. Two trait variables also had significant relationships with August photosynthesis. The first was the CWM stomatal conductance, a positive effect, and the second FDvar potential biomass, a strong negative effect representing lower photosynthetic uptake in plots with species of a wide range of potential biomass. This effect interacted strongly with soil water (Table 2). The model for November photosynthesis, when fluxes were very low (Figure 1A), was much simpler and contained no community effects, only positive effects of PAR and soil temperature, both of which were low in this period (Figure 1E, F). These variables interacted so that fluxes were highest where temperature was low and PAR was high.

Evapotranspiration

The models for evapotranspiration (Table 3) were very variable in fit ($R_M^2 = 0.19\text{--}0.80$) and generally less parameterized than those of respiration and photosynthesis. They typically contained fewer biotic and more abiotic variables, which were also the best descriptors, with the exception of highly significant trait measure terms in the November model. The model for March evapotranspiration, a period when fluxes were low (Figure 1C), contained a highly significant positive effect of PAR,

and weak positive effects of moss biomass and CWM potential height. The final term in this model was a positive relationship with CWM of SLA; evapotranspiration was higher in communities of thin leaved species. The highly significant positive PAR effect was also present in the June evapotranspiration model alongside positive effects of soil moisture and soil temperature. In August, a period of high evapotranspiration (Figure 1C), the model contained a quadratic relationship with soil temperature; fluxes peaked around temperatures of 22°C. There was a strong positive relationship with grass biomass but a strong negative effect of CWM potential biomass that indicated lower evapotranspiration fluxes were potentially large species dominated. By November fluxes were very low (Figure 1C) but the model was closely fitting, containing terms for soil moisture, a negative relationship with CWM relative growth rate, and an interaction between these terms. There was also a weak but significant relationship with the FDvar of root to shoot ratio.

Correlations Between Traits

To investigate why trait predictors varied between fluxes and seasons correlations between community trait measures were calculated. Strongly correlated traits should have similar predictive power but correlations between traits retained in respiration models were weak (Pearson's $r < 0.1$). This indicates that different functional properties determined these fluxes at different times of year. In contrast, there was a correlation between the CWM of plant-N and CWM stomatal conductance ($r = 0.63$), which explained photosynthesis in June and August, respectively. Similarly, there was a correlation between CWM potential height and CWM SLA ($r = -0.68$), which explained evapotranspiration in March and June, respectively. Correlations were also found between the traits that explained fluxes at a particular time of year, thus indicating that in certain seasons a trait may predict several fluxes. FDvar plant tissue P and CWM potential height, which explained photosynthesis and evapotranspiration in March correlated negatively ($r = -0.69$). FDvar potential aboveground biomass, which predicted August respiration, and FDvar total biomass, which predicted August photosynthesis, were also strongly correlated ($r = 0.85$).

DISCUSSION

By combining abiotic and biomass measures with community trait measures, we identified several

variables that explained grassland C and water fluxes. These results indicate that plant traits can predict ecosystem C and water fluxes, but that the relationship between them is stronger in periods of high biological activity. Throughout the study fluxes were low, most probably due to the low biomass of the vegetation and the nutrient poor status of the site (Figure 1; Table S1) and it is possible that in more active systems trait–flux relationships will be stronger. In the following sections, we discuss each of the predictors in our hierarchy of controls in turn.

Abiotic and Plant Biomass Predictors

Strong relationships were observed between fluxes and abiotic drivers such as light, soil water content and temperature. These were particularly common terms in evapotranspiration models. Such effects are reasonably well understood and are extensively reported in the literature (Wohlfahrt and others 2008; Bonan and others 2012; Niu and others 2012). These abiotic variables were often the only ones retained in models for periods of low biological activity (for example, in November) but their effects were seen inconsistently throughout the year. This may not mean that they were not influencing function but merely that they did not vary over ranges that influence function during data collection. Had the study been conducted over larger spatial scales and used continuous flux measures then it is highly likely that these would emerge as more important predictors.

The observed relationship between plant biomass and fluxes can also be explained intuitively, and it is not surprising that biomass was a strong predictor of ecosystem photosynthesis rate. Seasonal variation in the plant functional groups which displayed significant biomass–flux relationships may reflect seasonal differences in phenology and activity. In March photosynthesis fluxes did not correspond to herb biomass, but were higher where there was high grass biomass. This is probably because grasses (for example, *Holcus mollis* and *Agrostis* spp.) made up most of the winter AGB. By June this had changed: photosynthesis was positively associated with high grass and herb biomass, with herbs showing a much stronger per unit biomass effect, thus indicating that they were active in this period, when their biomass was also highest (Figure 1I). Evapotranspiration showed similar seasonal trends to the C fluxes with March evapotranspiration correlating with moss biomass, presumably because of their relatively high biomass in this period and their strong water holding capacity. The importance

of biomass terms, relative to trait and diversity terms, is a similar finding to that of Laughlin (2011), who found that biomass was a stronger predictor of forest N dynamics than community trait measures.

CWM Traits

The results support the view that measures of species composition can improve the fit of models explaining fluxes (Hui and others 2003; Ma and others 2011) and the importance of CWM measures was high in many models. However, it should be noted that the high variation in species composition in the site, alongside the relative standardisation of other drivers such as soil and weather, may have influenced the relative importance of vegetation measures within our models. The identity of the traits that explained fluxes were highly variable, thus suggesting the absence of a simple general relationship between community traits and ecosystem C and water fluxes. Instead, the traits driving, or at least correlating with function varied seasonally. This conclusion is broadly similar to those of Eviner and others (2006) who found that multiple plant traits were required to explain seasonal patterns of soil nitrogen and phosphorus cycling and Ma and others (2011), who found the relationship between photosynthetic capacity and leaf N to vary between years.

Explaining the possible mechanisms underlying trait–flux relationships is more challenging than understanding abiotic and biomass effects. However, hypotheses can be formulated as to mechanisms underlying trait–flux relationships as most of the traits retained in the models have a hypothetical link to resource capture or loss. The March respiration model shows that communities with a high root:shoot ratio respired more in winter. This may be due to the activity of the high belowground biomass of grass-dominated communities. By November respiration correlated with the CWM of plant tissue P, this may represent faster decomposition of nutrient-rich plant litters in a low photosynthesis period. The poor fit of respiration models may be due to the lack of important soil variables (for example, soil chemistry and microbial community structure) as descriptors but it is likely that plant traits will represent at least some of the variation in these variables, for example, CWM leaf N and SLA are related to the relative abundance of bacteria and fungi in grasslands (de Vries and others 2012).

The relationship between photosynthesis rates and correlated CWM traits of leaf N and stomatal conductance (negative in June and positive in

August, respectively) can be understood in terms of gas exchange. We hypothesise that low conductance low leaf N species with a conservative strategy were more active in June but the opposite, fast species were active in August. Similar links to the leaf economics spectrum (Wright and others 2004) may explain respiration patterns. In June, there was also a positive correlation between evapotranspiration and the CWM of SLA. This may be because high SLA plants have a greater surface area for water loss. In August, it was the CWM of potential biomass that correlated with evapotranspiration, perhaps because these potentially large species were still growing and had their stomata open. It is difficult to explain the negative relationship between the CWM of RGR and evapotranspiration in November, a period in which plants are largely inactive. Similarly, it is difficult to explain the negative relationship between CWM plant-N and photosynthesis in June, as a positive relationship would be expected (Wright and others 2004). Such relationships may reflect the correlation between trait measures and other unmeasured drivers of fluxes.

Trait Functional Diversity

A number of significant relationships were found between fluxes and FDvar measures. Particularly, strong was the positive relationship between FDvar potential total biomass and respiration in August and its negative relationship with photosynthesis in the same period. This finding suggests that biodiversity could play an important role in driving fluxes at certain times. However, the general finding was that trait means and the biomass of functional groups were more consistently retained as descriptors of grassland C fluxes than diversity measures. As a result, our findings are consistent with both experiments that found a weak or absent relationship between diversity measures and soil respiration (but also that functional group presence was a key descriptor of function) (De Boeck and others 2007; Johnson and others 2008; Fry and others 2013), and with biodiversity–ecosystem function experiments. In these the diversity of functional groups or traits is seen to strongly and positively affect water and CO₂ fluxes (Craine and others 2001a, b; Kunert and others 2012; Milcu and others 2014). The results of such experiments contrast with many observational field studies, which find a weak relationship, if any, between species or functional diversity and ecosystem processes (Diaz and others 2007; Grace and others 2007; Schumacher and Roscher 2009; Maestre and others 2012). In this study, the relationship

between trait diversity and fluxes was sometimes negative. Such effects may reflect the correlation of plant trait diversity with other drivers of function. The discrepancy between field and experimental results may result from similar causes—other drivers of function may dominate over biodiversity effects under field conditions, making them difficult to detect (Diaz and others 2007; Schumacher and Roscher 2009; Maestre and others 2012). Evidence for such effects could be seen in the interaction between the FDvar of tissue P and grass biomass in the March photosynthesis model; both main terms were positive, but the interaction was negative, suggesting that complementarity effects on growth (Loreau and Hector 2001) could only be expressed in the absence of highly competitive grass species. It is also possible that diversity effects would be stronger if fluxes over much longer timescales were examined. Here, temporal complementarity of species may result in greater C fixation over time (Allan and others 2011).

Advancing Trait–Flux Research

The results of the present study, and others in which plant traits correlate with function in observational field studies, should be interpreted with caution. As mentioned above, plant traits are known to correlate with and respond to a wide range of environmental factors (for example, soil biological and chemical properties and climate) many of which also control fluxes and other ecosystem processes (de Vries and others 2012; Douma and others 2012; Soudzilouvskaia and others 2013). We predict a stronger relationship between traits and fluxes over longer environmental gradients and larger scales. At these larger scales, trait values and fluxes would strongly correlate with abiotic environmental factors (for example, de Vries and others 2012) and would be harder to disentangle from them. An opposing problem occurs in the relatively narrow disturbance gradient of our study. We only sampled communities of grasses and herbs, which differ subtly in comparison to the full length of the leaf economics spectrum (Wright and others 2004). As a result, the importance of traits in driving fluxes may be underestimated. Relatively small differences between communities, alongside standardised measuring conditions, may also have contributed to the sometimes low model fits. Experimental manipulation of trait distributions in controlled and if possible orthogonal, designs may be the best approach to teasing apart cause and correlation and identifying the traits that control function (Fry and others 2014).

Another challenge to the incorporation of traits into flux models and predictions is the identification of the correct traits. Identifying traits that explain function is complicated by a strong correlation between traits (Wright and others 2004). In practical terms, this simplifies the use of traits in predicting fluxes but such correlations appear to be fairly weak in this study, probably due to its relatively narrow range of conditions. There is also difficulty in measuring the root traits that may control belowground processes (for example, rhizodeposition control over soil respiration), although consistent correlations between aboveground and belowground traits have been found (Tjoelker and others 2005; Mokany and Ash 2008).

Intraspecific variation in traits present a further challenge to the use of database trait values to predict fluxes; trait values from databases and glasshouse conditions may not be representative across a range of field conditions (Albert and others 2010). The magnitude of the error this introduces depends upon the degree of trait plasticity, intraspecific variation and the difference between field conditions and those where the database or glasshouse trait value was taken (Mokany and Ash 2008; Cordlandwehr and others 2013). Species trait values also vary seasonally across time, a factor that explained temporal flux variation in woody savannah (Ma and others 2011). Such seasonal variation was not measured here and this may partly explain the stronger explanatory power of trait measures in summer fluxes. Conversely, our glasshouse traits could be reasonable predictors of winter fluxes if traits shift systematically for all species (for example, values decrease by 30% in the winter for all species) across the seasons, thus maintaining relative differences.

Despite these various potential problems, a number of studies have now shown that most trait variation is interspecific, at both global and local scales (Kattge and others 2011; Kichenin and others 2013) and interspecific trait differences are consistent across a range of environments (Ordoñez 2013; Kazakou and others 2014). Therefore, glasshouse and database measures may be reliable and seasonal and intraspecific trait variation may be a minor source of error in ecosystem level comparisons, at least where there are strong differences in species composition, as in the present study.

It is clear that identifying general relationships between traits and function is a non-trivial task that requires comprehensive data. A key problem with a study such as this is that flux measures only

represent a snapshot of actual flux activity; it is highly likely that a more reliable picture of how traits, biomass and the abiotic environment interact to determine fluxes would be achievable with the comprehensive data taken from flux towers that continuously measure fluxes. However, such an apparatus is typically replicated only once per site requiring a network of sites, for example, FLUXNET (Baldocchi and others 2001), to be utilised to tease apart the influences of local soil conditions, weather, climate, biomass and plant traits. Data on how traits vary across seasons would also be useful, particularly if these changes follow consistent patterns that are predictable from a combination of climate and database trait measures. If general patterns could be found with such an approach then it might then be possible to generate maps of predicted fluxes using measures of weather, standing plant biomass (for example, from satellite data) and trait maps, with the latter being generated using data from trait databases, for example, TRY (Kattge and others 2011) and information from biodiversity surveys, for example, the UKs Countryside Survey (Carey and others 2008). If the response of plant communities to climate change is predictable from the same traits (for example, SLA) then it may also be possible to predict future changes to fluxes by extending such an approach (Soudzilouvskaia and others 2013). Similarly, better characterization of trait variation and its functional consequences would aid the development of dynamic global vegetation models and their capacity to predict future fluxes (Verheijen and others 2013).

CONCLUSIONS

This study represents an initial attempt at explaining ecosystem fluxes of C and water using trait measures. In many cases, the inclusion of trait data improved model likelihood, thus indicating that fluxes are driven not just by the interaction of plant biomass and the abiotic environment but also the physiology and chemistry of that biomass. Our results also indicate that an array of traits control fluxes throughout the year. Currently, species composition is typically represented very simply in ecosystem models and global C and water flux analyses, usually as a small number of plant functional types (Sitch and others 2003; Migliavacca and others 2011; Bonan and others 2012; Niu and others 2012; Williams and others 2012). The significance of trait terms adds further support to calls (De Deyn and others 2008; Ostle and others 2009) that this approach may be insufficient to accurately

represent and predict future fluxes. This may require the revision of ecosystem model functional types to a more continuous representation of traits (for example, Verheijen and others 2013), a challenge that may be necessary given the potential for ecosystem C and water fluxes to influence future climate and human activities.

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