VOL. 173, NO. 1 THE AMERICAN NATURALIST JANUARY 2009

Notes and Comments

Vegetation Responses to Extreme Hydrological Events: Sequence Matters

ShiLi Miao,[1,*] **Chris B. Zou,**[2,†] **and David D. Breshears**[3,‡]

1. South Florida Water Management District, West Palm Beach, Florida 33406;
2. School of Natural Resources, University of Arizona, Tucson, Arizona 85721;
3. School of Natural Resources, Institute for the Study of Planet Earth, and Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721

Submitted March 26, 2008; Accepted July 28, 2008; Electronically published December 5, 2008

ABSTRACT: Extreme hydrological events such as flood and drought drive vegetation dynamics and are projected to increase in frequency in association with climate change, which could result in sequences of extreme events. However, experimental studies of vegetation responses to climate have largely focused on responses to a trend in climate or to a single extreme event but have largely overlooked the potential for complex responses to specific sequences of extreme events. Here we document, on the basis of an experiment with seedlings of three types of subtropical wetland tree species, that mortality can be amplified and growth can even be stimulated, depending on event sequence. Our findings indicate that the impacts of multiple extreme events cannot be modeled by simply summing the projected effects of individual extreme events but, rather, that models should take into account event sequences.

Keywords: climate change, Everglades, extreme hydrological events, mortality, sequence.

Introduction

Hydrological fluctuation is an important ecological driver in ecosystems associated with lakes, river floodplains, coastal bay areas, constructed dams, and wetlands. However, the increasing anthropogenic manipulation of hydrology and the exacerbation of climatic change forcing have resulted in substantial increases in the frequency and magnitude of hydrological fluctuations in many of these ecosystems. Therefore, more extreme and unpredictable hydrological events, such as drought and flooding, as well as various sequential combinations of both are anticipated (Meehl et al. 2007). Although there has been a growing focus on extreme events such as drought and flood as critical drivers of vegetation change (e.g., Jentsch et al. 2007), this shift in emphasis from trends to events may still be missing an important driver of vegetation change via impacts on growth and/or mortality—the particular sequence of hydrological events (Redmond 2007). The sequence of extreme events might be an important determinant of vegetation response. For example, a sequence of extreme rainfall followed by drought appears to have triggered tree mortality in one study (Auclair 1992). Most studies, models, and assessments of plant growth and mortality in response to extreme events are, at best, based on limited data related to responses for an individual event and, more often, on undocumented thresholds for plant mortality (Running and Coughlan 1988; Neilson et al. 2005; Liedloff and Cook 2007). Consequently, these approaches generally implicitly ignore potential responses of plants to multiple extreme events as well as the potential for specific sequences to perturb responses in unexpected ways.

In subtropical freshwater and coastal wetland ecosystems, predominant tree species are generally adapted to and rely on a series of hydroperiods generated by hydrological fluctuations to maintain their structure and functional integrity (Miller and Zedler 2003). Such hydrological fluctuation patterns, however, are increasingly being provoked by changes in precipitation patterns and increases in the number and frequency of hurricanes and tropical storms associated with intensification in the El Niño–Southern Oscillation (Huntington 2006). This trend is likely to be exacerbated by projected changes in climate, and the number of sequential extreme hydrological events, such as drought followed by flood or flood followed by

---

[*] Corresponding author; e-mail: smiao@sfwmd.gov.

[†] Present address: Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, Oklahoma 74078; e-mail: chris.zou@okstate.edu.

[‡] E-mail: daveb@email.arizona.edu.

Am. Nat. 2009. Vol. 173, pp. 113–118.
DOI: 10.1086/593307

drought, is predicted to increase (McCabe et al. 2004; Huntington 2006), thereby creating novel environmental conditions that may reduce plant growth and trigger mortality (Parmesan and Yohe 2003). Given the substantial impacts of climate change and related hydrological events that are projected for tropical and subtropical coastal and aquatic ecosystems, an improved ability to assess the effects of sequential extreme events on vegetation is needed.

To address the lack of understanding about the effects of sequences of hydrological events, we investigated the seedling responses of three co-occurring, major tree species located on tree islands in the Everglades, Florida—an ecosystem that is representative of subtropical freshwater and coastal wetland ecosystems and projected to be greatly impacted by hydrological events associated with both management and climate change (Meehl et al. 2007). These three tree species were selected on the basis of their physiologies, distributions, and habitat characteristics to represent three different tolerance categories relative to one another in the Everglade tree islands: *Bursera simaruba*, a relatively drought-tolerant species; *Annona glabra*, a flood-tolerant species (Jones et al. 2006; both of the former species are widespread in the New World tropics and subtropics); and *Acer rubrum*, a species with intermediate tolerance to both drought and flood relative to the other two species chosen (Niinemet and Valladares 2006). Although these species were expected to have different tolerances to the two major types of hydrological extreme events—flood and drought—their responses to multiple extreme events of both disturbance types and associated sequences are unknown. This study tested the responses of height, biomass, and mortality in seedlings of each species to (1) individual extreme events of both types—drought or flood—of varying magnitude, (2) sequences of paired extreme events (flood-drought vs. drought-flood) that were abruptly changed from one to the other, and (3) sequences that included a period of normal conditions (baseline) between two extreme events (flood-baseline-drought vs. drought-baseline-flood).

Methods

The experiment was conducted in a research greenhouse facility on the campus of Florida Atlantic University, Boca Raton, Florida (26.37°N, −80.10°W; elevation 2 m). Seeds of *Acer rubrum* and *Annona glabra* were collected from tree islands in the Everglades and germinated in the greenhouse in 2003, whereas *Bursera simaruba* seedlings were gathered from various tree islands in the Everglades. All seedlings were <1 year old when they were transplanted to pots (15 cm in diameter and 23 cm in height, with a volume of 4,064 cm^3) filled with soil from a tree island that had not flooded in the previous 5 years. Vigorously growing, healthy plants of similar heights (9.09 ± 1.69, 18.6 ± 3.88, and 24.94 ± 3.21 cm for *B. simaruba*, *A. rubrum*, and *A. glabra*, respectively) were chosen for experimental treatments in September 2003.

The experiment utilized a randomized block design with a total of 12 blocks (tanks) arranged in two rows in the greenhouse. Each block was a 200 × 200 × 40-cm opaque PVC tank, with water circulated between each tank and the filtration reservoir through a closed-loop irrigation system. Water in the reservoir was transported from an experimental pond having a total phosphorus concentration similar to that found in the extant Everglades (10 parts per billion).

For each tank (block), a split-plot design was applied for five constant watering treatment applications (flood, moderate flood, baseline, moderate drought, drought). Specifically, plants receiving the flood treatment were positioned at the bottom of the tank with about 10 cm of water above the soil surface. Plants assigned the moderate flood treatment stood at an elevation where the water depth was at the soil surface. Plants with baseline, moderate drought, and drought treatments were all positioned above water level in the tank but received different amounts and frequencies of watering: baseline treatment received 500 mL of water every week, moderate drought treatment received 300 mL of water every week, and drought treatment received 300 mL of water every 2 weeks. As a result, the mean gravimetric water contents (±SE) of these three treatments as measured at each watering application were 30.52% ± 1.66%, 27.53% ± 1.93%, and 15.27% ± 1.49%, respectively. In addition to the five stress treatments that were consistent for the entire experiment (about 12 months), there were four sequence treatments: two abrupt change sequence treatments (flood-drought and drought-flood; approximate duration of 4 months at each phase) and two gradual change sequence treatments (flood-baseline-drought and drought-baseline-flood; approximate duration of 4 months at each phase). As a result, nine treatments (five constant treatments and four sequence treatments) were created per tank. These treatments were randomly assigned to individual plants, with one plant per treatment except for the abrupt change treatments, which were assigned three plants (resulting in 13 plants per species, 39 plants per tank, and 468 plants for the entire study). The experiment started in September 2003 and concluded in October 2004.

Plant height and biomass were measured directly for all plants, except that the values of biomass for the two abrupt change treatments were calculated using the multiple regression formula $\alpha \times A^{\beta} + \gamma \times D^{\delta}$, based on actual height (A) and basal diameter (D). The biomass model for each species was established using directly measured biomass data from more than 200 seedlings of similar sizes

Table 1: Statistics of two-way ANOVA for overall (including eight treatments except for the baseline), constant stress, abrupt change sequence, and gradual change sequence treatments on seedling growth

		Height ratio		Biomass ratio	
Treatment and sources	df	MS	*F*	MS	*F*
Overall:					
Block	11	340	1.17	2,241	2.12*
Treatments	7	9,025	23.26***	32,799	34.53***
Block × treatments	73	388	1.33	950	0.9
Species	2	9,437	23.26***	72,088	68.08***
Treatments × species	14	2,627	9.00***	16,993	16.05***
Error	133	291		1,059	
Constant stress:					
Block	11	155	0.58	1,219	1.34
Treatments	3	8,745	25.87***	16,007	24.48***
Block × treatments	33	338	1.26	654	0.72
Species	2	6,428	23.82	18,665	20.48***
Treatments × species	6	3,737	13.85	6,219	6.82***
Error	113	270		911	
Abrupt change sequence:					
Block			2.86**	3,501	1.63
Treatments	1	10,546	19.86***	93,347	49.57***
Block × treatments	11	531	1.18	1,883	0.88
Species	2	7,871	17.52***	97,604	45.42***
Treatments × species	2	1,998	4.45*	48,862	22.74***
Error	31	449		2,149	
Gradual change sequence:					
Block	11	1,285	2.54*	3,501	1.45
Treatments	1	13,149	57.67***	103,378	148.80***
Block × treatments	11	228	0.45	651	0.27
Species	2	7,035	13.87***	96,599	39.98***
Treatments × species	2	2,309	4.55*	47,989	19.86***
Error	31	507			

* $P < .05$.

** $P < .01$.

*** $P < .001$.

(*B. simaruba*: $\alpha = 0.000955$, $\beta = 2.149$, $\gamma = 0.0123$, $\delta = 2.47$; *A. rubrum*: $\alpha = 0.00926$, $\beta = 1.552$, $\gamma = 0.1793$, $\delta = 1.73$; *A. glabra*: $\alpha = 0.0263$, $\beta = 1.559$, $\gamma = 0.0354$, $\delta = 2.45$). The treatment effects were quantified by mortality rate (%) and relative ratios (%) of both height and biomass for surviving plants under the treatments compared with those under the baseline condition. Overall treatment and species effects were conducted initially by a two-way ANOVA (SAS Institute, Cary, NC) including nine treatments and three species. In the two-way ANOVA, treatments and species were treated as fixed factors, whereas the block was random. Where the treatment effect was tested by the block, treatment variance, the species effect, and the interaction between species and treatments were tested using the residual (error). In the case where the main effects (treatments and species) and their interactions were all significant, the nine treatments were further grouped into three categories: (1) constant stress (df = 3; did not include the baseline treatment because it was used to calculate relative ratios), (2) abrupt sequence change (df = 1), and (3) gradual sequence change (df = 1; table 1). Similar two-way ANOVAs were conducted for each of the three categories.

Results

In response to a single extreme event, all three seedling types experienced reduction in growth, with substantial mortality under both drought and flood conditions. Relative growth metrics (ratios of height or biomass after treatment relative to the baseline condition) for all three tree species differed significantly with treatment type ($P < .0001$; fig. 1*A*, 1*B*). Not surprisingly, surviving trees of the drought-tolerant type (*Bursera simaruba*) had the lowest growth under the two flood treatments, but, notably, surviving trees of both the intermediate and flood-

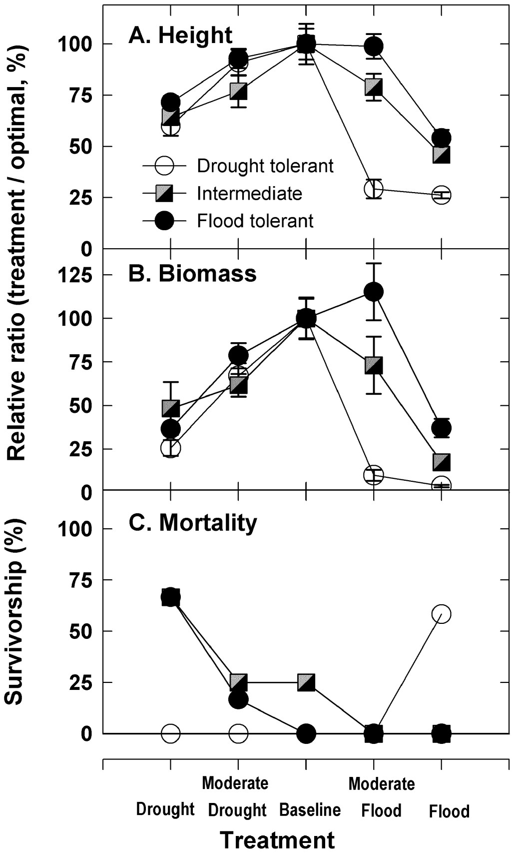

Figure 1: Differential responses to individual events that range from drought to flood for three wetland tree types (*Bursera simaruba* as drought tolerant, *Annona glabra* as flood tolerant, and *Acer rubrum* as intermediate in tolerance) for metrics of relative growth ratio—with growth rates normalized to baseline conditions associated with typical water conditions for a given species—for both height (*A*) and biomass (*B*) for trees that survived the event and for overall mortality rate (*C*). Error bars are 1 SE.

tolerant tree types exhibited relative growth metrics under flood that were as low as or lower than those under drought. High rates of mortality (fig. 1*C*) were triggered for the drought-tolerant type by flood (58% mortality) and, conversely, for the intermediate and flood-tolerant types by drought (both exhibiting 67% mortality).

Importantly, under paired sequences that abruptly transitioned from one event type to the other, growth responses differed with event sequence ($P < .0001$) regardless of tree type or growth metric (fig. 2*A*, 2*B*), with growth under flood-drought consistently lower than that under drought-flood. The sequence-dependent reduction in growth was also reflected in mortality rates, with higher mortality in flood-drought than in drought-flood for all three tree types. Inclusion of a period of baseline condition to impose a gradual transition between two extreme events (flood-baseline-drought or drought-baseline-flood) mitigated sequence-dependent differences in growth for the drought-tolerant type ($P = .3724$ for height and $P = .1915$ for biomass) but not for either the intermediate or the flood-tolerant types ($P < .0001$; fig. 3*A*, 3*B*). Surprisingly, under drought-baseline-flood, growth was substantially stimulated for both the intermediate and flood-tolerant tree types, in one case by as much as 240% in comparison to baseline. Mortality under these gradual sequences was similar to that under corresponding abrupt sequences (fig. 3*C*).

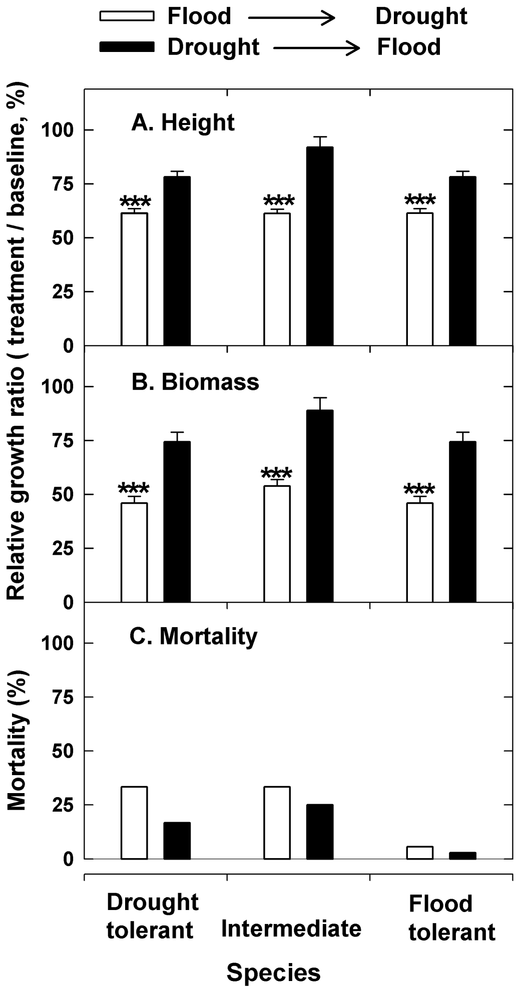

Figure 2: Responses of three wetland tree types (as in fig. 1) to a pair of disturbance events that included a drought followed by a flood with an abrupt transition between the two. Error bars are 1 SE. Compared with the drought-flood sequence, the flood-drought sequence resulted in a significantly lower growth ratio—with growth rates normalized to baseline conditions associated with typical water conditions for a given species—for both height (*A*) and biomass (*B*) in each of the three types. *Three asterisks*, $P < .001$.

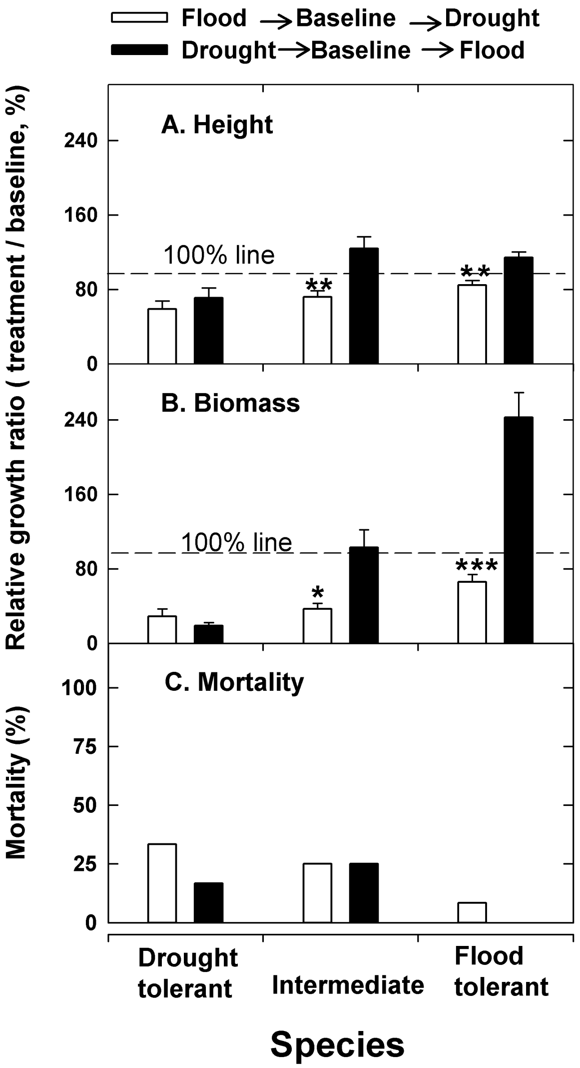

Figure 3: Responses of three wetland tree types (as in fig. 1) to disturbance events that included a drought and a flood, with an intermediate period of baseline conditions in between that generally differed on the basis of the sequential order for the extreme events. Error bars are 1 SE. For the intermediate and flood-tolerant types, the drought-baseline-flood sequence stimulated relative growth rates (*A*) and biomass (*B*), contrasting with the flood-baseline-drought sequence. *One asterisk*, $P < .05$; *two asterisks*, $P < .01$; *three asterisks*, $P < .001$.

Discussion

We found that the species studied responded to single events of drought or flood essentially as would be expected on the basis of their physiologies and distributions. Nevertheless, with respect to responses to a sequence of extreme hydrological events, our results collectively highlight three key and potentially underappreciated issues. First, species responses are dependent on event sequence with respect to both the order of flood and drought and the presence or absence of an interceding baseline condition between extreme events. For each sequence type, the treatment initiated with flood produced significantly different growth responses than that initiated by drought. Second, species responses in growth and mortality to sequences of extreme events are not simply an additive result of their responses to individual events, as evident in the sequence-dependent differences. In particular, in some cases, the event sequence actually stimulated rather than depressed growth by a factor of two or more (fig. 3*A*, 3*B*). Third, plant responses in growth and mortality to extreme events, especially in sequences, are related to but are not likely to be readily determinable a priori by knowledge of characteristics of physiology and distribution. That is, the responses that we observed were not always evident on the basis of knowledge about species (e.g., flood tolerant, drought tolerant, or intermediate). Our results were based on responses of seedlings, but the general insights they provided may also be relevant to adult trees (Kolb and Stone 2000), an issue that requires further investigation. The results could lead to improved model forecasting. For example, in our study, the sequences that started with drought (for both abrupt and gradual change sequence treatments) showed a consistent, lower impact than those initiated with flood.

The results of our study have significant implications for predicting vegetation responses and managing ecosystems that are subject to artificially created and/or climate-induced extreme hydrological disturbances and future climate change. The Everglades and the entire south Florida coastal region are experiencing increasingly extreme hydrological disturbances and are among the most vulnerable ecosystems to climate change–induced hurricane events and sea level rise (Meehl et al. 2007). Critical, interrelated ecological issues such as nutrient enrichment, managed hydrological alterations, and exotic plant invasions in the Everglades are directly associated with species-level responses of predominant tree types (Miller and Zedler 2003). Success of the ongoing restoration and future management of the Everglades and other aquatic systems will rely heavily on an understanding of tree island understory dynamics and succession via growth and dieback in response to sequences of hydrologic variability and to the increase in extreme climate events (Ellison and Bedford 1995; Dixon and Turner 2008).

In conclusion, our study experimentally demonstrates the importance of event sequence in determining the impacts of extreme hydrological events on seedling responses such as growth and mortality. Furthermore, it highlights the fact that models dealing with seedling growth, tree establishment, and survival as well as with ecosystem structure and dynamics may need to explicitly study, model, and account for the sequence of events—sequence matters.

Acknowledgments

R. Johnson helped designed and build the irrigation water system, B. Gossman and J. Huels helped design and set up the experiment, and J. Creasser and R. Wanvestraunt helped with plant measurements and the final harvest. We thank S. Carstenn, J. Davison, T. W. Dreschel, M. K. Nungesser, and F. Sklar for valuable comments. F. Valladares and an anonymous reviewer provided very valuable suggestions to improve this manuscript.

Literature Cited

Auclair, A. N. D. 1993. Extreme climatic fluctuations as a cause of forest dieback in the Pacific Rim. Water Air and Soil Pollution 66: 207–229.

Dixon, M. D., and M. G. Turner. 2008. Simulated recruitment of riparian trees and shrubs under natural and regulated flow regimes on the Wisconsin River, USA. River Research and Applications 22: 1057–1083.

Ellison, A. M., and B. L. Bedford. 1995. Response of a wetland vascular plant community to disturbance: a simulation study. Ecological Applications 5:109–123.

Huntington, T. G. 2006. Evidence for intensification of the global water cycle: review and synthesis. Journal of Hydrology 319:83–95.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and the Environment 5:365–374.

Jones, D. T., J. P. Sah, M. S. Ross, S. F. Oberbauer, B. Hwang, and K. Jayachandran. 2006. Responses of twelve tree species common in Everglades tree islands to simulated hydrologic regimes. Wetlands 26:830–844.

Kolb, T. E., and J. E. Stone. 2000. Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine-oak forest. Tree Physiology 20:1–12.

Liedloff, A. C., and G. D. Cook. 2007. Modelling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the FLAMES simulation model. Ecological Modelling 201:269–282.

McCabe, G. J., M. A. Palecki, and J. L. Betancourt. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. Proceedings of the National Academy of Sciences of the USA 101:4136–4141.

Meehl, G. A., T. F. Stocker, W. D. Collins, P. Friedlingstein, A. T. Gaye, J. M. Gregory, A. Kitoh, et al. 2007. Global climate projections. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, eds. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York.

Miller, R. C., and J. B. Zedler. 2003. Responses of native and invasive wetland plants to hydroperiod and water depth. Plant Ecology 167: 57–69.

Neilson, R. P., L. F. Pitelka, A. M. Solomon, R. Nathan, G. F. Midgley, J. M. Fragoso, H. Lischke, and K. Thompson. 2005. Forecasting regional to global plant migration in response to climate change. BioScience 55:749–759.

Niinemets, U., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76:521–547.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Redmond, K. Y. 2007. Understanding hazard and predictability of drought. Pages 70–78 *in* National Research Council, ed. Understanding multiple environmental stresses: report of a workshop. National Academies Press, Washington, DC.

Running, S. W., and J. C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecological Modelling 42:125–154.

Associate Editor: Martin J. Lechowicz
Editor: Monica A. Geber

ShiLi Miao with experiments involving plant response to weather extremes at the South Florida Water Management District.