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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Potassium enrichment stimulates the growth and reproduction of a clone of *Daphnia dentifera*

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Abstract Nutrient limitation commonly constrains organisms in natural ecosystems. Typically, ecologists focus on limitation by N and P. However, other nutrients can limit growth or reproduction. Here we focus on K limitation of invertebrate consumers (*Daphnia dentifera*) and phytoplankton in freshwater lakes. All organisms require K for several metabolic processes. In freshwater, K could limit growth because low external concentrations can increase the energetic costs of accumulating K. Furthermore, in a study linking K to disease, we previously found that K enrichment of water from one low-K lake stimulated the growth and reproduction of *Daphnia*. Here we test whether K could limit the production of *Daphnia* and phytoplankton across lakes and years. We repeated a life table experiment using water collected from a low-K lake during a different year. K again stimulated *Daphnia* reproduction. We also enriched water from 12 lakes with K or P and measured short-term growth of *Daphnia* and the resident algal community. Both nutrients increased *Daphnia* growth in five lakes. However, only P enhanced algal production. P stimulation of *Daphnia* positively correlated with algal quantity and the ratio of C to P in seston. However, K stimulation of *Daphnia* was not correlated with these factors or the background concentration of K. Thus, this study shows repeatable K-limited animal physiology in nature. Further, we can exclude the hypothesis that K stimulates *Daphnia* indirectly by enhancing algal production. These patterns call for future physiological studies to uncover the mechanistic basis of K limitation in natural systems.

Keywords Algae · Growth rate · Nutrient limitation · Condition · Freshwater

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Introduction

Nutrient limitation of growth and reproduction is a widespread constraint for organisms in natural ecosystems (Elser et al. 2000). Enrichment of key nutrients may alleviate this constraint. Enrichment often stimulates growth, physiological condition, and reproduction for producers and consumers (Elser et al. 2001, 2007). These effects can cascade through food webs, altering species interactions (Frost et al. 2008) and ecosystem processes (Oren et al. 2001). For example, P enrichment in aquatic habitats can stimulate the reproduction and condition (e.g., increased internal concentrations of ribosomes and P) of photosynthetic algae (Sterner and Hessen 1994). These effects can increase both the quantity and quality of algal food resources for consumers (Sterner 1997). It may also alter community composition, nutrient cycling, and water quality (Hall 2009; Schindler 2012). Thus, nutrient limitation—and its release by enrichment—can play a central role in

population, community, and ecosystem ecology (Sterner and Elser 2002).

Since limitation and enrichment impact ecosystems so profoundly, we must identify the limiting nutrient(s) for both producers and consumers in nature. In general, when looking for limiting nutrients, most effort focuses on N and P (Sterner and Elser 2002). Indeed, these two nutrients often limit primary and secondary production in terrestrial, freshwater, and marine habitats (Elser et al. 2007), and both provide fundamental components of proteins and nucleic acids, respectively (Sterner and Elser 2002). Still, other minerals (e.g., Ca, Fe, and K) and biochemicals (e.g., fatty acids and sterols) can also limit productivity, community composition, or ecosystem processes (Coale et al. 1996; Muller-Navarra et al. 2004; Jeziorski et al. 2008). Often, our mechanistic understanding of limitation by these insufficiently studied nutrients lags behind that for N and P (Sterner and Elser 2002). However, the strong signatures of limitation by these nutrients suggest that a broader focus on limitation could reveal novel insights into the nutritional requirements, performance, and ecological interactions of producers and consumers in natural ecosystems.

In this study, we focus on the nutrient K for two reasons. First, while greatly insufficiently studied, K could limit the growth of a diverse array of freshwater organisms. All organisms require K for a variety of metabolic processes [e.g., enzyme activity, pH and charge balance, and energy assimilation (Williams 1970; Marschner 1995)]. However, the K^+ ion leaks readily, requiring potentially substantial energetic costs to constantly pump it back into cells (Williams 1970). In freshwater, low external (dissolved) concentrations of K can substantially exacerbate this cost (Williams 1970), thereby diminishing the growth rate of animals or primary producers. Second, a previously detected ecological pattern prompts further focus on K. Low K concentrations constrain fungal epidemics in *Daphnia dentifera*, a freshwater zooplankton (and our focal animal here). K influenced disease through traits linked to the energetic condition of hosts (Civitello et al. 2013). In particular, in a set of experiments, K addition stimulated growth of the host; this stimulation then increased the birth rate of hosts but also the production of fungal spores (Hall et al. 2009, Civitello et al. 2013). Both factors catalyze disease spread. Conversely, K limitation can constrain disease.

Here we tested whether K stimulates the production of *D. dentifera* and its food resource, phytoplankton (algae), across time (within one lake between years) and space (across lakes). First, we repeated a life table experiment manipulating K in water collected from a low-K lake used in our previous study (Civitello et al. 2013). We hypothesized that K enrichment would again stimulate *Daphnia* reproduction because K levels remain fairly constant within lakes among years in our study area [including this lake (Civitello et al. 2013)]. Second, we broadened the search for K limitation. We enriched field-collected water from 12 lakes with K or P (a common limiting nutrient in freshwater systems). We then tracked the growth responses of individual *Daphnia* and the resident algal community in separate experiments.

We hypothesized that K enrichment would stimulate *Daphnia* growth in a variety of lakes. Furthermore, based on previous results (Talling 2010), we hypothesized that algal production should not respond to K addition. Thus, response of *Daphnia* should reflect underlying physiological mechanisms rather than stimulation of food resources. Then, we compared K stimulation of *Daphnia* (and algae) to that of P enrichment. P commonly stimulates the production of producers and consumers in freshwater systems (Sterner and Elser 2002). Thus, here we used P enrichment as a benchmark for K limitation. Finally, we tested whether stimulation by K was related to (1) the background concentration of K in the lake, (2) algal quantity, or (3) an index of algal quality (C:P ratio of seston).

Materials and methods

We used nutrient enrichment assays to quantify stimulatory effects of K and P on growth and performance of *Daphnia dentifera*. We focused on lakes that are dominated by *D. dentifera* from late summer up to and including December (Civitello et al. 2013). For these experiments, we collected integrated epilimnetic water daily from the focal lake(s) with a tube sampler and sieved it through an 80-μm screen to remove zooplankton but not edible algae. We determined the background concentration of dissolved K for each lake using inductively coupled plasma-mass spectrometry on a subsample of water (Jenner et al. 1990; Activation Laboratories, Ancaster, ON). We then enriched the lake water with nutrients (either K or P) and cultured individual *Daphnia* or the natural algal community under favorable conditions (20 °C with a 16-h:8-h light:dark photoperiod, light intensity, ~50 μmol quanta/m^2 per s). We used neonates (<24-h-old individuals) collected from a single *D. dentifera* genotype (originally collected from Baker Lake, Barry County, MI; 0.7 mg K^+/L; total P, 27 μg P/L), and did not provide additional food resources. Thus, *Daphnia* consumed only the naturally available seston present in the lake water. We acid-washed all containers and glassware.

Interannual repeatability: K stimulation of population growth in a low-K lake

Previously, we found that K enrichment of water collected from a single low-K lake stimulated the growth and reproduction of *Daphnia* [in 2010 (Civitello et al. 2013)]. We

performed an additional life table experiment using the same low-K lake (University Lake, Monroe County, IN) in 2011 to assess the interannual consistency of K stimulation of *Daphnia* reproduction. We collected water daily from 21 July to 9 August 2011 and added K (as KCl; treatment levels, 0, 2, or 4 mg K^+/L). We then placed individual neonates (<24 h old) in 50-mL centrifuge tubes containing the experimental water ($n = 15$ replicates per treatment). Each day, we transferred the *Daphnia* to freshly collected water and recorded survival and reproduction. We terminated this experiment after 20 days and omitted two males from the analysis. We used the daily survival and reproduction data to calculate the population growth rate (r) for each treatment following the Euler-Lotka equation (McCallum 2000). Next, we estimated a constant background death rate (d) using maximum likelihood techniques (McCallum 2000; see Civitello et al. 2012, 2013 for details). Using these estimates of r and d, we calculated the instantaneous birth rate (b) for *Daphnia* in each treatment by assuming $b = r + d$ (McCallum 2000; Civitello et al. 2012, 2013). We bootstrapped SEs for r and b for each treatment (Dixon 1993). We calculated SEs for d using maximum likelihood (Civitello et al. 2012). We tested the hypothesis that K enrichment altered r, b, and d using linear regression and randomization tests with 10,000 iterations (Gotelli and Ellison 2004).

Spatial robustness: nutrient stimulation of *Daphnia* growth across 12 lakes

From 11 to 24 July 2010, we performed juvenile growth rate experiments in 12 lakes to assess spatial variation in K stimulation of *Daphnia* growth. These hard-water lakes, located in southwestern Indiana [Monroe, Greene, and Sullivan counties; see Civitello et al. (2013) for geographic coordinates], contained ~2–8 mg K^+/L in the epilimnion, well within the range seen in hard-water lakes worldwide [0.4–15 mg dissolved K^+/L (Talling 2010)]. Background concentrations of K of these lakes are very stable seasonally and among years, as shown previously (Civitello et al. 2013). We also determined C:P ratios for edible (≤80 μm) seston from nine of the 12 lakes from early August 2010 (roughly 3 weeks after these experiments) from a larger field survey of fungal epidemics in populations of *D. dentifera* (Duffy et al. 2012; Civitello et al. 2013). We measured seston C content using a 2400 series CHN analyzer (Perkin Elmer, Waltham, MA) on pre-combusted GF/F filters (0.7-μm pore size; Whatman, Piscataway, NJ). We measured seston P content using the ascorbic acid method following persulfate digestion (Prepas and Rigler 1982) on acid-washed GF/F filters. The mean molar C:P ratio among these lakes was 442:1 (range 298–834:1), suggesting the potential for P limitation of *Daphnia* (Sterner and Elser 2002). For each lake, we collected integrated epilimnetic water for 5 consecutive days and sieved it (80 μm) to remove zooplankton but retain edible algae. We then enriched water from each lake with either K (+4 mg K^+/L, as KCl), P (+40 μg P/L, as K_2HPO_4), or did not enrich it. P additions of this magnitude significantly decrease C:P of natural seston within hours (Elser et al. 2001; DeMott and Tessier 2002). If all P was incorporated into seston, all C:P ratios would decrease below 60:1. These P additions did contribute 0.1 mg K^+/L. These levels ranged between 0.75 and 5 % of the background K concentration, which are tiny compared to that of the K-addition treatment which added 50–200 % of background K levels. Such small K additions likely did not stimulate algae or *Daphnia* (Talling 2010; Civitello et al. 2013), and if they did, they only upwardly biased estimates of P limitation. We then placed individual neonates, 15 per treatment (<24 h old, same genotype as above), in 50-mL centrifuge tubes. We weighed 15 neonates to estimate initial mass (M_0). After four daily transfers to freshly collected and enriched water, we dried and weighed each individual to obtain mass at day 5 (M_5). We then calculated daily mass-specific growth rate (g), for each replicate: $g = \ln(M_5/M_0)/5$ (Lampert and Trubetskova 1996).

We assessed the effects of nutrient enrichment for each lake separately using planned non-orthogonal comparisons of each nutrient enrichment treatment (P or K) to the control. We used the Holm-Sidak correction for multiple comparisons. Next, we calculated growth differentials (Δg_i; i = P or K), for each nutrient-enrichment treatment in each lake using treatment means, $\bar{g}_i$, relative to mean growth in the control treatment, $\bar{g}_c$, i.e., $\Delta g_i = \bar{g}_i - \bar{g}_c$(Downing et al. 1999). We then calculated an overall Δg_i value for each nutrient (yielding $\overline{\Delta g_i}$) by averaging Δg_i values across all lakes or only among lakes in which *Daphnia* responded significantly to enrichment ("responsive lakes;" Fig. 3a, b). We tested for significant effects of each nutrient across all lakes with randomization tests of the null hypotheses $\overline{\Delta g_i} = 0$ (10,000 iterations; Gotelli and Ellison 2004). We bootstrapped SEs for all Δg estimates (see Appendix for additional results).

Nutrient stimulation of algal production across 12 lakes

Concurrent with each *Daphnia* growth rate experiment, we enriched lake water with the same nutrient treatments, K (+4 mg K^+/L) or P (+40 μg P/L). We then measured algal production following standard methods for algal bioassays (Elser et al. 2009). Briefly, we collected and sieved lake water as above, then estimated the initial concentration of algae (A_0) of triplicate 60-mL samples by measuring chlorophyll *a* (Webb et al. 1992; Welschmeyer 1994). We filtered each sample through Whatman GF/F glass fiber filters (Whatman), extracted chlorophyll with 4 °C ethanol

for 24 h, and measured fluorescence on a Turner Biosystems Trilogy fluorometer (Turner Biosystems, Sunnyvale, CA). We added K, P, or nothing to triplicate 60-mL samples of lake water in acid-washed 80-mL screw-top vials per treatment. We incubated the samples for 2 days (20 °C, 16-h:8-h light:dark cycle, light intensity ~50 μmol quanta/m^2 per s), gently mixing and randomizing the location of each tube twice daily. We estimated the final concentration of algae (A_2) and calculated the relative algal r during the 2-day assay ($t = 2$) for each replicate: $r = \ln(A_2/A_0)/t$. The subsequent calculations resembled those for *Daphnia* above. We assessed nutrient stimulation of algal production for each lake using planned non-orthogonal contrasts as for *Daphnia* above. Next, we calculated growth differentials for algae from each lake (Δr_i; i = P or K), and averaged them over all lakes or the subset of lakes in which algae responded to enrichment (responsive lakes, yielding a $\overline{\Delta r_i}$ in both cases). We tested the significance of these overall effects using randomization tests (null hypothesis: $\overline{\Delta r_i} = 0$; 10,000 iterations; Gotelli and Ellison 2004). Due to lower sample sizes, we calculated SEs for Δr_i values for each lake–nutrient combination using a normal approximation (Sokal and Rohlf 1995). Since samples from University Lake were accidentally destroyed, we omitted this lake from analyses involving algae.

Explaining variation in nutrient stimulation across lakes

Finally, we sought an explanation for variation in growth differentials among lakes. We regressed growth differentials (Δg_i for *Daphnia* and Δr_i for phytoplankton) with three environmental factors: a proxy for algal biomass (chlorophyll *a*); one measure of food quality (C:P ratio of edible seston; obtained for nine lakes); and background concentration of dissolved K [K]. We estimated chlorophyll *a* and [K] for all lakes during the initiation of the algal production experiments. Chlorophyll *a* and the C:P ratio of seston were positively correlated. Therefore, when we found significant correlations among both factors and a growth response, we determined their partial correlation coefficients [controlling for the other factor (Legendre and Legendre 1998)].

Results

Interannual repeatability: K stimulation of population growth in a low-K lake

K enrichment of water collected from the low-K lake significantly increased the population r of *Daphnia* (Fig. 1a; $r = 0.016 \times$ [added K] $+ 0.22$, $n = 43$, $P = 0.031$). It increased 28 % in the +4 mg K^+/L treatment relative to unmanipulated lake water. K enhanced population growth rate by stimulating b (Fig. 1b; $b = 0.013 \times$ [added K] $+ 0.27$, $n = 43$, $P = 0.002$). The stimulatory effect of K enrichment on b was quantitatively similar to that observed in the previous year (e.g., +0.071 for the +4 mg K^+/L treatment in 2009 vs. +0.052 in 2010). However, K enrichment did not alter d (Fig. 1c; $n = 43$, $P = 0.59$).

Spatial robustness: nutrient stimulation of *Daphnia* growth and algal production in 12 lakes

K enrichment significantly enhanced the juvenile growth rate of *Daphnia* in five of 12 (42 %) lakes—the same number of lakes as did P addition (Fig. 2a). Overall, both P and K enrichment stimulated *Daphnia* by a similar

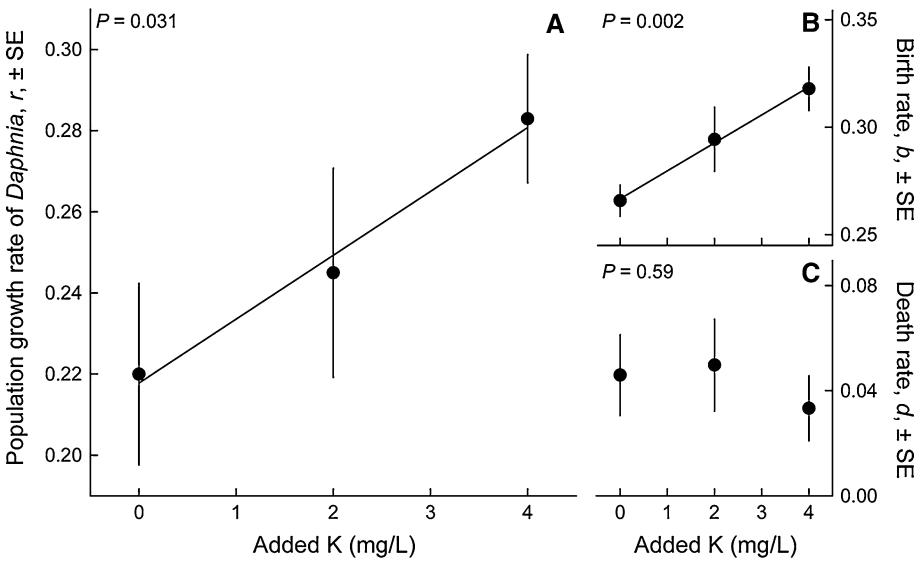

Fig. 1 Interannual repeatability of K limitation: results of the life table experiment with water collected from the low-K University Lake (total $n = 43$). **a** K enrichment stimulated the population growth rate (r) of *Daphnia dentifera*. K stimulated r because it enhanced **b** reproduction by *Daphnia* (b), **c** without altering death rates (d)

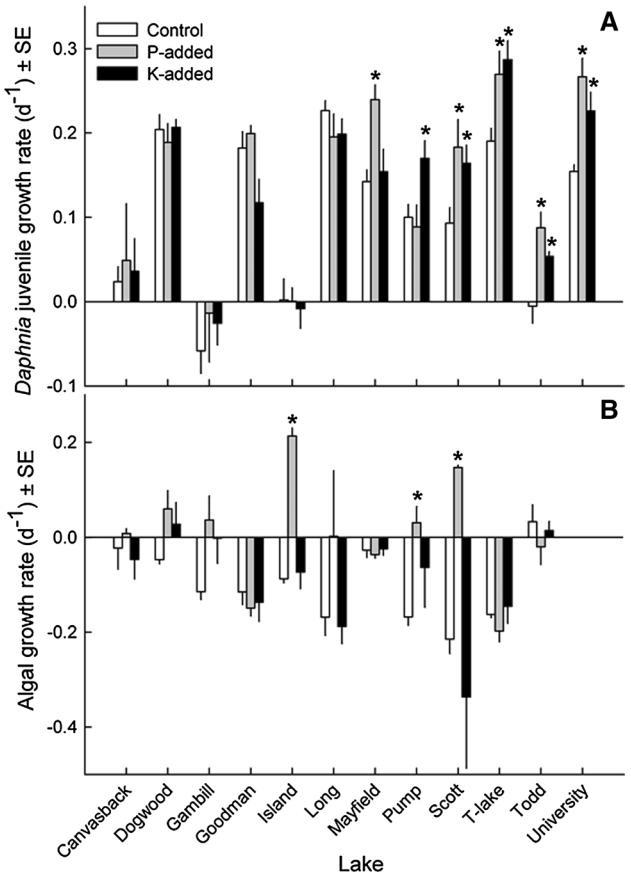

Fig. 2 Spatial robustness: results of limitation assays conducted in 12 Indiana lakes. **a** Separate additions of K (+4 mg/L) and P (+40 µg/L) stimulated the growth of juvenile *Daphnia* in five lakes each. **b** P enrichment significantly enhanced algal production in three lakes. However, K enrichment had no effects on algae. *Asterisks* indicate a significant difference between a nutrient enrichment treatment and the unmanipulated control for that lake

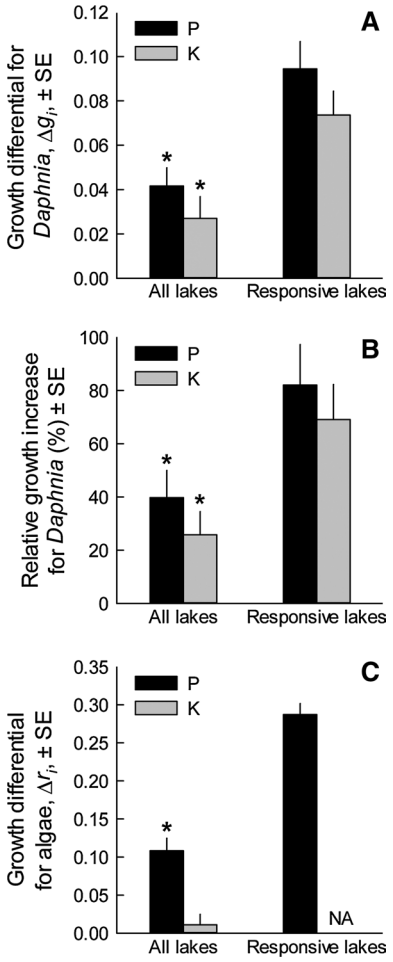

Fig. 3 Spatial robustness, continued: effects of nutrient enrichment on production of *Daphnia* or algae, averaged across all lakes and only in responsive lakes (i.e., those with significant effects in Fig. 2). **a** Across all lakes ($n = 12$), both nutrients significantly increased *Daphnia* growth. In responsive lakes ($n = 5$ each), *Daphnia* growth rates increased by approximately 0.08–0.10/day with enrichment. **b** Results from **a** re-scaled on a percentage basis, relative to controls. **c** Averaged across all lakes, P enrichment substantially increased algal production ($\overline{\Delta r_P} > 0$), while K had no effect. Algae were never K limited. *Asterisks* indicate a significant effect of nutrient enrichment, averaged across all lakes. No further tests were needed for "responsive" lakes (by definition)

magnitude. The growth differentials (Δg) averaged across all lakes were significantly greater than zero for both nutrients (Fig. 3a). Across all lakes, *Daphnia* growth increased by 40 % with P enrichment and 26 % with K enrichment (Fig. 3b). For lakes in which *Daphnia* were significantly stimulated by enrichment, P increased growth by 82 % and K increased growth by 70 % (Fig. 3b). P addition also significantly stimulated algal production in three lakes (Fig. 2b). However, K enrichment did not alter algal production in any of the lakes we examined (see Appendix). Overall, P enrichment significantly enhanced algal production (Fig. 3c). In contrast, K enrichment had a small, non-significant average effect on algal production (Fig. 3c).

Explaining variation in nutrient stimulation across lakes

Across the 12 lakes, P and K tended to stimulate growth of *Daphnia* in similar lakes, i.e., growth differentials (Δg_j) were significantly correlated ($n = 12$, $R = 0.59$, $P = 0.04$; Fig. 4a). Stimulation of *Daphnia* growth by P (Δg_P) was higher in lakes with more chlorophyll *a* ($n = 12$, $R = 0.71$, $P = 0.01$; Fig. 4b) and in lakes with a higher C:P ratio ($n = 9$, $R = 0.77$, $P = 0.01$; Fig. 4c). However, chlorophyll *a* and C:P ratio were positively correlated ($n = 9$, $R = 0.68$, $P = 0.044$). When controlling for chlorophyll *a*, the C:P ratio remained highly correlated with Δg_P (partial correlation, $r = 0.67$, $P = 0.025$). In contrast, after controlling for the C:P ratio, chlorophyll *a* no longer correlated with Δg_P (partial correlation, $r = -0.028$, $P = 0.94$). Further, Δg_P was not correlated with the background concentration

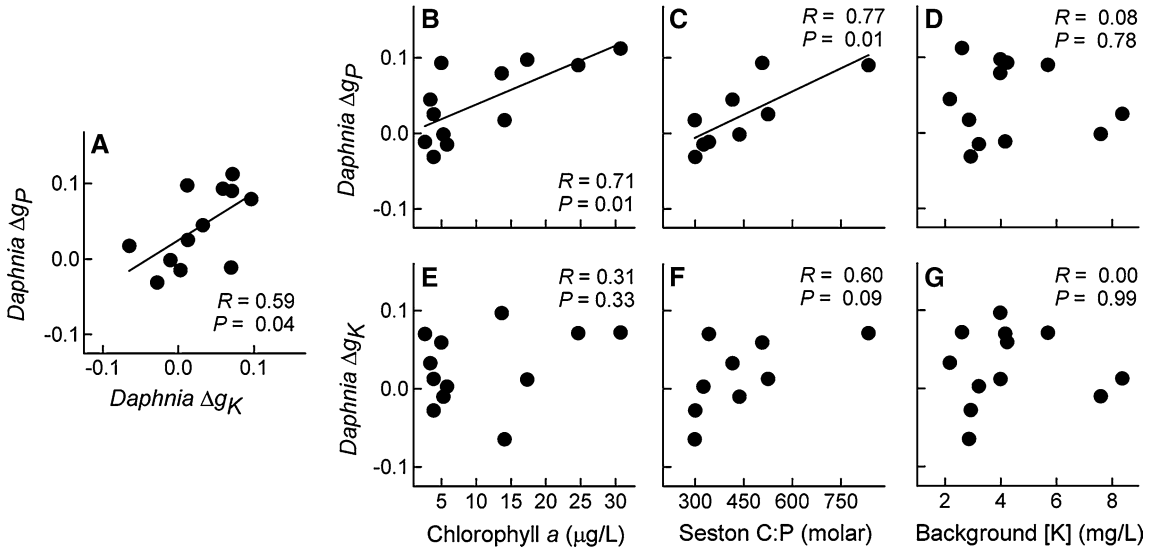

Fig. 4 Exploring variation in nutrient limitation: analysis of nutrient stimulation of *Daphnia* growth. *Each point* represents an estimate for one lake ($n = 12$). **a** Growth differentials for P (Δg_P) and K (Δg_K) were positively correlated across lakes. P stimulation of growth increased with background levels of **b** chlorophyll *a* and **c** C:P of edible seston. However, it was not correlated with **d** background K concentration [*K*]. In contrast, *Daphnia* growth differentials for K (Δg_K) were not correlated with **e** chlorophyll *a*, **f** C:P ratio, or **g** background [K]. *Regression lines* indicate relationships with statistical significance. See Appendix for SEs for Δg_P and Δg_K

of K ($n = 12$, $R = 0.28$, $P = 0.41$; Fig. 4d). Stimulation of *Daphnia* growth by K (Δg_K), on the other hand, showed no relationship with chl *a* ($n = 12$, $R = 0.31$, $P = 0.33$; Fig. 4e) and background concentration of K ($n = 12$, $R < 0.01$, $P = 0.99$; Fig. 4g). Growth stimulation of *Daphnia* by K was weakly correlated with the C:P ratio of seston ($n = 9$, $R = 0.60$, $P = 0.09$; Fig. 4f).

Discussion

Nutrients can limit the growth and reproduction of organisms in natural ecosystems. N and P can often limit growth in terrestrial, freshwater, and marine ecosystems (Downing et al. 1999; Elser et al. 2007). Indeed, P enrichment enhanced algal production and the growth of this genotype of a dominant grazer, *Daphnia dentifera*, in these short-term bioassays using field-collected water. Thus, we recaptured anticipated results for freshwater systems (Sterner and Elser 2002). However, K exerted similar enrichment effects on the growth and reproduction for this *D. dentifera* genotype. Specifically, K enrichment significantly increased the population growth rate of *D. dentifera* for 2 years in a row (this study; Civitello et al. 2013). Thus, K-limited growth of *D. dentifera* is repeatable across years. Then, K enhanced *D. dentifera* growth in five out of 12 lakes (42 %)—the same number of lakes as did P. Furthermore, the magnitude of growth stimulation by K rivaled that of P across all lakes (increases of 26 vs. 40 %) and among responsive lakes (increases of 70 vs. 82 %). Thus, as described in more detail below, K stimulation rivaled P stimulation of *Daphnia* growth in frequency and magnitude in nature.

Even if K and P similarly enhanced *D. dentifera* growth, these nutrients worked through different mechanisms. Typically, P enrichment stimulates growth of aquatic grazers by increasing the growth (quantity) or elemental content (quality) of algal resources (Sterner and Hessen 1994). These signals arose here. *D. dentifera*'s response to P correlated with chlorophyll *a* (a proxy for algal quantity) and the C:P ratio of edible seston (a proxy for quality). In contrast, neither chlorophyll *a,* seston C:P ratio, nor the background concentration of K correlated with *D. dentifera*'s response to K enrichment (Δg_K). An interaction with Na could explain the lack of correlation between the background K concentration and growth stimulation. Exposure to excess Na can reduce internal K concentrations in aquatic animals (Donini et al. 2006). Thus, high Na:K ratios, rather than low K concentrations, might yield K limitation. Unfortunately, we did not quantity Na in these experiments. Further, K never limited phytoplankton. Thus, we can rule out the hypothesis that K stimulates *D. dentifera* growth by increasing algal quantity. Hence, we suggest that P stimulation of *D. dentifera* growth was connected to well-studied mechanisms [i.e., increased quantity and/or quality of algal resources (Sterner and Hessen 1994; DeMott and Van Donk 2013)]. However, K stimulation probably acts through different, potentially direct, mechanisms on *D. dentifera* physiology (Williams 1970).

Stimulation of *D. dentifera* growth and reproduction by understudied nutrients like K matters because it connects

to broader ecological dynamics. For instance, epidemics of the virulent fungus *Metschnikowia* grew larger in lakes with more K. In an experiment, enrichment of water from a low-K lake with K stimulated the reproduction of *Daphnia* hosts and fungal parasites. These changes in K-dependent traits then drove larger experimental disease outbreaks in that same low-K lake (Civitello et al. 2013). The results presented here greatly bolster the generality of K stimulation of *D. dentifera* across space and time. Thus, an enhanced understanding of K physiology could reveal novel insights into the ecology and epidemiology of animals. Other mineral and biochemical nutrients may also influence the performance of invertebrate grazers (Muller-Navarra et al. 2004; Jeziorski et al. 2008; Martin-Creuzburg et al. 2009). These factors may also connect to community structure (Jeziorski et al. 2008) or energy flow through ecosystems (Muller-Navarra et al. 2004). Thus, a broader perspective that incorporates these nutrients could enhance predictive power at a time of unprecedented change in global nutrient cycles (e.g., Canfield et al. 2010).

After establishing its relevance in multiple lakes, future research on K-limited growth of animals could proceed on two central fronts. First, K should be manipulated in nutrient-addition studies in the field. These experiments, coupled with surveys, could reveal the frequency and magnitude of K stimulation for other genotypes, species, locations, and ecosystems. Second, lab-based physiological studies could reveal the mechanisms underlying K utilization for growth and reproduction. Currently, little is known about the mechanisms by which K modulates the physiology of animals under natural conditions. However, we know that K has a critical role in a number of cellular and metabolic processes [e.g., enzyme activity, pH regulation, and energy assimilation (Williams 1970)]. Furthermore, the relative importance of dietary vs. dissolved sources of K for aquatic consumer growth and reproduction is not currently understood. Evidence is scant, but the K quota of phytoplankton is somewhat flexible (Gerloff and Fishbeck 1969). Thus, K enrichment could increase the K content of algae, enhancing dietary assimilation of K by consumers. Alternatively, external (dissolved) K might be most important for consumers like *D. dentifera*. Freshwater organisms can acquire K directly from water. However, constantly pumping dissolved K^+ into the body across a strong concentration gradient is energetically costly, and this cost increases as the external concentration of K^+ declines (Williams 1970). In the future, physiological studies could establish the relative importance of aqueous and diet-based sources of K and uncover which physiological functions drive whole-organism performance. Such a combination of expanded field study and K-dependent animal physiology could powerfully assess the physiological and ecological importance of this greatly understudied macronutrient.

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