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DIRECT AND INDIRECT EFFECTS OF DROUGHT ON COMPENSATION FOLLOWING HERBIVORY IN SCARLET GILIA

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Abstract. Compensation following herbivory is an important element of plant defense; however, variation in compensation under naturally stressful conditions has yet to be evaluated directly. During Arizona's worst drought on record, we explored compensation following ungulate herbivory in a typically overcompensating population of scarlet gilia (*Ipomopsis aggregata*) near Flagstaff, Arizona, USA. In a natural survey of browsed and unbrowsed plants, we documented severe undercompensation. We tested two factors that potentially contributed to this atypical pattern: (1) the direct effect of drought stress on the capacity to compensate (following the typical single bout of herbivory) and (2) the indirect effect of drought stress on compensation through increased ungulate browsing. Using a 2 × 2 factorial experiment (with or without supplemental water, with or without clip-simulated herbivory typical of non-drought years), we found that water availability limited compensation (direct effect). In a second experiment examining the indirect effects of drought, we found that ungulates browsed scarlet gilia at unprecedented levels during the drought year, resulting in severe undercompensation. We conclude that, although water was an important limiting factor for compensation during the drought year, the overriding factor determining fitness achieved through compensation was the indirect effect of drought, i.e., drought-year-associated ungulate browsing.

Key words: compensation; drought; *Ipomopsis*; plant–herbivore interactions; tolerance; ungulate; water stress.

INTRODUCTION

Climatic extremes have the potential to impose profound impacts at individual, population, and community levels. Severe conditions such as drought, mid-summer frosts, and floods can induce morphological shifts (Boag and Grant 1984), local extinctions (Singer and Thomas 1996, Harrison 2000), and the translocation of whole communities (Allen and Breshears 1998). Plant–animal interactions may be especially vulnerable to these extreme climatic events because impacts on the plant or animal can arise directly, through physiological changes imposed by the environment, or indirectly, through changes in the number or quality of each member of the interaction. For example, Harrison (2000) found that, following a severe drought in Borneo, the interaction between dioecious fig species and

their fig-wasp pollinators was disrupted when fig inflorescence production dropped and the wasp species went locally extinct. Six months after flower production rebounded, no pollination (and consequently no fruit production) was observed. Moreover, numerous studies from both the agricultural and ecological literature demonstrate that drought-induced leaf chemistry changes in a host plant can trigger increased growth and reproductive rates of its herbivore, leading to population explosions and ultimately to unprecedented levels of host biomass removal (Mattson and Hack 1987). Thus, the precipitous fall in resource availability caused by a drought event can disrupt mutually beneficial interactions and exacerbate antagonistic ones through a combination of direct and indirect effects.

This complex interplay of drought-induced direct and indirect effects also may have a profound impact on plant compensation following herbivory, a plant response now appreciated as an important element of plant defense (Stowe et al. 2000). Plant compensation, or the regrowth and reproduction following herbivory, typically increases with resource availability (Maschinski and Whitham 1989, Juenger and Bergelson

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1997, Huhta et al. 2000a); therefore, extreme water limitation under drought conditions should preclude a plant's capacity to tolerate herbivory. Furthermore, previous studies suggest that annual variation in compensation is associated with precipitation changes (Maschinski and Whitham 1989, Lennartsson et al. 1998). In addition to these possible direct effects of water stress on host-plant compensatory capacity, herbivore foraging may also intensify under extreme conditions (Mattson and Hack 1987). Compensation, however, typically occurs only under a limited range of herbivory levels (Huhta et al. 2000b). If drought intensifies herbivory pressure, compensation will likely diminish. Moreover, an extreme abiotic environment may impact plant compensatory capacity only, herbivore foraging only, or both simultaneously, ultimately leading to changes in compensation achieved. No previous study has addressed directly plant compensation under severe drought conditions in a system that tolerates herbivory; thus, we have limited understanding of the potentially complex effects of a temporally variable environment on regrowth and reproduction following herbivory.

During a severe drought in Arizona, we investigated the effect of drought on compensatory capacity and on the interactions between scarlet gilia (*Ipomopsis aggregata*) and ungulate herbivores. Our study addressed the following questions in a population known to consistently overcompensate (produce more seeds following browsing than 208 when unbrowsed [Paige 1994, Gronemeyer et al. 1997, Anderson and Paige 2003]):

1) How does compensation in a drought year compare to non-drought years?

2) What is the effect of drought stress on the compensatory capacity of scarlet gilia (direct effect of drought)?

3) What is the effect of drought stress on ungulate browsing levels and what are the consequences for compensation (indirect effect of drought)?

Investigating these questions enabled us to determine whether the degree of compensation achieved by scarlet gilia in an extreme drought year can be attributed to compensatory capacity, drought-associated ungulate foraging, or both. The interaction between scarlet gilia and their ungulate herbivores represents an ideal system for addressing these questions, as we have four years of background data on compensation from our study site (Paige 1994, Gronemeyer et al. 1997, Anderson and Paige 2003). Furthermore, based on bristlecone pine data, the 2002 drought in the American Southwest may be among the most severe in over 1400 years (Merriam Powell Research Center, Flagstaff, Arizona, USA; unpublished data).

METHODS AND MATERIALS

Drought, compensatory capacity, and browsing-level-dependent compensation

To assess the effect of drought stress on compensatory capacity (the direct effect of drought), we used

a 2×2 fully factorial design with all combinations of treatments of with or without clipping (+clip or -clip) and with or without supplemental water (+water or -water). Our clipping treatment simulated herbivory typical of non-drought years (one major bout) and was used to understand the "capacity" of the plant to compensate under water limitation. To understand the effects of drought-associated ungulate browsing on compensation (the indirect effect of drought), we created a fifth treatment, "natural herbivory," to which the +clip/-water and -clip/-water treatments were compared. These three treatments enabled us to compare compensation following typical browsing levels (all clipped treatments were protected from natural herbivory) vs. drought-year-associated browsing levels using the unprotected natural herbivory treatment. Moreover, these five treatments enabled us to isolate not only the effect of drought on the capacity to compensate (the 2×2), but also the effect of drought-year-associated browsing levels on compensation achieved (the natural herbivory treatment). Finally, to compare compensation achieved in the 2002 drought year to several non-drought years, we used the -clip/-water treatment and the unprotected, naturally browsed plants. Whereas in past years a natural survey was conducted at the end of the season to assess fruit production of naturally browsed and unbrowsed plants (multiple stemmed and single stemmed [Paige 1994, Gronemeyer et al. 1997, Anderson and Paige 2003]), in 2002 it was necessary to use the -clip/-water treatment plants (caged) because virtually every plant in the population had been browsed (see *Results*).

During the first week of June 2002, 13 transects spaced 3 m apart were established. At approximately 1.5-m intervals along a given transect, the closest (yet to be naturally browsed) individual was randomly assigned to one of the five treatments: (1) +clip/+water ("clip" denotes simulated browsing; see next paragraph), (2) +clip/-water, (3) -clip/+water, (4) -clip/-water, and (5) -water/+natural-herbivory. This last "natural-herbivory" treatment was established by selecting and tagging previously browsed individuals (identified by the stem scar left after primary stem removal). We left these tagged individuals exposed to ungulates, unlike the plants in treatments 1-4 that were protected from multiple browsing events with welded wire cages. Welded wire cages ensured that the unbrowsed plants remained unbrowsed and that the clipped plants experienced only one major bout of (simulated) herbivory. *Ipomopsis* pollinators moved freely in and out of these cages. We selected 12 individuals along each of the 13 transects until 30 plants were assigned to each treatment, for a total of 150 plants. Every plant used in this study was the intermediate-pink hybrid (the most abundant) floral morph. Plants did not vary in size across treatments (root crown diameter, $F_{4,150} = 0.54$, $P = 0.71$).

We simulated ungulate herbivory in the clipping treatments by removing about 95% of biomass in late May, clipping plants at a height of 1–2 cm and thus replicating natural ungulate browsing. Our clipping treatment accurately simulated one bout of ungulate browsing, as a separate treatment of plants browsed once by ungulates and then caged and watered had statistically similar fitness levels as our +clip/+water treatment (flowers, $F_{1,46} = 0.21$, $P = 0.16$; seeds, $F_{1,45} = 0.011$, $P = 0.92$). Additionally, previous studies have failed to show significant differences in fitness between naturally browsed and experimentally clipped plants (Paige and Whitham 1987, Paige 1992). Substantial late-season ungulate browsing occurred on about 3% of the unbrowsed treatment plants that grew above the cage top. These plants were removed from the analysis.

From the time of stem elongation (and major browsing, late May), plants in the supplemental water treatment received 250 mL of water per day for two months. The unwatered plants, according to weather data from the Flagstaff weather station, received 0.0 mm of rain in June 2002, compared to the 13.49 mm June mean, and 38.1 mm of rain in July 2002, compared to the 61.4 mm July mean (1950–2001; data available online from the Western Regional Climate Center).² Furthermore, this Arizona *Ipomopsis* population had been experiencing drought stress since the previous fall. Therefore, the supplemental water treatment did not eliminate prior drought effects. However, the daily 2-mo water addition treatment spanned the entire flowering season and part of the fruiting season—two critical stages of development (reviewed in Levitt 1980).

Assessment of fitness

In mid-September—the end of the *Ipomopsis* fruiting season—plants were harvested. The number of fruits per plant and the number of seeds per fruit were quantified. In past *Ipomopsis* studies, fitness was measured only as number of fruits because the number of seeds per fruit did not vary across treatments (Gronemeyer et al. 1997, Anderson and Paige 2003). During this drought year, however, the number of seeds per fruit varied significantly across treatments (clipping, $F_{1,97} = 8.86$, $P = 0.004$; supplemental water, $F_{1,97} = 4.56$, $P = 0.04$), with fruits from the natural herbivory treatment, +clip/–water treatment, and remaining treatments bearing 4.7 ± 1.2 seeds/fruit, 7.2 ± 0.66 seeds/fruit, and 9 ± 0.52 seeds/fruit, respectively (mean \pm 1 SE, hereafter). Consequently, we measured fitness as the mean number of seeds per plant. To quantify mean seeds for each individual, we multiplied the total number of fruits times the mean number of seeds per fruit for 12 randomly chosen fruits. We also quantified treatment-level seed germination rates. After a 3-wk cold regime at 8°C, 50 seeds per individual were assessed for germination success on #3 Whatman filter paper in

moist petri plates. For across-year comparison of compensation, we used fruit number because this currency was used in past years (see Gronemeyer et al. 1997, Paige 1994), giving us a conservative (larger) estimate of fitness for the year-2002 browsed plants.

Statistical analysis

All variables were square-root transformed to normalize data. To examine compensation across years (1992, 1994, 1995, 1999, 2002), we used a two-way ANCOVA with stem diameter as a covariate for size, followed by within-year *t* tests. The 2×2 experiment (with and without clipping and with and without supplemental water) was assessed using a two-way ANOVA. A one-way ANOVA was used to assess differences in relative fitness among the unbrowsed treatment, the simulated single bout of herbivory (typical of non-drought years) treatment, and the unprotected, natural herbivory treatment. Multiple comparisons of the least-square (LS) means were adjusted using a Scheffé's test for both statistical tests. Data were analyzed using SAS 8.02.

RESULTS

During the 2002 drought year, this typically overcompensating population of *Ipomopsis* severely undercompensated following herbivory ($F_{1,60} = 130.0$, $P < 0.0001$; Fig. 1). In non-drought years, browsed *Ipomopsis* produced 1.5 to two times the number of fruits of unbrowsed plants, yet in 2002, browsed plants produced 1/16th the number of fruits produced by the unbrowsed treatment (Fig. 1).

We found a highly significant herbivory-by-year interaction for mean number of fruits ($F_{1,243} = 40.2$, $P < 0.0001$; Fig. 1), suggesting that browsed and unbrowsed plants respond differently to variation across years. Specifically, between-year variation is substantially larger in browsed plants ($CV = 0.7$) than in the unbrowsed plants ($CV = 0.5$), demonstrating the relative sensitivity of the former and drought tolerance of the latter.

Direct effects of drought stress on plants

In 2002, we found a significant clipping-by-water interaction ($F_{1,102} = 3.95$, $P = 0.049$, Fig. 2) for mean number of seeds produced, suggesting that lack of water limits compensation. Germination rate was constant across the four treatments ($F_{3,65} = 0.191$, $P = 0.902$). Simulated herbivory (single bout typical of non-drought years) had a significant detrimental effect on fitness in the nonwatered treatment, while it had no significant effect in the supplemental water treatment (Fig. 2). Unclipped/unwatered plants produced almost twice the number of seeds of the clipped/unwatered plants; hence, only the unwatered plants significantly undercompensated. In contrast, plants receiving supplemental water equally compensated, indicating that water was important for compensation. Surprisingly,

² (<http://www.wrcc.dri.edu>)

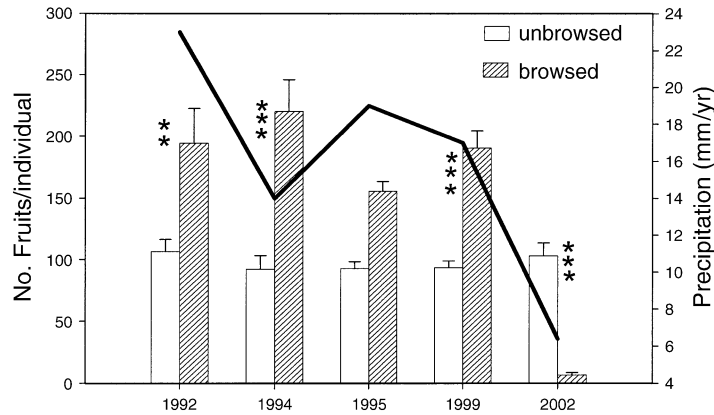


FIG. 1. Natural variation in the number of fruits per plant in browsed and unbrowsed plants across four non-drought years (1992, 1994, 1995, 1999) and one record drought year (2002). Asterisks indicate significant differences between treatments, analyzed with initial plant size as covariate: ** $P < 0.01$; *** $P < 0.001$. Precipitation measures (mm/year; solid line) were obtained from the Flagstaff weather station (see footnote 2). Values represent means \pm 1 SE.

water had no significant effect on the unclipped plants (Fig. 2), again suggesting that if protected from herbivores, *Ipomopsis* is highly drought tolerant.

Indirect effect: drought year browsing levels and the consequences for compensation

In 2002, plants left open to natural browsing (the natural herbivory treatment) experienced unusually high levels of herbivory. One hundred percent of the browsed-once (uncaged) plants were browsed at least twice, as evidenced by the severe damage to lateral stems always released after the first major bout of herbivory. This finding contrasts strongly with those results from previous studies in non-drought years (Paige 1992, 1994, Gronemeyer et al. 1997, Anderson and Paige 2003), in which secondary browsing occurs on $33 \pm 2.8\%$ of the population and accounts for biomass removal only at the very terminal ends of fully regrown plants.

Moreover, the naturally browsed plants suffered severe detrimental effects from multiple bouts of herbivory. These naturally browsed plants significantly undercompensated, with unclipped plants producing $33\times$ the number of seeds of multiply browsed plants ($F_{2,83}$

$= 47.73$, $P < 0.0001$, Table 1). This result was magnified by an extremely low germination rate of the seeds produced by the naturally browsed plants (Table 1), which was half the rate of unbrowsed and once-clipped plants ($F_{2,42} = 9.45$, $P < 0.0001$). Taking this level of germination into account, the unclipped treatment yielded $70\times$ the number of viable seeds of the multiply browsed plants. Additionally, the clipped treatment that simulated typical herbivory levels (single major bout) produced $28\times$ the number of viable seeds of the naturally browsed plants, demonstrating the fitness consequences of multiple browsing events in a drought year (Table 1).

DISCUSSION

In contrast to the previous findings of overcompensation, this *Ipomopsis* population severely undercompensated during the extreme drought of 2002. By performing two separate analyses, we demonstrated that both decreased compensatory capacity and unusually high levels of herbivory underlie the exceptionally low compensation during this record drought year. The relative drought tolerance of unbrowsed plants and the drought sensitivity of browsed plants support theoretical findings of Huhta et al. (2000a), who proposed that temporally variable conditions between years will more strongly impact damaged plants.

Direct effect of drought stress on compensatory capacity

The significant interaction between simulated herbivory (typical of non-drought years) and supplemental water treatments suggests that lack of water limited compensatory capacity in *Ipomopsis*. Although defoliation may improve plant water status by decreasing the transpiration surface (Toft et al. 1987), clipping during the 2002 drought year functioned as an additional stress that ultimately reduced fitness in *Ipomopsis*.

Drought-induced limitations on several physiological processes important to compensation may explain the undercompensation observed. Rather than the typ-

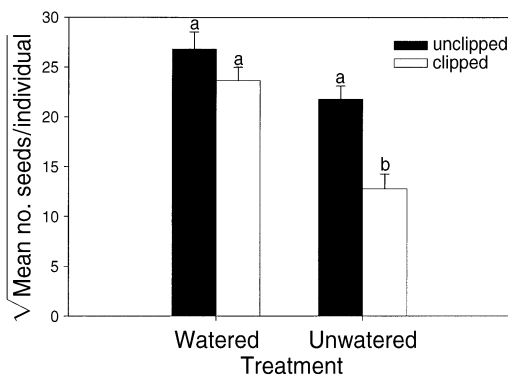


FIG. 2. Square root of the number of seeds per individual in the 2002 supplemental water and clipping treatments. Letters indicate significant differences from multiple comparisons of the LS-means adjusted with a Scheffé's test. Values are means \pm 1 SE.

TABLE 1. Number of seeds, germination, and viable seeds for the 2002 drought-year treatments: unclipped, clipped (typical herbivory level), and naturally browsed (uncaged).

Parameter	Unclipped	Clipped	Natural herbivory
Mean no. seeds	517.6 ^a ± 45.8	224.1 ^b ± 38.8	15.7 ^c ± 8.3
Germination rate (%)	78.2 ^a ± 5.0	81.3 ^a ± 4.5	41 ^b ± 12
Mean no. viable seeds	403.2 ± 61.5	182.2 ± 41.6	6.4 ± 5.3

Notes: Values are means ± 1 SE. Standard error for mean number of viable seeds was calculated using propagation of errors. The number of viable seeds was calculated as mean no. seeds × germination rate. Different letters indicate significant difference at $P < 0.001$ from multiple comparisons of the LS-means adjusted with a Scheffé's test.

ical increase following the herbivory event, photosynthesis and relative growth rate (Caldwell et al. 1981, Wallace et al. 1984, Oesterheld and McNaughton 1991, but see Nowak and Caldwell 1984) may have decreased under water stress. Similarly, the typical increase in nutrient translocation from belowground to aboveground parts following herbivory (Dyer et al. 1991) probably not did occur as a result of water stress (Turner and Kramer 1980, Simpson 1981). Furthermore, the number of lateral stems released following herbivory usually increases with resource availability (Juenger and Bergelson 1997, Huhta et al. 2000a) and we found that fewer lateral stems were released following clipping in the unwatered treatment (M. Levine, unpublished data). These three factors may also explain why the supplemental water treatment only equally compensated rather than overcompensated. Arizona had been experiencing drought since the previous fall (see footnote 2), so our watered treatment that began in early June likely only partially released these plants from drought stress.

Findings from past studies investigating the effect of water availability on compensation are mixed, though likely because some studies used naturally water stressed systems while others simply added water to non-stressed ones. In multi-year studies, both Lenartsson et al. (1998, with *Gentianella campestris*) and Maschinski and Whitham (1989, with *Ipomopsis arizonica*) found trends of lower compensation in years with low precipitation. Cox and McEvoy (1983) found increasing compensation with increasing irrigation in *Senecio jacobaea* during a water-stressed year, suggesting that water is a key resource for regrowth following herbivory. However, since all irrigation-level treatments were subject to herbivory, no comparisons were made to an uneaten control—the baseline treatment to which damaged plants are compared for establishing under-, equal-, or overcompensation. Maschinski and Whitham (1989) and Juenger and Bergelson (1997) found no effect of water addition on compensation in *Ipomopsis*; however, these studies occurred during non-drought years in which water was presumably not a limiting resource. In light of these latter findings, our study highlights the advantages of using natural variation in the field to understand the ecologically relevant abiotic factors that may limit compensation.

Results from this portion of our study (the direct effect of drought) support the Compensatory Continuum Hypothesis, which states that compensatory capacity increases as resources increase, and thus plant-herbivore compensatory interactions can range from ecologically antagonistic to mutualistic, depending on resource level (Maschinski and Whitham 1989). This theory has been demonstrated experimentally by measuring compensation under artificially enhanced conditions, such as N and P additions (Maschinski and Whitham 1989, Juenger and Bergelson 1997, Huhta et al. 2000a) and hand pollination (Juenger and Bergelson 1997), but never under stressful conditions, particularly naturally induced stresses. By caging plants, we were able to show that if herbivory were to remain similar across non-drought and drought years (a single major bout), then compensation varied with resource availability (water).

Indirect effect of drought-year-associated browsing on compensation

Ultimately we found that the dynamics underlying the severity of undercompensation were explained only partially by the Compensatory Continuum Hypothesis. An additional analysis of the indirect effects of drought, which incorporated not only plant water limitation, but also drought-year-associated browsing, showed that both factors contributed to undercompensation. Rather than the single bout of herbivory typically imposed in non-drought years, plants experienced repeated ungulate browsing under the severe drought conditions of 2002. Previous studies on this population of *Ipomopsis* have shown that these herbivores frequently browse twice; however, the deer and elk typically eat only the terminal ends of the regrown, multiply stemmed plants and so have no effect on final fitness (Paige 1992). In contrast to past non-drought years, during the 2002 drought the ungulates browsed the multiple lateral stems of previously browsed plants down to 2–3 cm. This exceptionally high level of herbivory left individuals with on average six viable seeds (see Table 1), compared to over 1000 seeds typical of normal years (Paige and Whitham 1987, Paige 1992, Anderson and Paige 2003). Furthermore, the ungulates browsed over 99% of the population, leaving the 2002 cohort virtually decimated.

Variation in browsing intensity has long been appreciated as an important factor in compensation (McNaughton 1979, Huhta et al. 2000b). In a common-garden setting, Huhta et al. (2000b) showed that high levels of herbivory (75% biomass removed) are associated with a decrease in compensation relative to intermediate levels (50%). Similarly, Iacobelli and Jefferies (1991) demonstrated the detrimental effects of overgrazing on vegetation biomass surrounding the nesting grounds of lesser snow geese.

There are several possible explanations for the unusually high levels of browsing during the 2002 drought year. During the drought, all local water sources had dried or experienced drastic reductions in flow (data available online from USGS WaterWatch),³ the typical NDVI (normalized difference vegetation index) means for the Coconino National Forest were nearly halved (M. Snyder, *personal communication*), and ungulate mortality rates were unusually high (R. Miller, *personal communication*). The apparent water stress on ungulates and drastic reductions in green cover may have catalyzed shifts in feeding preference (and ultimately, herbivory pressure)—a typical ungulate response to stressful conditions (Kossak 1983, Gillingham and Bunnell 1989, Wilmshurst et al. 1999). In addition to water stress on ungulates, drought-induced changes in plant resistance such as increased available nitrogen and decreased secondary compound levels may also have contributed to increased ungulate browsing pressure. Research examining the relative importance of such mechanisms is underway.

Measuring plant–herbivore interactions under environmental variability

To our knowledge, this is the first study to examine directly the combinatorial effects of compensatory capacity and intensity of herbivory under naturally stressful conditions. The 2002 drought provided the unique opportunity to investigate both its direct and indirect effects. Under these severe conditions, both the capacity to compensate and ungulate browsing levels were impacted by the shift in the abiotic environment, highlighting the importance of considering all participants in an interaction. Much of the literature on plant–animal interactions under variable environments, especially tolerance/compensation studies, simulate this variability for the host only (Maschinski and Whitham 1989, Louda and Collinge 1992, Huhta et al. 2000a, Meyer 2000). While physiologically interesting and critical for isolating variables, this approach risks missing potentially important combinatorial factors generated by both participants of a plant–animal interaction. Our study, however, is only a first step in understanding the likely complicated mechanisms underlying combinatorial effects of climatic extremes. Exploring the direct effects of drought, for instance,

on the ungulates alone would have further elucidated mechanisms responsible for the indirect effect (increasing herbivory pressure). Therefore, future studies that isolate the direct effects of environmental variability on both members of an interaction through field experiments combined with field observations will lead to a more thorough understanding of the mechanisms underlying the natural consequences of climatic extremes.

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³ (<http://water.usgs.gov/cgi>)

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