Responses of Grassland Production to Single and Multiple Global Environmental Changes

Jeffrey S. Dukes1,*, Nona R. Chiariello2, Elsa E. Cleland2, Lisa A. Moore1, M. Rebecca Shaw1, Susan Thayer3, Todd Tober1, Harold A. Mooney2, Christopher B. Field1

1 Department of Global Ecology, Carnegie Institution of Washington, Stanford, California, United States of America, 2 Department of Biological Sciences, Stanford University, Stanford, California, United States of America, 3 Department of Plant Biology, Carnegie Institution of Washington, Stanford, California, United States of America

In this century, increasing concentrations of carbon dioxide (CO2) and other greenhouse gases in the Earth’s atmosphere are expected to cause warmer surface temperatures and changes in precipitation patterns. At the same time, reactive nitrogen is entering natural systems at unprecedented rates. These global environmental changes have consequences for the functioning of natural ecosystems, and responses of these systems may feed back to affect climate and atmospheric composition. Here, we report plant growth responses of an ecosystem exposed to factorial combinations of four expected global environmental changes. We exposed California grassland to elevated CO2, temperature, precipitation, and nitrogen deposition for five years. Root and shoot production did not respond to elevated CO2 or modest warming. Supplemental precipitation led to increases in shoot production and offsetting decreases in root production. Supplemental nitrate deposition increased total production by an average of 26%, primarily by stimulating shoot growth. Interactions among the main treatments were rare. Together, these results suggest that production in this grassland will respond minimally to changes in CO2 and winter precipitation, and to small amounts of warming. Increased nitrate deposition would have stronger effects on the grassland. Aside from this nitrate response, expectations that a changing atmosphere and climate would promote carbon storage by increasing plant growth appear unlikely to be realized in this system.

Introduction

Since the start of the Industrial Revolution, human activities have changed the composition of the atmosphere at an accelerating rate, with increasingly recognized consequences for Earth’s climate and biogeochemical cycles [1–3]. Ecosystem responses to these changes may further affect climate and biogeochemical cycling [3,4], and alter the character of ecosystem services provided to society [5]. During the past two decades, researchers have studied ecosystem responses to changes in climate, nitrogen (N) deposition, and atmospheric carbon dioxide (CO2) [6]. In some natural systems, responses of plant growth and resource use to one of these global changes have been extensively quantified. However, few studies have examined responses of ecosystems to the simultaneous and interacting global changes likely to be seen later this century. Even fewer studies have observed these responses over many years.

Production responses to single environmental changes vary widely among systems, and by year.

First, doubled atmospheric CO2 increased aboveground biomass production by an average of 14% across nine herbaceous systems [6]. However, CO2 enrichment suppressed production in some systems, while increasing it in others by as much as 85%. Some grasslands responded more positively in dry years than wet years [7–9], possibly because plants narrow their stomatal openings under elevated CO2, which leads to water savings.

Second, observed patterns of plant growth across natural gradients of precipitation and across years within locations suggest that increases in precipitation have the most positive effect on plant growth in systems with the lowest annual inputs [10]. Where precipitation exceeds about 3,000 mm per year, additional precipitation may suppress growth [11].

Third, warming increases aboveground biomass production in many systems, with the strongest effects in colder climates. Across 20 experimental warming sites in tundra, grassland, and forest, increases in aboveground productivity averaged 19% [12]. Across natural systems, production tends to increase with increasing mean annual temperature [11]. Within some productive systems, aboveground growth is correlated with maximum growing season temperature [10].

Fourth, responses to N additions are generally positive across temperate, boreal, and arctic systems [13,14]. While all terrestrial systems are experiencing a fairly uniform increase in CO2, the character of other global changes varies from one region to the next. Thus, the mix of global changes impacting a given region will depend on both

Abbreviations: C, carbon; CO2, carbon dioxide; JRGCE, Jasper Ridge Global Change Experiment; N, nitrogen; NPP, net primary production; P, phosphorus

* To whom correspondence should be addressed. E-mail: jeffrey.dukes@umb.edu
¤ Current address: Department of Biology, University of Massachusetts, Boston, Massachusetts, United States of America

Received September 27, 2004; Accepted July 13, 2005; Published August 9, 2005
DOI: 10.1371/journal.pbio.0030319

Copyright: © 2005 Dukes et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

PLOS Biology | www.plosbiology.org
space and time. Understanding the responses of ecosystems to potentially interacting global changes is critical to predicting ecosystem feedbacks to climate and biogeochemical cycles. In particular, the response of carbon (C) storage in ecosystems is dependent on (and proportionally related to) two ecosystem processes: C inputs from primary production, and the residence time of C in the system [15].

Several previous studies have examined interactions between N availability and other global change factors [16–18], and some have examined interactions between CO₂ and changes in water availability [8,9], climate [19–21], or loss of biodiversity [22,23]. However, we are still developing a conceptual framework to describe the conditions under which a given interaction is most important. For instance, mineral element availability may progressively limit positive CO₂ responses in some systems, but other systems are unlikely to develop such an interaction [24]. Similarly, where elevated CO₂ leads to important soil moisture savings [25], increases in precipitation might negate any CO₂ effect. Temperature and CO₂ responses are frequently assumed to be additive, although few ecosystem-scale experiments exist [26]. No previous studies, to our knowledge, have simultaneously tested responses to enhanced CO₂, warming, increased precipitation, and increased N deposition.

Since 1998, the Jasper Ridge Global Change Experiment (JRGCE) has exposed a moderately fertile grassland to atmospheric and climate conditions expected later this century, and to enhanced nitrate deposition. Because small-statured, annual species dominate California grasslands, this ecosystem is well suited for the study of responses to global changes. Thousands of individual plants can be examined within a small area, and changes in the chemistry of plants and plant litter quickly reach the soil as the plants die. Additionally, the plants complete one generation each year, so competition and selection can “tune” the performance of the grassland to new environmental conditions more quickly than would occur in systems with longer-lived species. While systems dominated by larger, longer-lived organisms might adjust to a step change in CO₂ or N deposition over a span of decades, annual grassland can be expected to reach a steady, “representative” response more quickly.

With a wide range of treatments and treatment combinations, the JRGCE provides a foundation for characterizing how ecosystems may perform in the future in a range of possible scenarios. Of particular interest is determining whether ecosystem responses to individual factors are additive. How reliably can we predict ecosystem responses to many concurrent environmental changes based on responses to individual changes? Previously, Shaw et al. [27] focused on CO₂ responses in this grassland and found an unexpected result: elevated CO₂ suppressed positive production responses to other global changes during the third year of the JRGCE. Here, we present a comprehensive description of the responses of grassland production to all four global changes over the first 5 y of experimental treatments, and discuss these responses in the context of natural, as well as experimental, climate variation. With this expanded dataset, we are able to put the results from Shaw et al. [27] in a larger context, and determine whether there have been consistent changes in grassland net primary production (NPP) that could directly affect the amount of C stored in this ecosystem.

Results

Production Responses to Global Changes

Mean production (NPP) of the control treatment varied from 577 to 933 g m⁻² across the 1999–2003 growing seasons (see related data in Figure 1). The four main treatments differed in their average effects on NPP (Figures 2 and 3). Only nitrate deposition consistently affected NPP, causing increases of 21%–42% in all years but 2000. Shoots generally responded more positively to N addition than roots did, leading to decreases in root-to-shoot ratios (Figure 2; Tables S1 and S2). Increased precipitation had little effect on NPP, as negative root responses largely counteracted positive shoot responses. Neither warming nor elevated CO₂ significantly affected shoot, root, or total production in any year. Increased precipitation and nitrate deposition frequently decreased root-to-shoot ratios, while heat and CO₂ did not affect allocation (Figure 2; Tables S1 and S2).

Nitrate strongly increased NPP in all years but 2000, when a four-way interaction was significant (Figure 3; Table S3). Aboveground biomass responses drove the NPP results, as nitrate increased shoot production in all years but 2000 (Figure 4; Table S4). In 2001, nitrate also affected shoot responses to rainfall and CO₂; precipitation responses were more positive under increased N, but only in ambient CO₂ levels. In this year only, elevated CO₂ suppressed the shoot response to combined N and precipitation (Figure 4). Roots responded positively to nitrate deposition in 1999, but not in subsequent years. In 2000, 2001, and 2003, increased rainfall suppressed root production (Figure 5; Table S5).

Figure 1. Biomass Production, Cumulative Precipitation, and Cumulative Temperature from 1998 (the Year before Treatments Began) to 2003

Bars for shoot biomass (grey) and root biomass (black) represent mean values (±SE, n = 8) for quadrants in the “infracore control” treatment, which experienced ambient conditions (see Materials and Methods). Cumulative precipitation includes the germinating rain event (defined here as the event that brought cumulative rainfall after October 1 above 12.5 mm) and subsequent precipitation until the last harvest of the year. Cumulative temperature is the sum of average temperatures (in °C) over all days from germination until the final harvest. Shoot biomass (g m⁻²) was not related to growing season precipitation (mm; linear regression: p = 0.87) or cumulative temperature (°C; p = 0.27), but there was a weak relationship between shoot growth and fall precipitation (linear regression: p = 0.06, slope = 0.646, r² = 0.627).

DOI: 10.1371/journal.pbio.0030319.g001
Across all 5 y of the experiment, nitrate deposition strongly increased shoot biomass and NPP, and slightly increased root biomass (repeated measures analysis; Figure 6). The only other treatment to affect biomass production across years was precipitation, which increased shoot growth but suppressed root growth, leading to no effect on NPP (Figure 6).

How Are Responses to Global Changes Affected by the Background Climate?

In most cases, grassland responses to the global change treatments did not depend on climatic factors as measured by regressions against accumulated degree-days or total precipitation ($p > 0.05$). The exception was the response of shoot growth to temperature, which increased in warmer years ($p < 0.05$, slope $= 0.001$, $r^2 = 0.10$). While the total precipitation and degree-day sums facilitate simple comparisons of responses across years and climate treatments, these metrics do not necessarily capture the critical aspects of climate during the growing season. The sensitivity of grassland production to interannual variation in weather is further discussed below.

Progressive Effects

The pattern from 5 y of treatments in the JRGCE hints at the possibility of progressive or cumulative effects but is rarely definitive. For NPP, aboveground production, and belowground production, no regression of treatment effect on time is significant. Across all of the single-factor treatments and treatment combinations, treatment effects appeared to progressively decrease root production ($p = 0.09$). The strongest evidence for progressive effects comes from changes in allocation patterns. The effect of nitrate on root-to-shoot ratios became increasingly negative over time ($p = 0.02$), and the response of root-to-shoot ratios to elevated CO$_2$ shifted from positive to negative ($p = 0.07$).

Discussion

Over the first 5 y of the JRGCE, production responded minimally to elevated temperature and CO$_2$, positively to increased nitrate deposition, and in a context-dependent manner to supplemental precipitation. The response of production to elevated CO$_2$ is negative in some but not all.
treatments and years [27]. As a consequence, NPP did not respond to elevated CO$_2$ over the 5-y period (means: ambient CO$_2$, 925 g m$^{-2}$; elevated CO$_2$, 887 g m$^{-2}$; $p = 0.62$). The lack of response to CO$_2$ enrichment indicates that this and similar grasslands are unlikely to experience strong C sinks from CO$_2$ fertilization over the next century. Neither is the response to any future precipitation increase likely to lead to increased C storage. Future increases in nitrate deposition could increase NPP and perhaps C storage, while the experimental warming was probably too slight to interpret as an analog for the end of the century.

Responses to Global Environmental Changes

Except in groups of treatments [27], production did not respond to elevated CO$_2$ over the 5-y period (means: ambient CO$_2$, 925 g m$^{-2}$; elevated CO$_2$, 887 g m$^{-2}$; $p = 0.62$). The lack of response to CO$_2$ enrichment indicates that this and similar grasslands are unlikely to experience strong C sinks from CO$_2$ fertilization over the next century. Neither is the response to any future precipitation increase likely to lead to increased C storage. Future increases in nitrate deposition could increase NPP and perhaps C storage, while the experimental warming was probably too slight to interpret as an analog for the end of the century.

Figure 4. Mean Shoot Biomass in Individual and Combined Global Change Treatments

Error bars denote one standard error. Shading, labels, and statistics as in Figure 3. DOI: 10.1371/journal.pbio.0030319.g004

Figure 5. Mean Root Biomass in Individual and Combined Global Change Treatments

Error bars denote one standard error. Shading, labels, and statistics as in Figure 3, with one addition ($^{*}$, 0.10 > $p$ > 0.05). DOI: 10.1371/journal.pbio.0030319.g005

summer-active species that take advantage of wetter soils in late spring. In the JRGCE, such late-flowering forbs were rare. They were absent from all harvested areas in 1999 and constituted 0.37% of the aboveground biomass harvest in 2003. Our peak biomass harvests took place before these forbs reached full size, but the species were so rare that their responses could have impacted overall NPP only if they were massively sensitive to the observed water savings from elevated CO$_2$ [29].

Warming did not affect grassland production, but it did affect the phenology of many species ([30]; Chiariello et al., unpublished data). Zavaleta et al. [29] found that warming led to earlier senescence of many of the dominant species, leaving additional water in soils over the summer. In a setting with responsive plant species, this water savings could combine with that from elevated CO$_2$ to increase the production and/or establishment of late-season annuals, shrubs, and trees [31].

Precipitation affected plant growth more strongly than warming or CO$_2$, with positive effects on shoots and negative effects on roots across years (Figure 6), although analyses of
individual years indicated that these effects were not always significant (see Figures 2 and 5). Averaged across treatments, these counteracting shoot and root effects led to no effect on NPP (see Figures 3 and 6). Why did supplemental precipitation decrease root growth? It is possible that allocation to roots decreased as soil resources became more available. In this case, root growth could have been downregulated by increases in water availability or availability of nutrients that are mobile in water. A leading candidate for such a nutrient would be nitrate, which consistently decreased root-to-shoot ratio, with significant effects in two of the 5 y. It is also possible that root growth is affected by small changes in water availability, or that soils in the precipitation treatment occasionally became waterlogged, suppressing root respiration.

Of the four global changes, nitrate deposition had the most consistent, positive effects on plant production. Nitrate increased shoot growth more consistently and by a greater amount than root growth, leading to lower root-to-shoot ratios. Several previous studies have found similarly positive responses of California grasslands to various forms of N (e.g., [32–35]).

Explaining the CO2 Response

The biomass responses presented here include the results from the 2000–2001 growing season discussed by Shaw et al. [27]. The analysis by Shaw et al. primarily focused on CO2 responses, demonstrating that elevated CO2 partially suppressed NPP increases in response to warming, extra precipitation, and nitrate deposition. Across the 5-y dataset, as in the analysis of Shaw et al., there was not a significant, experiment-wide CO2 effect over the entire dataset or in any individual year.

Why doesn’t elevated CO2 increase production in this grassland? Several lines of evidence suggest phosphorus (P) limitation could play a role. Both N deposition and elevated CO2 decrease plant P concentration, and, at least in some treatment combinations, elevated CO2 reduces total plant P uptake [30]. In some years, elevated CO2 appears to favor P uptake by microbes over plants [30]. A comparison of grassland production responses after a summer wildfire at the JRGCE also supports the P limitation hypothesis (H. Henry et al., unpublished data). In this study, elevated CO2 suppressed production in unburned grassland, but not in burned areas. Plant growth also responded more strongly to N deposition in burned areas. Ratios of N to P in shoots of the dominant annual grasses were lower in the burned area, suggesting that the fire may have made available more P in ash deposits. The burn alone did not increase plant growth, indicating P limitation may be triggered by elevated CO2 or N deposition. Henry and colleagues cannot definitively separate effects of P availability from changes in microclimate in the burned area, but further studies on the role of P in this grassland are under way. Ongoing research in the JRGCE is also exploring how changes in herbivory, phenology, allocation, and other factors may prevent the grassland from responding positively to CO2.

The Role of Weather

Rangeland scientists have developed many equations to predict shoot growth (forage yields) in annual grasslands based on weather variables [36–40]. In general, measures of heat (as degree-days) and/or precipitation predict annual shoot growth with reasonable accuracy [39,40]. Warmer years and wetter fall and spring seasons usually lead to greater shoot growth. Why, then, did increased temperatures and precipitation not consistently increase shoot growth in this experiment? Most of the precipitation additions in this experiment were associated with rain events, and most of these events occurred in the colder months of winter. In contrast to precipitation in the fall and spring, winter rainfall is not significantly related to shoot production in California grasslands ([36]; J. Dukes, unpublished data). Supplemental precipitation could have its greatest effect by advancing the start of the growing season, eliminating occasional mid-season droughts, or delaying the end of the growing season in years with dry spring months. Our precipitation treatments never advanced the start of growing seasons, but occasionally reduced drought severity. The most positive effect of precipitation was in 2001 (see Figure 2), when a dry period occurred at the end of the growing season and the added precipitation extended the growing period in addition to eliminating the drought.

Despite predictions that CO2 responses would be most positive in drier years [7], this was not the pattern in the JRGCE. Across the range of annual precipitation that the
Progressive Effects

Responses of NPP to global changes could be progressive for a number of reasons. Changes in community structure could lead to increases in the abundance of unusually responsive (or unresponsive) species. Continuing additions may directly affect the availability of a potentially persistent resource (e.g., nitrate). Or there might be feedbacks through the quantity or quality of soil organic matter [24]. The strengthening effect of N deposition on root-to-shoot allocation patterns could result from a progressive increase in N availability as a consequence of an increasing ecosystem stock. It may also reflect stimulated N mineralization resulting from increased rates of decomposition [41].

In the JRGCE, the evidence for progressive effects is limited in the results to date. Tests to quantify the magnitude, direction, and persistence of progressive effects are a central goal of continuing studies.

Other Considerations

The change in the harvest strategy from one to two harvests between 2000 and 2001 may account for subtle differences between the responses in the first two and the last three years of the dataset. In some cases, responses to treatments were stronger at the second harvest than in the first. High variability in harvested root biomass complicates the task of quantifying treatment effects on root production. Frequently, variation within a treatment was extreme. For instance, in 2003 the control treatment averaged 278 g m\(^{-2}\) root biomass, with a range of 122–552 g m\(^{-2}\).

Our biomass-based root production results underestimated actual production for two reasons. First, annual root production exceeds peak live biomass by approximately 50% in this grassland [42]. Second, we used root data from soil cores taken to 15 cm, a depth that captures 80%–90% of total root biomass (L. Moore, unpublished data). To assess the impacts of these simplifications, we recalculated our data using correction factors. First, we estimated root biomass to 30 cm. For three of the five years, we had measured root biomass from soil cores to 30 cm depth. In the other 2 y, we estimated peak root biomass to 30 cm based on the ratio of roots to 15 cm and 30 cm in the years for which we had measurements. Second, we multiplied the biomass to 30 cm by 1.54, to account for turnover [42]. These corrections had little effect on patterns of NPP responses to the treatments, and altered the significance of the results in only two cases (the temperature \(\times\) nitrate interaction became significant \([p = 0.047]\) in 2000, and the nitrate effect became only marginally significant \([p = 0.086]\) in 2002).

Implications

What are the implications of these changes in grassland production for C storage and other ecosystem services? Production increases are likely to lead to increased productivity on their own. While interactions among changes in climate and CO\(_2\) may influence biomass production in specific years, the consequences of these interactions appear limited when averaged over longer time scales.

The JRGCE is one of the most comprehensive global-change experiments to date. It is one of relatively few ecosystem scale experiments to use naturally occurring—as opposed to artificially constructed—ecosystems. We see no reason to think that the kinds of responses observed in the JRGCE are not quite general, at least for natural communities in temperate climates on soils of moderate nutrient availability. Comparing the single-factor responses in the JRGCE with single-factor responses in other ecosystems should provide an efficient approach to assessing the generality of the JRGCE responses to simulated global changes.

Materials and Methods

Study site and system. The JRGCE is located in Jasper Ridge Biological Preserve, near Woodside, California, United States (37°24′N, 122°14′W, 120 m elevation). This region experiences a Mediterranean climate, with cool, wet winters and warm, dry summers. The experiment was conducted in 36 plots dispersed across −0.75 ha of natural grassland. Each plot was circular, 2 m in diameter, and divided into four equal-sized quadrants. The dominant species in this location are typically annual grasses (Bromus hordeaceus, Avena barbata, A. fatua) and annual forbs (Geranium dissectum, Erodium botrys). Perennial grasses and forbs are common but rarely dominant. A few of the ~35 herbaceous species present in the study area increased in dominance over the course of the experiment, most prominently the perennial grass Danthonia californica and the biennial forbs Cryptantha vesicaria ssp. taraxifolia.

Plots were established in the summer of 1997, with the 1997–1998 growing season used as a pretreatment year. The exceptional rainfall and warmth of the 1997–1998 El Niño (see Figure 1), however, made this year somewhat unusual. From 1974–2003, the site received an
annual average of 655 mm precipitation (as measured by a weather station located within 1 km of the experimental area).

Global change treatments. In a complete factorial design, we exposed the grassland to ambient and elevated levels of four factors: atmospheric CO₂, temperature, precipitation, and nitrate deposition. Experimental treatments were imposed during every growing season (roughly June-July) starting in the cruise year. We used slow-release pellets of calcium nitrate (Nutricote 12–0–0, Agrivert, Riverside, California, United States) to increase nitrate deposition. Nitrate was added in solution to mimic the flush of accumulated dry matter during the growing season (January–February), 5 g N m⁻² was added as slow-release pellets (Nutricote 12–0–0, Agrivert, Riverside, California, United States). Warming and elevated CO₂ treatments were included as whole-plot effects, and precipitation and nitrate deposition treatments were included as split-plot effects. We tested for treatment effects with the restricted maximum likelihood method, using the containment method for determining degrees of freedom and using ordinary least squares starting values where necessary. For analyses of the full 5 y of NPP data, we used PROC MIXED to run a repeated measures version of the split-plot model. For each regression, we used default starting values, unstructured covariance, and the Kenward-Roger technique for determining denominator degrees of freedom. Unlike other indicators, CO₂ was regulated in these cases, analyses with log-transformed data provided virtually identical results. Other statistical techniques are discussed with the results. We excluded data from 13 quadrants in the 1999 dataset, due to errors in the application of the nitrate treatment and inconsistencies in the output of one heater. In all other years, all 128 quadrants were analyzed.

To examine whether grassland responses to global change treatments were dependent on climatic factors, we regressed proportional responses of shoots, roots, and total biomass to the global change treatments against accumulated degree-days (C) and growing season precipitation (mm). Proportional response values were calculated using treatment means. Means from treatments with elevated levels of a factor were divided by means of the corresponding treatments with ambient levels of that factor. For instance, when regressing the N response against precipitation, our proportional response value was the mean of the CTN (elevated CO₂, temperature, and nitrogen) treatment divided by the mean of the CT (elevated CO₂ and temperature) treatment. The rainfall and heating treatments caused four data points to fall on each of two values on the independent axis (precipitation or temperature) each year. For each regression, n = 49.

Supporting Information

Table S1. Results (p-Values) from Mixed Model Analyses of Treatment Effects on Root-to-Shoot Ratio (In-Transformed)

Table S2. Results (p-Values) from Mixed Model Analyses of Treatment Effects on Root-to-Shoot Ratio (In-Transformed)

Table S3. Results (p-Values) from Mixed Model Analyses of Treatment Effects on NPP

Table S4. Results (p-Values) from Mixed Model Analyses of Treatment Effects on Aboveground Production
Table S5. Results (p-Values) from Mixed Model Analyses of Treatment Effects on Belowground Production

Treatment labels as in Table S1. Numerator degrees of freedom: 1 (all years). Denominator degrees of freedom: (999-2003): 23; 28, 28; 28, 28, 27, respectively.

Found at DOI: 10.1371/journal.pbio.0030319.s004 (42 KB DOC).

Acknowledgments

We thank the dozens of researchers, technicians, and assistants who have helped out over the course of this project, including: A. Ferreira, B. Mortimer, B. Poultier, M. Rilling, B. Thomas, E. Zavaleta, B. Bohaman, H. Henry, D. Khathy, H. Peters, K. Amatangelo, J. Ayers, E. Ferreira, H. Fields, S. Finlayson, L. Forwand, A. Gallego, S. Gere, W. Gomez, J. Juarez, C. Lund, T. Mahe, M. Milne, W. Nott, S. Robinson, V. Schoung, J. Silva, J. Silvis, J. Thayer, P. Yelton, and many volunteers. We appreciate the comments of three anonymous reviewers. The JRGC has been supported by grants from the National Science Foundation, the Morgan Family Foundation, the David and Lucile Packard Foundation, Jasper Ridge Biological Preserve, and the Carnegie Institution of Washington. EEC was supported by a US Department of Energy Graduate Research Environmental Fellowship.

Competing interests. The authors have declared that no competing interests exist.

Author contributions. CBF, HAM, NRC, and MRS conceived and designed the experiments. JSD analyzed the data and wrote the paper. JSD, NRC, EEC, LAM, MRS, ST, TT, and CBF contributed substantially to the maintenance of the experiment and the collection, organization, and verification of data relevant to this paper.


