Morphological and Physiological Traits Account for Similar Nitrate Uptake by Crested Wheatgrass and Cheatgrass

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ABSTRACT

Millions of hectares throughout the Intermountain West are either dominated or threatened by the invasive annual grass Bromus tectorum *(cheatgrass). This invasion is largely linked to disturbance and few regions appear immune. Disturbance liberates resources in a community and cheatgrass appears exceptionally able to capitalize on these resources. One species, however, is consistently competitive with cheatgrass.* Agropyron cristatum *(crested wheatgrass), an improved plant material developed from several populations in central Asia, is drought resistant, grazing tolerant, and largely excludes cheatgrass in stands established within the Great Basin. While previous studies document high resource uptake ability by crested wheatgrass, it remains unknown if high uptake in this species is due to morphological or physiological adaptation. We examined N uptake and tissue morphology of four grasses common in the Intermountain West, including cheatgrass and crested wheatgrass. We also included two native grasses,* Pseudoroegneria spicata *(bluebunch wheatgrass) and* Elymus elymoides *(bottlebrush squirreltail). We observed similar rates of N uptake by cheatgrass and crested wheatgrass and their uptake was greater than the native perennial species. A multivariate analysis suggests that, of the three perennial grasses examined here, crested wheatgrass is morphologically most similar to cheatgrass, but that morphology only accounts for 57 percent of the variation in N uptake capacity among species. Consequently, physiological traits such as induction of N uptake or N efflux likely play a role in the ability of crested wheatgrass to achieve N uptake rates similar to cheatgrass.*

INTRODUCTION

The most substantial plant invasion in North America is the replacement of perennial sagebrush communities with invasive, exotic annual grasses such as cheatgrass (D'Antonio and Vitousek 1992; Chambers et al. 2007). *Bromus tectorum* L., a winter annual native to central Asia, has come to occupy millions of hectares in the Intermountain West over the past century (Stewart and Hull 1949; Bradley and Mustard 2006). This species germinates in the autumn, produces copious seed, and maintains high density stands that rapidly dry near-surface soil in the spring (Knapp 1996; Leffler et al. 2005). Because *B. tectorum* senesces in late spring and seeds can cause livestock injury, the resource value is greatly reduced compared to communities of native perennials (Knapp 1996).

Mounting evidence suggests that plant invasion is largely linked to resource availability and dynamics. Specifically, disturbances cause abrupt increases in resource availability and invasive species are capable of taking advantage of the resource pulse (Davis et al. 2000; Davis and Pelsor 2001; Leffler and Ryel 2012). Consequently, any disturbance that alters resource availability can trigger an invasion if an appropriate species is present locally. *Bromus tectorum* initially establishes in degraded range communities (Knapp 1996) where perennial grasses are not able to use near-surface soil resources effectively (Leffler and Ryel 2012). When *B. tectorum* reaches sufficient density and fire occurs, remaining perennial vegetation that is not fire-resistant can be eliminated and the site is converted to an annual species plant community (Knapp 1996). In the absence of perennial vegetation, there is abundant soil NO_3^- during autumn in *B. tectorum* stands (Booth et al. 2003; Hooker et al. 2008), which promotes establishment of the next generation because *B. tectorum* is highly responsive to soil N pulses (James 2008).

Since Elton (1958) ecological theory has held that diverse communities of species are resistant to invasion because they more fully occupy niche space, leaving few resources available to be exploited (i.e., niche complementarity, Naeem et al. 2000; Fargione

and Tilman 2005). Conversely, diverse communities are more likely to include a hyper-competitive species that inhibits further invasion (i.e., the sampling effect, Naeem et al. 2000; Fargione and Tilman 2005). In the Intermountain West, few communities seem capable of resisting invasion by *B. tectorum* when they are disturbed; rather one species seems most capable of competing with *B. tectorum*. Crested wheatgrass (*Agropyron cristatum* and closely related species) is an exotic perennial grass planted throughout the region because it is resistant to drought, cold, and grazing (Rogler and Lorenz 1983). This species appears competitive with invasive annual grasses (Rummell 1946; D'Antonio and Vitousek 1992; Davies 2010) and previous studies indicate its ability to acquire soil resources is greater than native grasses (Caldwell et al. 1985; Eissenstat and Caldwell 1988).

The competitive ability of *A. cristatum* is somewhat curious given its perennial life form. Tissue economics theory (Wright et al. 2004) holds that short-lived species will have rapid rates of resource acquisition compared to long-lived species and largely attributes this difference to tissue morphology. *Bromus tectorum* is known to use water and acquire N rapidly when actively growing (Leffler et al. 2005; James 2008), a trait expected in an annual grass. Studies, however, suggest that *A. cristatum* does not have a greater growth rate than native perennial grasses that do not effectively compete with *B. tectorum* (Eissenstat and Caldwell 1987; Bilbrough and Caldwell 1997). Thus, the morphological and physiological mechanisms responsible for interference of *B. tectorum* by *A. cristatum* remain elusive.

In this contribution we address differences in nitrogen uptake capacity and tissue morphology among four grass species grown in two experimental temperature conditions. Grasses include the non-native species *B. tectorum* and *A. cristatum* and the native bunchgrasses *Pseudoroegneria spicata* (bluebunch wheatgrass) and *Elymus elymoides* (bottlebrush squirreltail). We wish to know if (1) nitrogen uptake capacity and tissue morphology differ among species, (2) whether tissue morphology can explain differences in uptake capacity among species, and (3) if differences among species are consistent between growth environments. We conclude with a discussion of the roles morphology and physiology play in competitive ability in these species.

METHODS

Study Species

We compared morphological and physiological differences between the annual grass *Bromus tectorum* L. and three perennial grasses common in the Intermountain West. The perennial grass of most interest was Hycrest II crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), a widely planted non-native cultivar developed from several populations in central Asia. *Agropyron cristatum* was chosen for its vigorous growth and evidence that rangeland plantings of *A. cristatum* are largely resistent to invasion by annual grasses (Davies 2010). Two native perennial grasses were included in the study for comparison with *A. cristatum*: Rattlesnake bottlebrush squirreltail germplasm (*Elymus elymoides* [Raf.] Sweezey ssp. *elymoides*) and Anatone bluebunch wheatgrass germplasm (*Pseudoroegneria spicata* [Pursh] A. Löve ssp. *spicata*). *Elymus elymoides* was selected because it is a short-lived perennial that can naturally establish in annual-dominated ecosystems (Hironaka and Tisdale 1963; Hironaka and Sindelar 1973) while *P. spicata* is a long-lived perennial grass. Seeds of *B. tectorum* were collected from populations in northern Utah. Seeds of the others grasses were obtained from local seed producers.

Growth Conditions, Experimental Treatments, and Measurement

Individual plants were grown in pots (4 x 21 cm 'cone-tainers', Ray Leach Inc., Canby, Oregon) for the duration of the experiment. Pots were filled with a 1: 1 mixture of a coarse and fine growth medium (Turface MVP and Greens Grade, Profile Products LLC, Buffalo Grove, Illinois) holding ca. 0.5 g H_2O g^{-1} medium. The medium was washed before use in the experiment to insure no nutrients were adsorbed to the particle surface. Three to five seeds of a single species were added to a pot and kept moist with periodic watering. Ten days following germination and emergence, pots were transferred to growth chambers programmed for constant experimental temperature and a 14/10 h day/night cycle. Photosynthetic flux density inside the chambers was ca. 900 μmol m^{-2} s^{-1} above the uppermost leaves. After several days of growth, seedlings were thinned to two individuals per pot.

Plants were kept in two growth chambers that each contained twenty pots of each species. One chamber was set to 10 ˚C, the other to 25 ˚C. Temperature was monitored (model Watchdog B101, Spectrum Technologies, Plainfield, Illinois), and each week, plants and temperature conditions were rotated among chambers to minimize chamber effects. While target temperatures were achieved at night, daytime temperatures were 3-4 ˚C warmer than intended (13.1/9.9 and 28.6/24.8 ˚C day/night, respectively). Moisture in pots was maintained near saturation daily with an NH_4^+-free nutrient solution containing 0.20 g l^{-1} KNO_3, 0.21 g l^{-1} $Ca(NO_3)_2$, 0.06 g l^{-1} NaH_2PO_4, 0.12 g l^{-1} $MgSO_4$, and 0.3 g l^{-1} of a complete micronutrient fertilizer (J.R. Peters Inc., Allentown, Pennsylvania).

Nitrogen acquisition was measured via uptake of NO_3^-, the most available inorganic form of N in semi-arid regions of the Intermountain West (West 1991). Nitrate acquisition was determined with incubations in a ^{15}N solution (BassariRad et al. 1993). Assays began with the 25 ˚C individuals ca. 5 weeks following germination. Individuals in the 10˚C treatments were measured approximately two weeks later to account for slower development of individuals in the colder temperature treatments. Ten pots of each species were randomly selected for measurement. Individual plants were removed from pots and washed free of growth medium. Eight individual plants were placed in eight flasks each containing 250 mL of 60 atom percent $K^{15}NO_3$, the remaining two plants were treated as controls and placed in flasks of $K^{14}NO_3$.

After a two-hour incubation at growth temperatures, plants were removed from assay flasks and immersed in a chilled 50 mM KCl solution to stop NO_3^- uptake. Plants were then washed five times in distilled water. Root and shoot tissue was dried at 75 ˚C for at least 48 hours, weighed, and ground to a fine powder using a shaker mill (model 2000, SPEX CertiPrep, Metuchen, New Jersey). Tissue samples were analyzed for [^{15}N] at the University of California, Davis. Standard deviation among repeated measurements of a standard was less than 0.0003 atom percent. Nitrate acquisition was calculated by determining the difference in tissue ^{15}N between labeled plants and control plants. Excess ^{15}N in root and shoot tissue were combined and acqusition is expressed as mass-specific absorption rate (SAR_M, μgN g^{-1} h^{-1}).

We quantified root and leaf morphological traits before tissue was dried. Surface area of leaf tissue was measured with a leaf area meter (model 3100, Li-Cor Inc., Lincoln, Nebraska) and root images were obtained with a flatbed scanner and analyzed for length and surface area using the software package WinRhizo (Regent Instruments, Quebec, QC). Mass of tissue was determined after drying.

Statistical Analysis

We used ANOVA to test for statistically significant differences among species in each temperature regime. Response variables included SAR_M, leaf area, leaf mass, root area, root mass, and root length in a fixed-effect, one-way ANOVA. Means were separated using a Tukey multiple comparison. Differences were considered significant at $P < 0.05$ and ANOVA was conducted with PROC GLM in SAS (version 9.2, SAS Institute Inc., Cary, North Carolina).

The five morphological variables were combined in a Principle Component Analysis (PCA) to produce new, uncorrelated variables, which could be used in further analyses. We performed PCA using the PRINCOMP function in the statistical computing language R (R Core Development Team 2005). Mass-specific absorption rate was regressed onto the first two principle component axes to determine how much of its variation was explained by tissue morphology.

RESULTS

We observed significant differences among species in SAR_M and all morphological variables in 10 and 25 ˚C conditions (table 1). The two exotic species (*B. tectorum* and *A. cristatum*) had statistically similar SAR_M as did the two native perennial grasses *P. spicata* and *E. elymoides* (figure 1). Mass-specific absorption rate was 213 percent and 53 percent higher in the exotic species compared to the natives at 10 and 25 ˚C, respectively.

We found the highest leaf mass in *A. cristatum* and the highest leaf area in *B. tectorum* (figure 2). The two native species were similar in leaf mass and area in both temperature conditions. While differences between *B. tectorum* and *A. cristatum* in leaf mass were significant but small, *B. tectorum* produced ca. double the leaf area of *A. cristatum* at 25 ˚C. Consequently, *B. tectorum* had a higher specific leaf area (grand means: *B. tectorum* = 210, *A. cristatum* = 91). Higher temperatures resulted in greater leaf mass and leaf surface area for all species.

Table 1. ANOVA examining differences among species in the two temperature conditions. Numerator degrees of freedom = 3 for all variables.

	10 ˚C			25˚C		
	n	*F*	*P*	*n*	*F*	*P*
SAR	32	14.94	< 0.001	31	8.70	<0.001
Leaf Mass	40	34.12	< 0.001	37	29.22	<0.001
Leaf Area	40	99.25	< 0.001	40	256.8	<0.001
Root Length	39	243.3	< 0.001	39	47.01	<0.001
Root Area	40	162.1	<0.001	39	33.20	<0.001
Root Mass	40	32.02	< 0.001	40	8.97	<0.001

Table 2. PCA loadings and proportion of variation explained by each principle component. The first two principle components explain 94% of the variation in the leaf and root morphology data set. The first principle component, a nearly equal weighting of all variables, represents the tissue economics spectrum (Wright 2004).

	PC1	PC2	PC3	PC4	PC5
Leaf Mass	−0.405	0.600	−0.346	0.568	0.182
Leaf Area	−0.472	−0.152	0.774	0.352	−0.178
Root Length	−0.426	−0.577	−0.206	0	0.665
Root Area	−0.483	−0.270	−0.454	−0.115	−0.689
Root Mass	−0.445	0.460	0.184	−0.734	0.134
% explained	0.760	0.179	0.041	0.019	0.002

Root mass was similar in *B. tectorum* and *A. cristatum* but *B. tectorum* produced longer roots and roots with more surface area (figure 3). Consequently, specific root length was highest in *B. tectorum* (grand means: *B. tectorum* = 12.0, *A. cristatum* = 6.8). Root mass, length, and surface area were generally lower in the native perennials. High temperature resulted in greater root mass for all species. High temperature resulted in greater root length and root surface area for the perennial species, but not for *B. tectorum*.

The principle component analysis produced two uncorrelated variables that explained 94 percent of the variation in the morphology data set (table 2). The first principle component (PC1) was a nearly equal weighting of all morphological variables which were correlated with one another. The second principle component (PC2) was more heavily weighted toward leaf mass, root mass, and root length but indicated a negative relationship between leaf mass and root length. All species and the two temperature conditions separated along PC1 (figure 4). Mean PC1 scores were most similar for the two non-native species and these scores were distinct from those for the native species, which were also similar. *Bromus tectorum* separated from other species along PC2. A regression of SAR_M onto PC1 and PC2 indicated that PC1 explained ca. 57 percent of the variation in SAR_M while PC2 was not a significant predictor (figure 5).

DISCUSSION

Bromus tectorum and *A. cristatum* had similar SAR_M, which was greater than SAR_M of native bunchgrasses. A previous study suggested differences in root length-specific absorption rate among the same species was dependent on N availability; at low N, uptake by native perennials

exceeded that of *A. cristatum* and *B. tectorum* (James 2008). In separate studies, *Agropyron desertorum*, a species closely related to *A. cristatum*, had a greater ability to acquire soil phosphorus (Caldwell et al. 1985) and fix carbon (Caldwell et al. 1981) than native bunchgrasses. Nitrogen uptake by *A. cristatum* can exceed uptake by *B. tectorum* (James 2008) but *B. tectorum* has a higher tissue N concentration (Monaco et al. 2003) and reduces soil N to a greater extent than native grasses (Blank et al. 2010).

Figure 1. Mean mass-specific absorption rate (SAR_M) under two growth temperatures for each species. Error bars indicate 95% confidence intervals. Bars with the same capital letters above are statistically not different in the 10°C growth condition; bars with the same lowercase letters above are statistically not different in the 25°C growth condition.
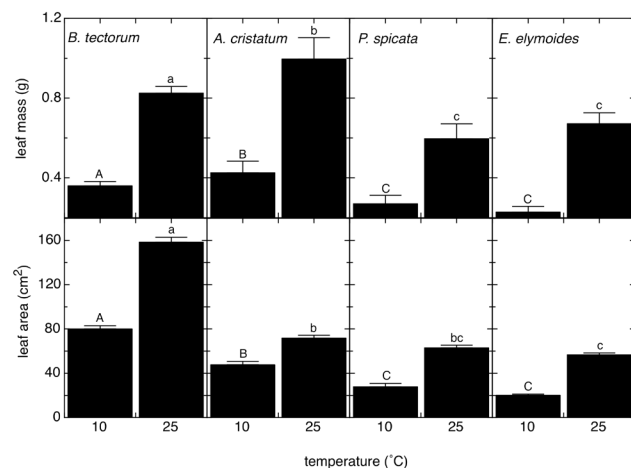

Figure 2. Mean leaf mass and area under two growth temperatures for each species. Error bars indicate 95% confidence intervals. Bars with the same capital letters above are statistically not different in the 10°C growth condition; bars with the same lowercase letters above are statistically not different in the 25°C growth condition.

Tissue morphology differences between an annual grass such as *B. tectorum* and perennial grasses were expected based on tissue economics (Wright et al. 2004). Consequently, *B. tectorum* had high specific leaf area and specific root length, a result previously

reported (James 2008). Most morphological differences, however, were subtle. For variables such as leaf and root mass, *B. tectorum* and *A. cristatum* were not statistically different. For other variables, *A. cristatum* values were intermediate to those for *B. tectorum* and the native grasses. Subtle and context-dependent differences in morphology among these species are common. James (2008) reported greater root mass, root length, and total biomass in *A. cristatum* compared to native perennials, but much greater values for the same variables in *B. tectorum*. Caldwell et al. (1981) attributed higher photosynthetic rates in *A. desertorum* compared to *P. spicata* to higher leaf surface area.
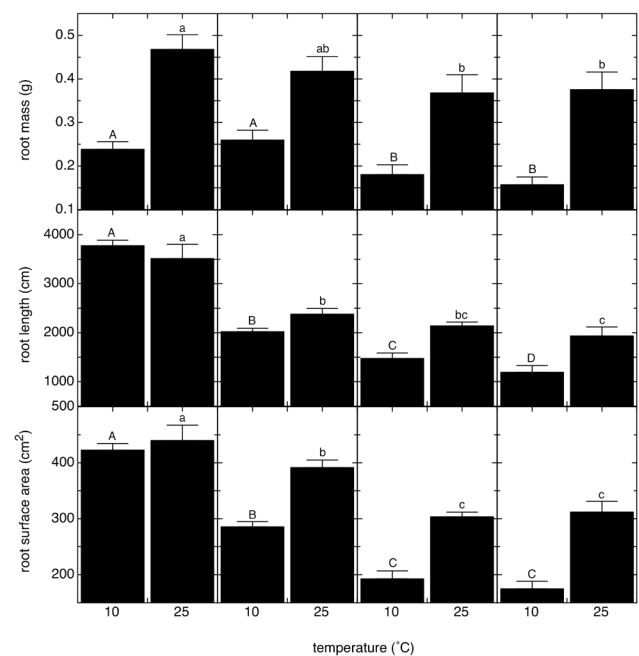

Figure 3. Mean root mass, length, and surface area under two growth temperatures for each species. Error bars indicate 95% confidence intervals. Bars with the same capital letters above are statistically not different in the 10°C growth condition; bars with the same lowercase letters above are statistically not different in the 25°C growth condition.

The first principle component, which accounts for 76 percent of the variation in the data set, describes the tissue economics spectrum for these species. The similar loadings of each morphological variable with the same sign indicate these variables tend to change with each other in a positive manner (i.e., species with high leaf mass also tend to have high root length). Consequently, separation of species along PC1 indicates differences among species based on tissue economics. *Bromus tectorum* and *A. cristatum* were close to each other on the 'acquisitive' end of

the spectrum while *P. spicata* and *E. elymoides* were close to each other on the 'conservative' end of the spectrum. The leaf economics spectrum explained ca. 57 percent of the variation among species in N uptake capacity.
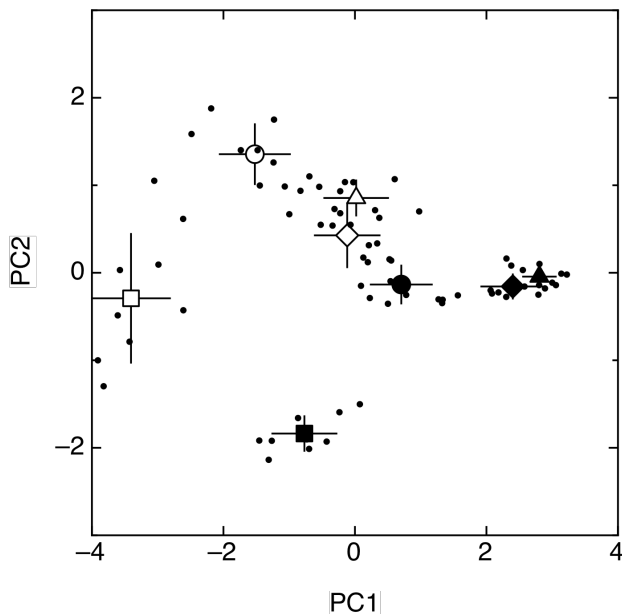

Figure 4. The first two principle components which explain 94% of the variation in the morphology data set. PC1 is a nearly equal weighting of the morphology variables and represents the tissue economics spectrum. Closed symbols represent plants in the 10˚C condition while open symbols represent plants in the 25˚C condition. Shapes are as follows: square, *B. tectorum*; circle, *A. cristatum*; diamond, *P. spicata*; triangle, *E. elymoides*. Symbols are mean values for a species in a growth condition; error bars represent one standard deviation. Dots indicate scores on PC1 and PC2 for individual plants. Species close to one another on PC1 are similar in morphology.

Growth temperature had little influence on the relationship among species in either N uptake or morphology. Higher temperature clearly shifted species toward the 'acquisitive' end of the tissue economics spectrum, but their position relative to each other on the spectrum did not change. Other growth conditions would likely have a different result, because differences among these species were not consistent when grown in various N environments (James 2008) and *B. tectorum* tends to be very plastic in dry mass production (Rice and Mack 1991).

Our results are specific to the experimental conditions in an N environment that exceed common field values (Booth et al. 2003; Hooker et al. 2008); our goal was

to examine SAR_M when N was not limiting production. Because only 57 percent of the variation in N uptake capacity could be explained by variation in morphology, the remaining variation can be attributed to physiology and measurement error. *Agropyron cristatum* could achieve similar N uptake to *B. tectorum* for several hypothetical physiological reasons: (1) NO_3^- efflux from *A. cristatum* roots could be very low. Our measurements of N uptake quantify a net rate, or a balance between influx and efflux, which is dependent on root $[NO_3^-]$ (Aslam et al. 1996; Glass et al. 2001). Root $[NO_3^-]$ may be related to NO_3^- reduction in leaves or different rates of turnover between influx and efflux systems (Aslam et al. 1996, Glass et al. 2001), which may vary among species; (2) The relative importance of constitutive and inducible NO_3^- uptake systems may differ between *A. cristatum* and *B. tectorum* (Crawford and Glass 1998); and (3) *Bromus tectorum* and *A. cristatum* may have different optimum temperatures for growth which were not measured here. Consequently, at higher or lower temperatures, uptake by *B. tectorum* may exceed that of *A. cristatum* because N uptake and relative growth rate are highly correlated (Glass et al. 2001; Tian et al. 2006). We cannot speculate on how much of the remaining variation is due to physiology; additional studies are necessary to investigate these hypotheses.
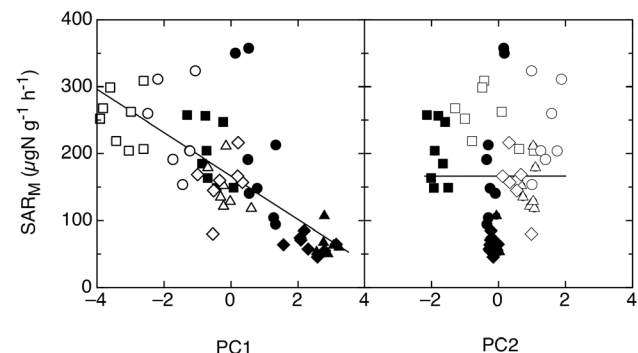

Figure 5. Linear relationship between mass-specific absorption rate (SAR_M) and PC1 or PC2. Symbols as in figure 4. The relationship is significant for PC1 ($n = 63$, $r^2 = 0.57$, $P < 0.001$), but not for PC2.

High N uptake capacity in *A. cristatum* may contribute to the ability of stands of this species to resist invasion by *B. tectorum* and other annual grasses. One difference between annual and perennial communities is the pronounced pulse of N availability in the autumn following senescence of annual grasses (Booth et al. 2003; Hooker et al. 2008). This

pulse of N may be important to establishment of annuals and *A. cristatum* may deny annuals this resource more efficiently than native perennials. Morphological similarity between *B. tectorum* and *A. cristatum* plays an important role, but likely not the only role, in the ability of *A. cristatum* to match N uptake by *B. tectorum*. Future efforts to develop materials for restoration of rangeland degraded by *B. tectorum* should examine temporal N uptake capacity as a desirable trait.

ACKNOWLEDGMENTS

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