Final Report "Physiological, demographic, competitive and biogeochemical controls on the response of California's ecosystems to environmental change"

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Overview: The Loma Ridge Global Change Experiment is a large, well-replicated water and nitrogen input manipulation in the Santa Ana Mountain foothills that operated with DOE support from 2006 to 2015 (Potts et al 2012; Allison et al 2013; Kimball et al 2014; Parolari et al 2015). The experiment considers the effects of increased and decreased water input and increased N input on two adjacent ecosystem types: California Annual Grassland (GL), which is dominated by exotic, Eurasian grasses and forbs, and Coastal Sage Shrubland (CSS), which is dominated by native, drought deciduous, perennial shrubs (Fig 1).

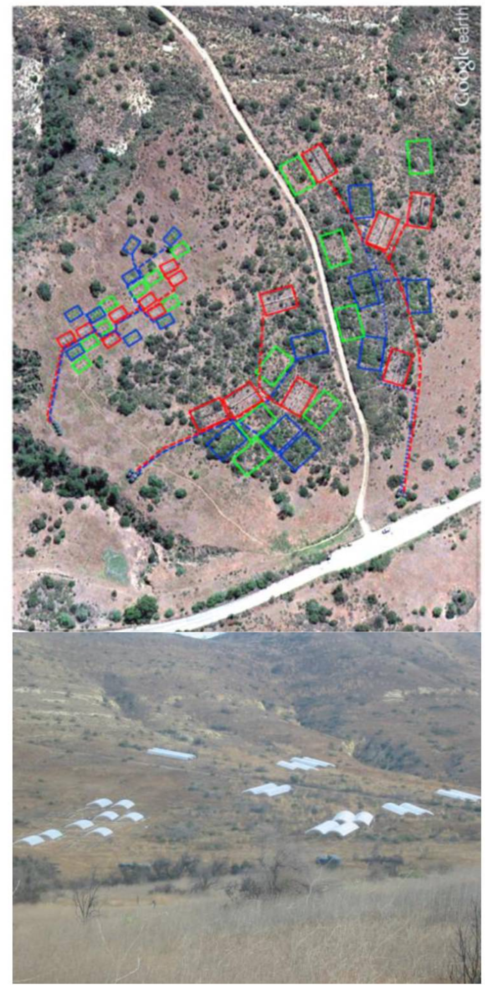

Figure 1 (a) Loma Ridge layout - rotated with east upwards. Coastal Sage Shrubland is textured green; Grassland is smooth tan. Red plots are reduced water; green are ambient; blue are added water. Water distribution pipes are dashed lines. CSS plots are 18.3x12.2 m. Shrub mortality and conversion to herbaceous is apparent in CSS dry plots. **(b)** Photograph showing closed shelters in anticipation of a storm (closed shelters correspond to red plots in a). This photo was taken from a hill to the NNW of the site - the 8 GL shelters are on the lower left and one set of CSS tanks are in the foreground.

Historic air photos show the boundary between CSS and GL at the site has been stationary since at least 1938 despite 5 wildfires and marked shifts in meteorology, air pollution, nutrient input, atmospheric CO_2 concentration and grazing intensity. Mosaics between grassland and shrubland are common throughout California, and previous analyses have implicated biotic factors in creating mosaic stability, though differences in fire history, soil texture and/or depth, nutrient input and topography may also play roles. The mosaic at Loma Ridge appears to be maintained mainly by biotic factors. The Mediterranean climate (wet winters, dry summers and marked interannual precipitation variation), soil texture (sandy loam), depth to bedrock (at least 3 m), fire history, topography (steady slope to NW) and nutrient deposition are all consistent from GL and CSS, and we have been unable to identify any independent aspect of the physical environment that is even weakly correlated with current vegetation distribution. Moreover, shrubs that are transplanted into GL grow well, rapidly expanding and producing seed, suggesting immigration and the successful establishment and expansion of CSS species into GL and vice-versa is a bottleneck. The goal of the Loma Ridge experiment was to investigate the causes and implications of this apparent biotic control over ecosystem type, and to determine whether altered water and/or N input could shift a local community from GL to CSS, or vice versa.

Experiment Phases: The experiment proceeded in two phases: "Phase I Severe treatment", and "Phase II Return to ambient". The "severe treatment" GL manipulations began in water year 2006-07 and the CSS manipulations in 2007-08. The "severe treatment" manipulations continued through 2013-14, when the "return to ambient" treatments were started. The "severe treatment" manipulations consisted of three water levels (-40% of ambient, ambient, +40%) crossed with two N inputs. The "severe treatment" manipulations represented an extreme shift in precipitation; a Monte Carlo simulation of the amount of precipitation received by the dry (-40% of ambient) plots over the "Severe treatment" suggests these plots experienced a once in ~10,000 year drought. The "severe treatment" experiment resulted in very rapid shifts in ecosystem structure and function, and after 2013-14 we initiated the "return to ambient" phase of the experiment by returning half of the previously treated plots to ambient. The outstanding questions with the "return to ambient" experiment were whether any species were extirpated from any of the "return" plots, and whether and how quickly species composition and ecosystem function in the "return" plots converged with those that experienced continuous ambient conditions.

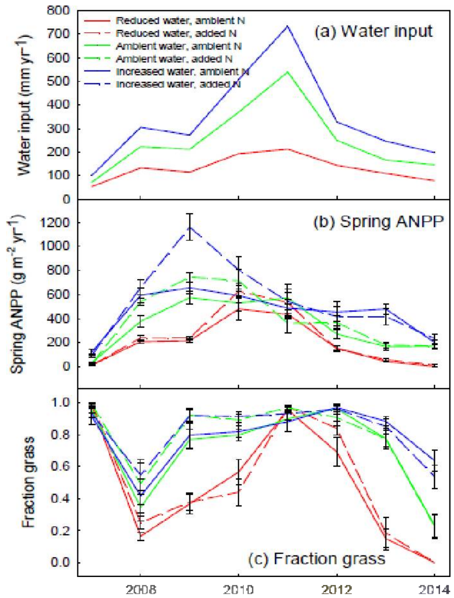

Figure 2 Year-to-year patterns of: (a) Water input, (b) Spring GL ANPP, (c) Relative fractional cover by grasses (forbs compose most remaining cover). Lines connect means across reps; years begin with previous Oct; water inputs are identical for GL and CSS.

Specific Methods: The experimental treatments at Loma Ridge were replicated 8 times in 8.5x6.1 m plots in GL and 18.3x12.2 m plots in CSS (Fig 1). The reduced water plots were covered with retractable, clear roofs during a subset of winter storms, which allowed us to reduce incoming water 40% while mimicking the shift to smaller storms observed in drier California locations and years. The roofs were open during the remainder of the year (more than 95% of the days), which reduced artifact. The water draining off the roofs was collected through a series of pipes, stored in tanks, and subsequently pumped to the added water plots where it was applied with a network of pressure compensated drip tubing. Each plot was split lengthwise, with 6 $gNm^{-2}yr^{-1}$ added to one half, creating a full factorial experiment of water input crossed with nitrogen amendment crossed with vegetation type.

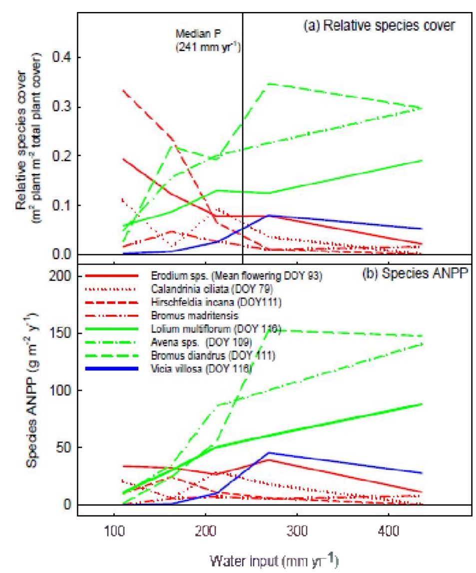

Figure 3 Rapid GL species shifts with water input: Lines connect means across year and treatment that were binned by water input. (a) End of season relative cover for 8 most common species. (b) Annual Aboveground Production by each species. Green are grasses, red are forbs, blue is N fixer, DOY is start of flowering.

Core measurements following consistent protocols were made over the entire project (both phases) and datasets are freely shared. Measurements were made at several time scales: 1) Continuous (every 30 minutes) in a subset of plots (2 replicates/treatment): surface soil moisture (top 30 cm; 96 total); deep matric profile (6 depths to 2 m; 12 profiles total); NDVI (24 total); air T and humidity (12 total); soil T (48 total). 2) Every 2-8 weeks in all plots: surface moisture (top 15 cm; 384 total); deep moisture (neutron probe to 3 m; 48 profiles total); spectral reflectance (EVI, NDVI, etc; 4800 locations total). 3) End of growing season: species composition (point intercept); ANPP (herbaceous clipping and shrub volumetric allometry).

Key findings from Phase I "Severe treatment": Phase I of the experiment was successful and produced a series of interesting and important observations. Ambient precipitation varied markedly over Phase I, with particularly dry conditions in 2006-07 and 2013-14, and wet conditions in 2010-11 (Fig 2a). GL community composition varied markedly with water input, with increased grass dominance in wet years and treatments (Fig 2c). Likewise, the relative abundance of shrubs vs herbaceous plants in CSS varied markedly with water treatment, with nearly complete shrub dominance in wet treatments, and marked shrub mortality and a shift to herbaceous plants in dry treatments (Kimball et al 2014). The community shifts in GL were rapidly reversible; for example, grass cover in the reduced water plots increased rapidly in 2010-11, which was comparatively wet, and decreased rapidly in subsequent years, which were dry, with a possible one year lag and carry-over effect (Fig 2ab). Likewise, the relative abundance of individual species in the GL plots was highly responsive to water input and rapidly reversible, effectively shifting back and forth from year-to-year with water input (Fig 3a).

The shifts in community composition were associated with large shifts in GL and CSS Aboveground Net Primary Production (ANPP), which declined markedly during dry years and in the reduced water treatments (Fig 2b). The effects of water on community composition and ANPP appear mechanistically linked. Representatives of some species, such as Bromus diandrus in GL and Acmispon glaber in CSS, rapidly increased in size in wetter years and treatments (Fig 3b), which led to both a shift in relative species cover (e.g., Fig 3a) and an increase in overall ANPP (e.g., Fig 2b). Other species, such as Erodioum sps in GL, were comparatively important in drier years and treatments; these species do not produce large amounts of biomass, leading to much lower ANPPs. The end result was a consistent relationship between ANPP and incoming water that rapidly shifted back and forth with year and treatment (Parolari et al 2015).

Key findings from Phase II "Return to ambient": Phase II is still at an early stage, though initial results are interesting and potentially very important. Phase II has shown that both CSS and GL are remarkably resilient to altered water and N. The short-term changes in ANPP and species composition with altered water or N input observed during Phase I are rapidly being reversed in the "return to ambient" treatments. Our severe dry treatments killed many of the CSS shrubs in the CSS shelters, and caused a proliferation of grasses and other herbaceous species; at the time we thought there was a good chance these plots had experienced an irreversible conversion of CSS to GL. However, these plots are now rapidly returning to CSS under the return to ambient conditions, underscoring the high ecological resilience of the system.

Equally interesting is the mechanism that is mediating this resilience. CSS is a fire adapted community with a characteristic successional pattern following crown fire that returns the community to its prefire conditions within 5-10 years. The ecological patterns, and consequently the ecological resilience, we are seeing during Phase II mimic this fire recovery pattern, and we now believe the ecological mechanisms that generate high resilience to crown fire also generate high resilience to an extreme, 10,000 year drought.

In summary, Phase I showed very rapid change in species composition or ANPP with altered water or N input (low resistance), whereas Phase II is showing a very rapid return to initial conditions once ambient water or N input were restored (high resilience). The severe drought treatment killed most of the shrubs in the dry plots and opened the canopy to herbaceous species, but this damage was ephemeral, and the shrubland community is recovering through the mechanisms and patterns that more typically mediate recovery from crown fire. The pattern of low resistance and high resilience carries implications for other "global change experiments", which have often also seen large and rapid treatment effects (low resistance), but have less frequently considered the subsequent recovery or resilience of the system. The phenomenon of pre-adaption to novel global-change stresses (i.e., CSS' ability to recover rapidly from crown fire pre-adapted it to recover from a 10,000 year drought) has received even less research attention.

Publications (22 published and another ~10 in various draft stages)

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