PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Physiology-based prognostic modeling of the influence of changes in precipitation on a keystone dryland plant species

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Abstract Fluctuations in mean annual precipitation (MAP) will strongly influence the ecology of dryland ecosystems in the future, yet, because individual precipitation events drive growth and resource availability for many dryland organisms, changes in intra-annual precipitation may disproportionately influence future dryland processes. This work examines the hypothesis that intra-annual precipitation changes will drive dryland productivity to a greater extent than changes to MAP. To test this hypothesis, we created a physiology-based model to predict the effects of precipitation change on a widespread biocrust moss that regulates soil structure, water retention, and nutrient cycling in drylands. First, we used the model to examine moss productivity over the next 100 years driven by alterations in MAP by ±10, 20 and 30 %, and changes in intra-annual precipitation (event size and frequency). Productivity increased as a function of MAP, but differed among simulations where intra-annual precipitation was manipulated under constant MAP. Supporting our hypothesis, this demonstrates that, even if MAP does not change, changes in the features of individual precipitation events can strongly influence long-term performance. Second, we used the model to examine 100-year productivity based on projected dryland precipitation from published global and regional models. These simulations predicted 25–63 % reductions in productivity and increased moss mortality rates, declines that will likely alter water and nutrient cycling in dryland ecosystems. Intra-annual precipitation in model-based simulations was a stronger predictor of productivity compared to MAP, further supporting our hypothesis, and illustrating that intra-annual precipitation patterns may dominate dryland responses to altered precipitation in a future climate.

Keywords Global change · Biocrust · Photosynthesis · Carbon balance · *Syntrichia caninervis*

Introduction

The changing energy balance of the Earth has and will continue to cause alterations to global precipitation patterns. Over the next century, mean annual precipitation (MAP) is expected to increase or decrease by up to 20 % in the majority of terrestrial ecosystems (Trenberth et al. 2003; Stainforth et al. 2005; Alexander et al. 2006; Meehl et al. 2007; Zhang et al. 2007), and the frequency of extreme precipitation events is projected to increase (Karl and Knight 1998; Easterling 2000; Alexander et al. 2006; Meehl et al. 2007). Along with these large changes in annual precipitation, many features of intra-annual precipitation (including individual event sizes, frequency, and seasonality) are projected to change (Hereford et al. 2002; Alexander et al. 2006; Meehl et al. 2007; Sun et al. 2007).

Drylands are likely to be among the most responsive of ecosystems to changes in precipitation because water is the primary limiting factor on productivity (Noy-Meir 1973; Fischer and Turner 1978; Hadley and Szarek 1981; Ehleringer and Mooney 1983). Precipitation events in drylands

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represent brief pulses of water and resource availability for plant and soil communities (Austin et al. 2004; Huxman et al. 2004; Reynolds et al. 2004; Schwinning and Sala 2004). Therefore, the features of individual pulse events (such as event timing and magnitude) constrain as well as drive short- and long-term growth patterns (Ogle and Reynolds 2004; Schwinning and Sala 2004; Cable et al. 2008). Because of the importance of individual precipitation events in these systems, future productivity of dryland communities may be disproportionately driven by intra-annual precipitation variability rather than MAP.

There is uncertainty in global models as to how precipitation may change into the future for dryland systems (Weltzin et al. 2003; Meehl et al. 2007). Changes in dryland MAP in the next century are predicted to occur in either direction as small changes (+5 to −10 %) or as no change in overall magnitude (Meehl et al. 2007). In contrast, changes in intra-annual precipitation in drylands are predicted to be more dramatic. Globally, projections for intra-annual precipitation for drylands are variable and represent a wide range of outcomes, but can be grouped into four distinct scenarios: (1) precipitation frequency will decrease and there will be an increase in the number of rare large events per year (Hereford et al. 2002; Meehl et al. 2007; Seager et al. 2007; Seager and Vecchi 2010), the scenario most commonly forecasted for North American drylands (Cayan et al. 2010); (2) precipitation frequency will increase and event size will decrease (Higgins et al. 2007; Schoof et al. 2010); (3) event size will decrease and there will be an increase in the number of long drought periods per year (Hereford et al. 2002; Meehl et al. 2007; Seager et al. 2007; Schoof et al. 2010; Seager and Vecchi 2010); and (4) precipitation magnitude will increase in summer and winter but decrease in spring (Johns et al. 2006; Garfin et al. 2010). In order to understand how dryland systems will respond to changes in precipitation, and in order to determine the role of intra-annual precipitation in structuring community change, an assessment of the response of dryland plant and soil communities to the full complement of intra-annual precipitation conditions in each of these scenarios is essential.

One feature of dryland ecosystems is the presence of a biocrust living at the soil atmosphere interface. Biocrusts are communities of cyanobacteria, lichens, and mosses that drive nutrient cycling and control soil stability in drylands (Harper and Pendleton 1993; Evans and Belnap 1999; Belnap 2003; Housman et al. 2006; Elbert et al. 2009; Grote et al. 2010). Mosses within biocrusts are globally distributed (Kramer 1980) and play a particularly important role in dryland ecology by influencing carbon and nitrogen fixation in the crust, driving large-scale patterns of nutrient cycling (Reed et al. 2012; Pietrasiak et al. 2014). Biocrust mosses also bind soil particles (Belnap 2003) which

increases water retention in crusts (Chamizo et al. 2012), serve as a habitat for epiphytic nitrogen-fixing cyanobacteria and other microorganisms (Brinda et al. 2011), and reduce the albedo of dryland surfaces due to their dark color, regulating surface energy balance (Finzi et al. 2011). Biocrust mosses, however, are extremely sensitive to subtle intra-annual changes in precipitation (Belnap and Eldridge 2001; Coe et al. 2012), and precipitation-driven declines or mortality in moss may have widespread consequences for ecosystem biogeochemistry (Pietrasiak et al. 2014), as well as temperature and hydrology on regional scales (Finzi et al. 2011).

For biocrust mosses, long-term performance and productivity can be assessed using the carbon balance of the organism during individual precipitation events (Green et al. 2011; Coe et al. 2012). These individual carbon balances can be summed over any time period of interest as a cumulative carbon balance (CCB), a quantitative measure of productivity. This, along with the important ecological role of these plants, makes moss an ideal system for studying the influence of changing precipitation patterns on dryland systems.

In this study, we examined the hypothesis that intra-annual precipitation changes will drive dryland productivity to a greater extent than changes to MAP, and tested this hypothesis using a keystone dryland plant, the common and widespread biocrust moss *Syntrichia caninervis* (Rosentreter and Belnap 2001). Our strategy was to develop a predictive model for performance and productivity under projected changes in precipitation for the next 100 years. First, we created a baseline model for moss performance based on physiology, then tested its ability to predict growth rates and mortality using historical precipitation records from western North America. Second, we examined the differential effects of changes in MAP and changes in intra-annual precipitation patterns on productivity by performing two sets of 100-year simulations: one that manipulated MAP by ±10, 20 or 30 %, and another that altered precipitation event size and frequency while holding MAP constant at three levels. Third, we determined how projected precipitation changes based on global models would influence moss productivity by simulating the conditions outlined in each of four complete scenarios using the model.

Materials and methods

Model construction

Physiological relationships relating intra-annual precipitation parameters to carbon balance in *Syntrichia caninervis* (see Coe et al. 2012) were used as a basis for the model. These relationships exist as equations that calculate moss

carbon balance as a function of precipitation magnitude (R), frequency (desiccation period prior to a rainfall event, DP), and seasonality (four equations—one each for spring, summer, fall, and winter). These four preliminary equations were: spring, C balance $= 3.34 + 0.10R_{sp}$; summer, C balance $= 3.26 + 0.06R_{su} + 0.01DP_{su}R_{su}$; fall, C balance $= 3.75 - 0.12DP_{fa} + 0.06R_{fa} - 0.03R_{fa}DP_{fa}$; winter, C balance $= 3.68 - 0.01DP_{wi} + 0.17R_{wi}$. Using these equations, carbon balance is calculated following each individual precipitation event that occurs, and CCB is calculated as the sum of all carbon balances over a given timeframe.

To ensure the physiological relationships generated reasonable estimates of moss biomass accumulation over time, we applied the equations to precipitation records from southeastern Utah (site details below) where field growth data were available for *S. caninervis* (Stark et al. 1998). We calculated moss CCB over the course of a year from reported precipitation event magnitudes and desiccation periods, then compared annual modeled and measured biomass accumulation. If the final predicted biomass fell outside the 90 % confidence interval of measured biomass from field data, x intercepts and/or coefficients for R and DP in C balance equations were altered, and the procedure was repeated until the model consistently produced biomass estimates with >90 % confidence. The final set of equations used to represent moss carbon balance for western North America that were used to create the model were: spring, C balance $= -8.95 + 3.89R_{sp}$; summer, C balance $= -7.78 + 1.51R_{su}$; fall, C balance $= -10.51 - 0.12DP_{fa} + 7.97R_{fa} - 1.14DP_{fa}R_{fa}$; winter, C balance $= -1.97 - 2.01DP_{wi} + 11.3R_{wi} - 0.69DP_{wi}R_{wi}$. This procedure, although most applicable to moss growing in Utah and Nevada drylands, ensured that the model produced conservative estimates of growth in *S. caninervis* that could be applied to precipitation occurring throughout western North America. Within a given year, the model used an intra-annual timestep of each individual precipitation event. When applied to multiple years of precipitation data, the model also used an inter-annual timestep at the end of each calendar year when annual CCB was calculated. The model's output was a CCB value for each inter- and intra-annual timestep up to 100 years.

We next tested the ability of the model to predict mortality in *S. caninervis* by simulating meteorological conditions previously shown to cause physiological stress and mortality in this species (Barker et al. 2005). Using the same precipitation records from southeastern Utah as above, we simulated a 4-year drought period where precipitation was reduced by 30 %, and tested the ability of our model to project mortality. Mortality was defined as a transition from positive to negative CCB from which the replicate did not recover (often, declines compounded) over the time course of the run. We calculated moss C balance over the course

of the 4-year drought (simulation repeated 100 times), then compared the proportion of negative moss CCB values after the 4-year drought to the proportion of populations exhibiting bleaching and mortality in field observations published by Barker et al. (2005).

To generate precipitation regimes during 100-year simulations, we determined precipitation magnitudes and frequencies that occur during each season of the year (spring, summer, fall, or winter) based on records from southeastern Utah (EPA CAN 407 weather station, Canyonlands National Park, San Juan County, UT, 38.458°N, 109.82°W, 1,809 m asl) from 2006 to 2010. These years are representative of the hydroclimate variability in the region as they included 1 year of above average precipitation (2007), 1 year of below average precipitation (2009), and displayed variability in ENSO/LNSO (National Oceanic and Atmospheric Administration 2014; Garman 2006, 2007, 2008; Witwicki 2009, 2010). Recorded precipitation was analyzed in 30-min intervals for every day in the 4-year period. This enabled us to generate a detailed account of precipitation magnitude, frequency, seasonality, and variability over this timeframe. Periods without precipitation of 4 h or more were used to define breaks between precipitation events, and precipitation events <0.02 mm were excluded from analyses. Using the resultant precipitation events, we generated probability distributions (using a gamma distribution) for precipitation event sizes and frequencies for each season. The parameters used for each of these distributions (*rate* and *shape*) are shown in Table 1. To produce simulations of precipitation event size and frequency over the course of a year (and for multiple years) we drew values from the precipitation event size and frequency distributions for each season. To change simulated precipitation event sizes or frequencies from the current baseline model, we altered the rate parameters (for magnitudes, see "Simulations") that define the shapes of the distributions to reflect the simulated precipitation conditions.

Simulations

To determine the relative influence of annual and intra-annual precipitation on the performance of mosses, and to predict productivity based on precipitation projections from global models, we ran 17 different 100-year simulations using the model. Simulations fell into three categories: (1) changes in MAP; (2) changes in intra-annual precipitation while holding MAP constant; and (3) changes to intra-annual precipitation predicted for dryland ecosystems.

First, to simulate changes in MAP, we increased or decreased precipitation event size by 10, 20, or 30 % compared to current precipitation conditions. We altered distribution parameters for these simulations by manipulating the original meteorological data from southeastern Utah

Table 1 Gamma distribution parameters (*shape* and *rate*) used to represent precipitation magnitude (*R*) and frequency (DP) in model inputs

	Spring		Summer		Fall		Winter	
	R	DP	*R*	DP	*R*	DP	*R*	DP
Shape	0.782	0.961	0.624	1.064	0.793	0.985	0.869	1.539
Rate								
Baseline	0.215	0.246	0.159	0.355	0.184	0.233	0.375	0.422
+10 %	0.196	0.224	0.145	0.323	0.167	0.212	0.341	0.384
+20 %	0.180	0.205	0.133	0.269	0.153	0.194	0.312	0.352
+30 %	0.162	0.185	0.120	0.267	0.138	0.175	0.282	0.325
−10 %	0.239	0.274	0.114	0.395	0.204	0.259	0.416	0.469
−20 %	0.269	0.308	0.119	0.444	0.230	0.291	0.468	0.528
−30 %	0.323	0.369	0.239	0.532	0.276	0.350	0.562	0.633

The same *shape* parameters were used for all simulations for a given season. For *rate*, baseline parameters represent current precipitation conditions, and modifications by ±10, 20, and 30 % were alterations imposed to simulate changes in precipitation

by the desired percent reduction or increase in event size to generate novel rate parameters to use in distributions for each season of the year (Table 1). To simulate altered precipitation event sizes in the model, we drew values from the novel distributions.

Second, to simulate differences in precipitation event size and frequency while holding annual precipitation magnitude constant, we ran the model where annual precipitation was limited to 200, 250, or 300 (±2) mm year^{-1} (representing below average, average, and above average precipitation for drylands in North America, respectively; Grote et al. 2010). This was achieved by constraining maximum precipitation that could occur annually in the model. Within each of these categories, two simulations were run: reduced event sizes (−20 %) at increased frequency (+20 %), and increased event sizes (+20 %) at reduced frequency (−20 %). Precipitation frequency, modified by changing the length of the desiccation period (DP) between precipitation events, was altered for these simulations in the same manner as described for event size, only the novel DP *rate* parameters (modified by ±20 %) were applied to seasonal DP distributions.

Third, to examine precipitation scenarios predicted by prognostic modeling, we ran simulations that matched as closely as possible four future precipitation scenarios (see Table 2c) In addition to manipulation of precipitation event size and frequency, these simulations also manipulated the number of rare large events and rare long droughts per year as well as seasonal variation in precipitation. To simulate an increase in either rare large precipitation events or rare long drought periods, we ran the model where 10 of the simulated precipitation events or DPs in a given year were replaced with a value four times the mean annual value. To simulate seasonal variation in precipitation event size and DP length, we manipulated precipitation event size and DP in the season(s) of interest (spring, summer, fall, winter)

by modifying baseline gamma distributions (see Table 1). MAP was not constrained in these simulations because (1) projections applied by the model reflected a minimal change to MAP, and (2) small changes in MAP induced by the simulations were of interest to us experimentally, allowing us to examine to what extent MAP versus intra-annual precipitation explained variation in long-term CCB. The simulated conditions were: +20 % DP, 10 rare large precipitation events per year (Scenario 1), −20 % DP, −20 % precipitation event size (Scenario 2), −20 % precipitation event size, 10 rare long DPs per year (Scenario 3), and precipitation event sizes: +10 % in winter, −20 % in spring, and +30 % in summer (Scenario 4).

All simulations were run for 100 years, using 100 independent runs (replicates) each. Mean annual precipitation, mean 100-year CCB, and the slope of the CCB-time relationship (m) were recorded following each simulation.

Statistical analyses

Model construction, simulations, and statistical analyses were all performed using the program *R* (R Development Core Team 2012). We used linear models to examine CCB as a function of time for all simulations, and one-way analyses of variance with Tukey's HSD post hoc comparison on means to determine significant differences between CCB simulations. We used a multiple linear regression to determine the relative ability of MAP and intra-annual precipitation (event size and DP) to predict moss CCB in the four simulated precipitation scenarios. When MAP was held constant, we used multiple linear regressions to examine the relative abilities of MAP and intra-annual precipitation to predict CCB at each individual MAP level. Next, we employed Welch two-sample *t* tests to examine differences in CCB among simulation pairs at each MAP level. Partial residual analyses were used to examine the ability of each

Table 2 Simulations of biocrust moss productivity (cumulative carbon balance; CCB, mg C m^{-2}) in the next century as a function of (a) changes in annual precipitation as ±10, 20, or 30 % from current baseline conditions; (b) alterations in intra-annual precipitation (event size and frequency) while MAP is held constant; and (c) four precipitation scenarios based on global models

(a) Changes in annual precipitation as ±10, 20, or 30 % from current baseline conditions

Annual precipitation, percent change from current baseline	Mean annual precipitation (mm ± SD)	Mean 100-year CCB (mg C m^{-2} ± SD)	Linear model	
			r^2	P
+30 %	344.20 (±45.65)	761.24 (±32.76)	0.989	<0.0001
+20 %	308.48 (±46.36)	608.47 (±27.38)	0.988	<0.0001
+10 %	286.41 (±39.17)	488.25 (±22.99)	0.985	<0.0001
Current baseline	260.00 (±40.70)	377.07 (±21.69)	0.979	<0.0001
−10 %	235.57 (±34.04)	258.97 (±19.24)	0.965	<0.0001
−20 %	209.30 (±29.62)	142.09 (±19.00)	0.910	<0.0001
−30 %	168.23 (±24.19)	−16.47 (±14.40)	0.156	<0.0001

(b) Alterations in intra-annual precipitation (event size and frequency) while MAP is held constant

Annual rainfall (mm)	Intra-annual manipulation	Mean 100-year CCB (mg C m^{-2} ± SD)	Linear model	
			r^2	P
200	+Event size, −frequency	206.15 (±19.24)	0.943	<0.0001
200	−Event size, +frequency	239.08 (±13.98)	0.979	<0.0001
250	+Event size, −frequency	443.16 (±21.36)	0.987	<0.0001
250	−Event size, +frequency	565.01 (±18.36)	0.994	<0.0001
300	+Event size, −frequency	615.47 (±25.12)	0.989	<0.0001
300	−Event size, +frequency	817.89 (±20.18)	0.997	<0.0001

(c) Four precipitation scenarios based on global models

Scenario	Modeled precipitation changes	Mean annual precipitation (mm ± SD)	Mean 100-year CCB (mg C m^{-2} ± SD)	Percent change from current baseline CCB	Linear model	
					r^2	P
1	−20 % precip. frequency, +frequency of rare large events	355.49 (±60.82)	218.32 (±23.29)	−42.10 %	0.941	<0.0001
2	+20 % precip. frequency, −20 % event size	221.82 (±31.59)	276.26 (±18.05)	−26.76 %	0.975	<0.0001
3	−20 % event size, +frequency of rare long dry periods	206.73 (±33.10)	139.18 (±17.37)	−63.09 %	0.907	<0.0001
4	Event sizes: +10 % in winter, −20 % in spring, +30 % in summer	271.90 (±40.49)	404.82 (±22.72)	+7.360 %	0.979	<0.0001

Linear models in each case represent the relationship between CCB and time for the 100-year simulation period

independent factor in the linear models (MAP, precipitation event size, precipitation frequency) to explain variance of CCB after accounting for the effects of the other two factors.

Results

Simulations using historical precipitation records showed that the model reasonably predicted current patterns of growth as well as precipitation-induced mortality. The model produced biocrust moss annual growth rates of 3.75 ± 0.22 mg C, similar to growth rates of 2.9–4.0 mg C calculated from recorded annual biomass and shoot increment lengths (Stark et al. 1998). Under drought conditions simulated for 4 years, the model predicted 40 ± 5 % mortality in accordance with field observations of 35–50 % mortality for a drought of the same duration (Barker et al. 2005). When run under current precipitation dynamics, the model produced a 100-year cumulative carbon balance of 377.1 ± 21.7 mg C (Fig. 1a; Table 2a).

When MAP was increased by 10, 20 and 30 %, mean 100-year CCB increased by 29.5, 61.4, and 101.9 % respectively (Fig. 1a; Table 2a). When MAP was reduced by 10 and 20 %, mean 100-year CCB was reduced by 31.3 and 62.4 %, respectively. When MAP was reduced by
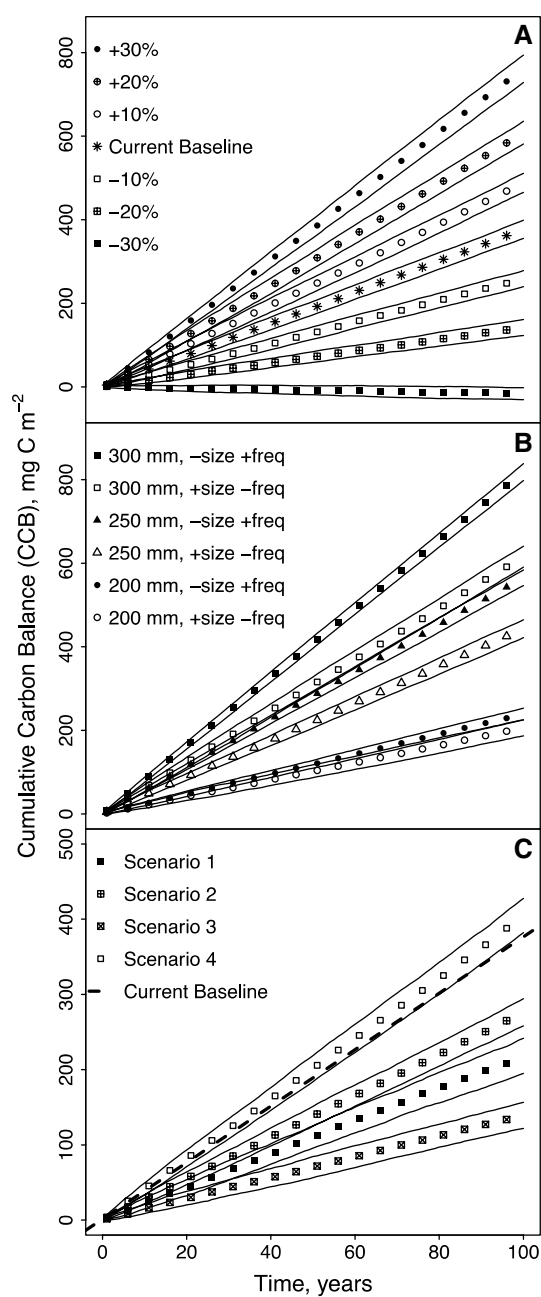
Fig. 1 One-hundred-year simulations of biocrust moss productivity (cumulative carbon balance; CCB, mg C m^{-2}) as a function of **a** changes in mean annual precipitation (MAP) by ±10 % (*open circles* and *squares*), 20 % (*crossed circles* and *squares*) or 30 % (*filled circles* and *squares*) from current baseline levels (*asterisk*), **b** changes in precipitation event size and frequency (+size –frequency shown as *open symbols*; –size +frequency shown as *closed symbols*) while MAP is held constant at 200 (*circles*), 250 (*triangles*), or 300 (*squares*) mm year^{-1}, and **c** four scenarios for dryland precipitation changes in the next century based on global models: simulations for Scenario 1 (*closed squares*), Scenario 2 (*crossed squares*), Scenario 3 (*hashed squares*), and Scenario 4 (*open squares*) are shown (see Table 2c for details) and the Current Baseline simulation is included for reference (*dashed line*). All symbols shown are mean CCB values (*n* = 100 replicates per simulation) at 5-year intervals, and *lines* above and below each simulation group show standard deviation in CCB over the 100-year period

30 %, 100-year CCB declined at a rate of -0.16 ± 0.07 mg C year^{-1} and ended in a carbon deficit of -16.5 ± 14.4 mg C (Fig. 1a; Table 2a).

When intra-annual precipitation (differences in event size and frequency) was altered while MAP was held constant at either 200, 250, or 300 mm year^{-1}, moss CCB differed significantly among different intra-annual precipitation simulations in all three MAP categories. At constant MAP, intra-annual precipitation consisting of less frequent (-20 %) larger events ($+20$ %) resulted in significantly different CCB values compared to more frequent ($+20$ %) smaller (-20 %) events ($P < 0.0001$) (Fig. 1b). The difference in productivity between these paired intra-annual precipitation simulations increased with annual precipitation, and productivity differences were most pronounced when MAP was 300 mm year^{-1}. Of the two intra-annual simulations in each MAP category, the simulation including smaller event sizes occurring at higher frequency always resulted in larger C gain per year and higher 100-year CCB than the simulation including larger event sizes at lower frequency (Table 2b). In the simulation in which intra-annual precipitation and MAP were both manipulated, these predictors explained 49.4 and 78.6 % of the variance in CCB, respectively, and both predictors combined were able to account for 87.3 % of the variance in CCB (Table 2a). Partial residual analyses indicated that after accounting for the variance explained by the other two factors, MAP, precipitation event size, and precipitation frequency were able to account for 96.7, 3.9, and 85 % of the variance in CCB, respectively (Table 3a).

When moss productivity was modeled based on four dryland precipitation scenarios predicted by climate models (Table 2c), all but one (Scenario 4) resulted in 100-year productivity values that decreased relative to current productivity levels (Fig. 1c; Table 2c). Scenario 4, in which precipitation was seasonally manipulated but frequency did not change, resulted in a 7.4 % increase in 100-year CCB from current levels. Scenario 1 (reduced precipitation frequency and increased number of rare large events) and Scenario 2 (increased precipitation frequency and reduced event size) resulted in a 42 and 27 % decline in 100-year CCB from current productivity levels, respectively (Table 2c). The lowest 100-year CCB values (63 % below current levels) occurred using Scenario 3, in which precipitation event size was reduced and the frequency of rare long droughts was increased. Modeled MAP in the four scenarios was 350, 222, 207, and 272 mm, respectively, and in all cases fell within the range projected by associated global models. Independently, intra-annual precipitation and MAP explained 39.2 and 2.0 % of the variance in CCB for global model-based simulations, respectively, and both predictors combined were able to account for 52.4 %

Table 3 Results from multiple regressions performed to assess the relative predictive ability of mean annual precipitation (*MAP*) and intra-annual precipitation (event size and frequency) for moss performance (cumulative carbon balance, CCB) in the next 100 years

Model	Factors	*df*	*F*	r^2	*P*	PR
(a) Intra-annual precipitation varied at each level of MAP						
MAP	1	598	2193	0.786	<0.0001	
Intra-annual precipitation	3	596	193.7	0.494	<0.0001	
MAP + intra-annual precipitation	6	593	681.5	0.873	<0.0001	0.967 (MAP) 0.039 (event size) 0.850 (frequency)
(b) Global model-based scenarios						
MAP	1	389	8.11	0.020	<0.01	
Intra-annual precipitation	3	396	84.99	0.392	<0.0001	
MAP + intra-annual	6	393	72.08	0.524	<0.0001	0.001 (MAP) 0.971 (event size) 0.285 (frequency)

The MAP model included MAP as a single factor, the intra-annual precipitation model included event size, frequency, and event size × frequency for a total of three factors, and the MAP + intra-annual precipitation model included all factors and interactions. Partial residuals (*PR*) report variance explained by each of the factors in the MAP + intra-annual precipitation model after accounting for the effects of the other two factors

of the variance in CCB (Table 3b). Analysis of partial residuals for the global model-based simulations showed that after accounting for the variance explained by the other two factors, MAP, precipitation event size, and precipitation frequency were able to account for <0.1, 97.1, and 28.5 % of the variance in CCB, respectively (Table 3b).

Discussion

Individual pulsed precipitation events drive resource availability and productivity in drylands (Huxman et al. 2004; Reynolds et al. 2004; Schwinning and Sala 2004), and, in support of our hypothesis, this study suggests that changes in intra-annual rainfall patterns could have a disproportionately large influence on plants in these ecosystems in a future climate. The physiology-based simulations presented here suggest moss productivity in western North America may decline by up to 63 % over the next 100 years, and this prediction is heavily influenced by the consideration of intra-annual precipitation in addition to MAP.

In simulations in which MAP was held constant at three magnitudes and intra-annual precipitation was altered within each MAP category, MAP explained 78.6 % of the variability of CCB (Table 3a). Moss productivity increased as a function of MAP and was greatest when MAP was 300 mm year^{-1}, the highest level simulated. This relationship between MAP and productivity exists because, in desiccation-tolerant mosses, carbon uptake occurs only when plants are hydrated and physiologically active during precipitation events (Oliver et al. 2000; Proctor 2000; Graham et al. 2006; Coe et al. 2012): if annual precipitation is greater, more opportunities for growth result in greater long-term productivity.

In these same simulations, intra-annual precipitation explained 49.4 % of the variance in CCB, and precipitation frequency accounted for 85 % of the variability in CCB after MAP and event size were accounted for (Table 3a). Additionally, CCB varied by 16–33 % when precipitation event size and frequency were altered by ±20 % but MAP was unchanged. These differences were accentuated as MAP increased, and intra-annual precipitation largely drove productivity when MAP was highest (300 mm), suggesting that intra-annual precipitation could become an increasingly important driver of productivity if MAP increases in dryland systems.

Among the simulations where MAP was held constant, growth rates and overall productivity were highest when precipitation event size was reduced and frequency was increased (Fig. 1b; Table 2b). This finding contrasts shorter-term field experiments on biocrust communities, where an increase in frequency of small events in April through September caused declines in productivity (Belnap et al. 2004; Reed et al. 2012). The modeled results presented here showed the opposite pattern, likely because future precipitation was created in the model to reflect natural stochasticity in precipitation event size and frequency. Therefore, it is very unlikely that the model produced only numerous small events in the summer, and instead produced at least one or two events large enough to maintain a C surplus throughout the season.

When intra-annual precipitation and MAP were both used in a combined linear model to predict productivity in the next century, the combined model was able to explain 87.3 % of the variance in CCB in simulations holding MAP constant. The combined model had higher predictive power than those using either intra-annual precipitation or MAP as independent predictors, indicating intra-annual precipitation is an important driver of productivity for dryland plants and must be included along with MAP when predicting productivity.

When the model was applied to predict biocrust moss productivity in the next 100 years based on precipitation

changes projected in current global models, three of the four scenarios tested resulted in reduced productivity compared current rates. This suggests an overall negative outlook for long-term performance of biocrust mosses (Fig. 1c; Table 2c). Annual growth and 100-year CCB was the lowest (63 % below current rates) in Scenario 3, in which the frequency of rare long droughts was increased annually, precipitation event size was reduced by 20 %, and MAP was reduced by 15 %. Under these conditions, carbon uptake was severely limited because smaller events lead to reductions in carbon gain (or even carbon loss), and longer droughts place constraints on physiological recovery when precipitation does return (Proctor 2001; Coe et al. 2012). Scenario 1, the one most commonly forecasted in global models and the one most commonly predicted for western North America (Cayan et al. 2010), resulted in a 42 % reduction in 100-year CCB compared to current productivity rates, in spite of a 15–20 % increase in simulated MAP. This result was driven by a 20 % reduction in precipitation frequency and the presence of rare large precipitation events. From a carbon balance perspective, single large events such as those simulated in this scenario sustain biocrust mosses through longer periods of unfavorable hydrological conditions by compensating for carbon losses. However, our results indicate that if large events are rare, positive effects on performance may be dampened by reductions in overall precipitation frequency. Scenario 2 (in which precipitation frequency was increased by 20 % and event size was reduced by 20 %) resulted in a 27 % decline in moss productivity over the next 100 years. Under these conditions, the gains from increased precipitation frequency were offset by the reduction in precipitation event size, highlighting the importance of precipitation event size in long-term performance. Finally, Scenario 4, in which precipitation magnitude was increased in the winter and summer yet decreased in the spring, and simulated MAP was unchanged, productivity surpassed current levels by 7.4 %, probably for two reasons: first, this simulation increased precipitation during the time of year (winter) when most growth occurs (Stark 1997; Kidron et al. 2012), resulting in greater long-term productivity; and second, large precipitation events increased during the summer in this scenario and have been shown to produce carbon gains (Coe et al. 2012). The moss productivity increases observed in Scenario 4 are also noteworthy for drylands in western North America in general given the importance of cool season precipitation for plant and soil communities in these regions (Johnson 1976; Gebauer and Ehleringer 2000).

In the simulations based on projections from global models, MAP was a weak predictor of productivity ($r^2 = 0.02$), and in one case (Scenario 1) above average MAP resulted in below average rates of productivity. Intra-annual precipitation was a stronger predictor and accounted for nearly 40 % of the variance in productivity. Precipitation event size, which accounted for 97 % of the variance in CCB after MAP and precipitation frequency were accounted for, dominated productivity responses. Collectively, these results demonstrate that (1) intra-annual precipitation changes will dominate responses in biocrust mosses, and (2) changes in productivity are not only possible, but likely, even if dryland MAP does not change in the future. These conclusions are important because global models for drylands project dramatic changes in the aspects of precipitation that appear to have the largest consequences for moss productivity (magnitude and timing of precipitation events on intra-annual scales) and small or negligible changes in precipitation aspects that are less likely to drive long-term productivity (MAP).

As global precipitation continues to change in dramatic and uncertain ways, it is becoming increasingly important to understand the responses of terrestrial vegetation to these changes. When taken in aggregate, two important points arise from this dryland-based modeling exercise. First, based on an array of tested precipitation projections for the next century, we have shown that, if drought conditions intensify or precipitation event sizes are reduced in western North America, biocrust mosses will exhibit declines in productivity of 25−63 %. If mosses are lost from this system, as has been observed in field precipitation manipulations (Reed et al. 2012), they are unlikely to be replaced by a functional equivalent (Zelikova et al. 2012; Pietrasiak et al. 2014), and, because of the intrinsic role these plants play in dryland communities, cascading effects on soil stability, nutrient cycling, and surface albedo will likely follow. These are all processes that feed back to influence regional and ecosystem scale processes, therefore precipitation-induced declines in biocrust mosses have the potential to push these systems into an alternative state (Belnap 1995; Rietkerk et al. 1997; Maestre et al. 2005; Miller 2005; and see Bowker 2007). Second, this study demonstrates that precipitation analyses solely using MAP are insufficient in making accurate predictions for dryland community responses to altered precipitation. Even if MAP does not change, as is predicted in some models, it is likely that changes in intra-annual precipitation patterns will strongly drive future performance in dryland plants. Individual events are extremely important for organisms exhibiting a pulse-dynamic response to precipitation, making it essential to include intra-annual precipitation in models to determine the productivity of dryland organisms in a future climate.

Conflict of interest The authors declare no conflict of interest with the organizations that sponsored the research.

Ethical standard The experiments presented in this manuscript comply with the current laws in the USA, where the experiments were performed.

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