

REVIEWS AND
SYNTHESES

Patterns in potassium dynamics in forest ecosystems

Christopher E. Tripler,^{1*}Sujay S. Kaushal,¹†Gene E. Likens¹ and M. Todd Walter²

¹Institute of Ecosystem Studies, Route 44A, Box AB, Millbrook, NY 12545, USA

²Department of Biological and Environmental Engineering, Cornell University, Ithaca, NY 14853-5701, USA

*Correspondence: E-mail: triplerc@ecostudies.org

†Present address: University of Maryland Center for Environmental Science, Appalachian Laboratory, 301 Braddock Road, Frostburg, MD 21532, USA.

Abstract

The biotic cycling of potassium (K) in forest systems has been relatively understudied in comparison with nitrogen (N) and phosphorus (P) despite its critical roles in maintaining the nutrition of primary production in forests. We investigated the ecological significance of K in forests from a literature review and data synthesis. We focused on (1) describing patterns of the effects of K availability on aboveground growth and change in foliar tissue of tree species from a variety of forests; and (2) documenting previously unreported relationships between hydrologic losses of K and N in forested watersheds from the Americas. In a review of studies examining tree growth under K manipulations/fertilizations, a high percentage (69% of studies) showed a positive response to increases in K availability in forest soils. In addition, 76% of the tree studies reviewed showed a positive and significant increase in K concentrations in plant tissue after soil K manipulation/fertilization. A meta-analysis on a subset of the reviewed studies was found to provide further evidence that potassium effects tree growth and increased tissue [K] with an effect size of 0.709 for growth and an overall effect size of 0.56. In our review of watershed studies, we observed that concentrations of K typically decreased during growing seasons in streams draining forested areas in the Temperate Zones and were responsive to vegetation disturbance in both temperate and tropical regions. We found a strong relationship ($r^2 = 0.42\text{--}0.99$) between concentrations of K and N (another critical plant nutrient) in stream water, suggesting that similar mechanisms of biotic retention may control the flow of these nutrients. Furthermore, K dynamics appear to be unique among the base cations, e.g. calcium, magnesium, and sodium, because the others do not show similar seasonal patterns to K. We suggest that K may be important to the productivity and sustenance of many forests, and its dynamics and ecological significance warrant further study. We suggest that knowledge about the dynamics of this understudied element is imperative for our understanding patterns and processes in forest ecosystems.

Keywords

Biogeochemistry, forest ecology, forest ecosystems, nutrient cycling, nutrient limitation, potassium.

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INTRODUCTION

The biotic cycling of potassium (K) has been less studied in ecosystem ecology compared with other nutrients such as nitrogen (N) and phosphorus (P). The importance of K as a limiting nutrient to plant growth, however, has been widely demonstrated in agricultural systems (e.g. Evans & Sorger 1966; Kilmer *et al.* 1968; Oosterhuis & Berkowitz 1996). Previous work in forests has suggested that the distribution

and seasonal dynamics of K in plant tissues, soils, soil organic matter, soil water, and surface waters, unlike other base cations, can be strongly influenced by biotic processes (e.g. Alban 1982; Hamilton & Lewis 1987; Likens *et al.* 1994; Jobbágy & Jackson 2001; Salmon *et al.* 2001; Vitousek 2004). The biotic availability for K may be influenced further by disturbances such as timber harvest, fire, N deposition, and contemporary and historical changes in land use (Johnson *et al.* 1985; Britton 1991; Bock & Van Rees

2002). Given the breadth of work that has examined the role of K in individual tree species and the biogeochemical nature of K in forests, there still remains a theoretical gap in our knowledge about the connection between biotic demand and ecosystem processing of K. In addition, the significance of K in natural environments and how its role may change in response to various anthropogenic disturbances remains to be clarified by ecological research.

Historically, large-scale removal of forests for fuel, agriculture and production of potash (a form of potassium carbonate and potassium salts) for fertilizer and glass-making was vital to the economies of Europe and North America (Hall 1948; Barker *et al.* 1956; Pisani 1985; Cummings 2002). Lucanus (1865) was the first to recognize the important role of K in the physiology and growth of plants. Since that time, farmers and silvicultural managers have applied nitrogen, phosphorus and potassium (NPK) on their fields and soils to ensure high crop yield.

Plants, especially terrestrial, utilize K in a number of physiological activities (e.g. phloem transport, osmotic balance and photosynthesis) leading to high demand and elevated concentrations of K in various tissues (Evans & Sorger 1966). For example, K content in leaf material ranges from 0.8% to 10% of dry weight in herbaceous and crop plants (Evans & Sorger 1966; Leigh & Wyn Jones 1984; Epstein 1994), and 0.3–2.3% of dry weight in various trees species (Koo 1968). Potassium availability to plants has been shown to be critical in the outcome of competition between grass and dandelions in lawn experiments (Tilman *et al.* 1999), reduction of herbivory (Warren *et al.* 1999), and mitigation of the rate of infection and severity of tree disease (Ylimartimo 1990/91; van den Driessche & Ponsford 1995; Shaw *et al.* 1998). Potassium has also been shown to play a role in the transfer of carbon-based exudates in tree roots to ectomycorrhizal fungi (Wallander & Wickman 1999). Despite a general concordance among studies that K plays a critical role in the physiological balance and overall health of trees, there is relatively incomplete knowledge of how prevalent or important this nutrient is for tree growth and for affecting forest community dynamics. In this paper, we collected information from a variety of studies of K fertilization and soil manipulation to examine its importance in forests from different regions around the world. We also examined patterns of K in streamwater outputs, which can be used as an indicator of biotic demand in terrestrial ecosystems.

Review and meta-analysis of potassium effects on tree growth in forests

We searched for journal articles related to K, forests, and streams using Thompson ISI's Web of Science, J-STOR and EBSCO search engines. We intended to collect a fairly

broad and representative body of literature to evaluate the role of K in forest systems. Like many reviews, we recognize that there may be studies that are not included, but we attempted to cover the majority of the primary ecological literature and be representative of studies investigating the general patterns of K dynamics likely to be observed in nature. Agriculture or horticultural studies were not included in the review database, but it should be noted that studies within these fields constituted most of the research on the effects of K on plant growth and metabolism. The majority of the papers we used in this review were from the last 30 years (Table 1). We included studies that reported changes in biomass (e.g. root, shoot, leaf and whole plant) in response to increases in K availability or a combination of K and other limiting nutrients. We also included a small number of studies that reported changes in K concentration in various plant tissues when N was amended to the system, or when other soil manipulations were done that did not include manipulating available K but reported effects on its dynamics. When a paper reported results for more than one tree species, we counted each tree species as a unique observation. We found 38 articles that evaluated 50 individual tree studies of which there were 26 species (see Table 1). Of the 26 evaluated species, 16 were coniferous and 10 were deciduous. Studies spanned 13 countries with 26 studies from North America, 10 from mainland Europe, eight from Scandinavia, three from Australia, one from New Zealand, one from Scotland, and one from Wales. There were 33 field studies and 17 greenhouse/nursery (pot) studies with 29 of those studies looking at responses in adult trees, four in saplings, and 17 in seedlings. All studies examining adult or sapling tree response were done in the field, and all seedling studies were done in greenhouses or nurseries.

We examined the effects of K on tree growth and physiology using three criteria: (1) growth response; (2) changes in K concentration in plant tissue (e.g. root, stem and foliage); and (3) any other physiological changes in trees. We classified growth as an increase in biomass, extension or radial growth, total tree volume, leaf expansion or number, or root number or volume over some observation period. Experiments or observations from within any given study lasted from 4 h to over 60 years. We scored growth response as a positive (+), when any measure of growth was measured as significantly different than a control (Table 1). We scored studies in which growth was not significantly different than controls as '0'. In certain studies (Voight *et al.* 1964, Kawana *et al.* 1969, Lea *et al.* 1980, Erdmann *et al.* 1988, Mika & Moore 1990/91, Ylimartimo 1990/91, Vroblecky *et al.* 1992, Hanley & Fenner 1997, Triboulot *et al.* 1997, Flückiger & Braun 1998, Hodson & Sangster 1998, Shaw *et al.* 1998, Zhang & Allen 1996, Garrison *et al.* 2000, Covelo & Gallardo 2002,

Table 1 Review of K limitation literature within forest systems

Species	Life stage	Growth response	Foliar, stem, root [K]	Other physiological responses	Treatment	Study location/length of study	Reference
Conifers							
<i>Abies grandis</i>	Adult	0	0		Control, N, N + K	USA/3 years	Garrison <i>et al.</i> (2000)
<i>Picea abies</i>	Adult	0	+		K, K + dolomite	Sweden/2–6 years	Salih & Andersson 1999
<i>Picea abies</i>	Adult	0	0		N + P + Mg + K	Sweden/3 years	Jacobson & Pettersson 2001
<i>Picea abies</i>	Adult	0	0		N deposition gradient	Switzerland/4–11 years	Flückiger & Braun 1998
<i>Picea abies</i>	Seedling	+	+		N deposition gradient	Switzerland/4–11 years	Flückiger & Braun 1998
<i>Picea abies</i>	Seedling	+	+		K, K + CO ₂ + O ₂	Germany/7 months	Pfirrmann <i>et al.</i> 1996
<i>Picea contorta</i>	Adult	0	+		control, N, N + K	USA/3 years	Garrison <i>et al.</i> 2000
<i>Picea engelmannii</i>	Seedling	0	+	↓ leaf yellowing	Factorial K, N, & K + N	Canada/3 years	van den Driessche & Ponsford 1995
<i>Picea glauca</i>	Adult	+	+	↓ [K] w/leaf age	Variied soil pH & K	Canada/N/A	Hodson & Sangster 1998
<i>Picea sitchensis</i>	Seedling	+	+	↑Water use efficiency	Control, K, K + P	Scotland/15 and 48 days	Bradbury & Malcolm 1977
<i>Picea sitchensis</i>	Adult	0	0	↑[N–P–Ca–Mg] uptake in needles	Control, low P + high K	Wales/12–42 months	Stevens <i>et al.</i> 1993
<i>Pinus brutia</i>	Seedling	0	0		Simulated. K deficiency	Greece/12 weeks	Hanley & Fenner 1997
<i>Pinus echinata</i>	Sapling	+	+		K, N + P + K	USA/1–16 months	Gleeson & Good 2003
<i>Pinus pinaster</i>	Seedling	+	0	↓lateral root biomass	Simulated. K deficiency	France/30 days	Triboulot <i>et al.</i> 1997
<i>Pinus ponderosa</i>	Adult	+	0		Control, N, N + K	USA 3 years	Garrison <i>et al.</i> 2000
<i>Pinus radiata</i>	Seedling	+	0	↓Mobilization of Mg from roots to shoots	Factorial K, Mg and K + Mg	New Zealand/21 weeks	Sun & Payn (1999)
<i>Pinus resinosa</i>	Adult	+	+	↑Needle retention	K	USA/12–17 years	Heiberg <i>et al.</i> (1964)
<i>Pinus resinosa</i>	Adult	+	+		K	USA/25 years	Kawana <i>et al.</i> (1969)
<i>Pinus resinosa</i>	Adult	+	+		K	USA/21 years	Comerford <i>et al.</i> (1980)
<i>Pinus resinosa</i>	Adult	+	+		K (39 years previously)	USA/39 years	Shepard & Mitchell 1990
<i>Pinus resinosa</i>	Adult	+	+		K (2–39 years previously – different sampling yrs)	USA/2–39 years	Nowak <i>et al.</i> (1991)
<i>Pinus rigida</i>	Seedling	+	+	↑Loss of K w/burning	3-Litter types × 2-burn × 2-watering	USA/4 months	Tuininga <i>et al.</i> (2002)
<i>Pinus rigida</i>	Sapling	+	+		Soil K variation	USA/N/A	Voigt <i>et al.</i> (1964)
<i>Pinus sylvestris</i>	Adult	0	+	↓Putrescine production	K	Finland/2 years	Sarjala & Kaunisto (1993)
<i>Pinus sylvestris</i>	Adult	+	+		N + P + K	Sweden/3 years	Jacobson & Pettersson (2001)
<i>Pinus sylvestris</i>	Adult	+	+		K + Mg	Germany/60 + years	Uebel & Heinsdorf (1997)
<i>Pinus sylvestris</i>	Seedling	+	+	↑Infestation. w/↑ needle N : K	K	Finland/3.5 months	Holopainen & Nygren (1989)
<i>Pinus sylvestris</i>	Seedling	+	+		N + K (various molar ratios)	Finland/1 year	Ylimartimo 1990/91
<i>Pinus sylvestris</i>	Seedling	+	+		K	Sweden/1 year	Wallander & Wickman 1999
<i>Pinus taeda</i>	Adult	+	+		N + P + K + Ca + Mg + B	USA/7 months	Warren <i>et al.</i> (1999)
<i>Pinus taeda</i>	Adult	0	0	83% K retrans-located prior to senescence	N	USA/10 months	Zhang & Allen (1996)

Table 1 Continued

Species	Life stage	Growth response	Foliar, stem, root [K]	Other physiological responses	Treatment	Study location/length of study	Reference
<i>Pseudotsuga menziesii</i>	Seedling	0	+	↑Phenolic production in roots	Factorial N + K (low/high)	USA/3 years	Shaw <i>et al.</i> (1998)
<i>Pseudotsuga menziesii</i>	Adult	+	+	↑Potential in mortality w/low soil [K]	N	USA/6 years	Mika & Moore (1990/91)
<i>Pseudotsuga menziesii</i>	Adult	0	0		Control, N, K + N	USA 3 years	Garrison <i>et al.</i> (2000)
Deciduous							
<i>Acer rubrum</i>	Adult	0	0		Site comparisons	USA/N/A	Erdmann <i>et al.</i> (1988)
<i>Acer rubrum</i>	Adult	0	+		Factorial N, N + P; N + P + K	USA/2 years	Lea <i>et al.</i> (1980)
<i>Acer saccharum</i>	Adult	+	+	↓Leaf [K] w/liming	K fertilization after dolomitic lime	Canada/4 years	Moore <i>et al.</i> (2000)
<i>Acer saccharum</i>	Adult	+	+		K (fertilizer balanced with some P + Mg)	Canada/2 years	Ouimet & Fortin (1992)
<i>Acer saccharum</i>	Adult	+	+	↓Crown dieback w/liming	K (smaller amounts of Ca + Mg to balance treatment)	USA/3 years	Wilmot <i>et al.</i> (1996)
<i>Acer saccharum</i>	Adult	0	+		Factorial N, N + P; N + P + K	USA/2 years	Lea <i>et al.</i> (1980)
<i>Alnus marina</i>	Seedling	+			Factorial K + N + P (+ NaCl)	Australia/7 months	Yates <i>et al.</i> (2002)
<i>Betula alleghaniensis</i>	Adult	+	0	↓Foliar [Mg] ↑ foliar ash%	Factorial N, N + P, N + P + K	USA/2 years	Lea <i>et al.</i> 1980
<i>Betula pendula</i>	Seedling	+		↑Leaf necrosis with low soil [K]	K	Sweden/N/A	Ericsson & Kähr (1993)
<i>Corylopsis tagal</i>	Seedling	+			Factorial K + N + P (+ NaCl)	Australia/7 months	Yates <i>et al.</i> 2002
<i>Fagus sylvatica</i>	Sapling	+	+		K + Mg	Germany/60 + years	Uebel & Heinsdorf (1997)
<i>Fagus sylvatica</i>	Adult		0	↑Bark necrosis w/↑ Leaf N/K ratios	N deposition gradient	Switzerland/4–11 years	Flückiger & Braun (1998)
<i>Fagus sylvatica</i>	Seedling		+		N deposition gradient	Switzerland/4–11 years	Flückiger & Braun (1998)
<i>Liriodendron tulipifera</i>	Adult		+		K gradient in soil	USA/N/A	Vroblecky <i>et al.</i> (1992)
<i>Quercus robur</i>	Sapling		+	↑Leaf N : K during senescence	↓Local plant competition for resources	Spain/2 years	Covelo & Gallardo (2002)
<i>Rhizophora stylosa</i>	Seedling	+			Factorial K + N + P (+ NaCl)	Australia/7 months	Yates <i>et al.</i> (2002)
Study totals	17 Seedling, 4 sapling, 29 adult	10: '0', 22: '+', 18: not measured	9: '0', 29: '+', 12: not measured				

Under 'growth response', 'foliar, stem, root[K]', and 'other physiological responses' a '+' indicates a positive or increase response, a '0' indicates that no response was measured, and a blank cell indicates that this response was not measured or the response could not be attributed to a K effect. Negative plant responses to K were not observed in any of these studies.

Yates *et al.* 2002; Table 1), K availability was altered either through nutrient deprivation, soil acidification, removal of competitors, N deposition/fertilization, or compared plants across soil K gradients. In these cases, a study that measured a decrease in growth under treatment conditions that depleted K when compared with a control was also counted as a '+'. In a number of these studies, the factorial design of the study allowed for the assessment of the impact of K on the growth or tissue concentration as a consequence of the measured response in the higher order treatment but less so in the main treatment. For example, Garrison *et al.* (2000) designed a study with a control, N fertilization, and a N plus K fertilization, in which some N treatments were not significantly different from controls, but the N + K treatment was, suggesting a K effect.

We also examined papers that reported changes in leaf, stem, phloem, or root concentration of K ([K]), in which increased [K] was considered a positive response, '+', to fertilization or treatment conditions. Similar to growth, any study that did not show a change in [K] in any measured biomass component was scored as '0'. We included in this review four studies in which K fertilizer was applied in conjunction with other cations or nutrients but did not have an adequate factorial design to evaluate the impact of K directly. However, in these studies K comprised the greater proportion of the fertilization and the authors had strongly suggested that the measured response was attributable to K (Uebel & Heinsdorf 1997, Warren *et al.* 1999, Jacobson & Pettersson 2001, Tuininga *et al.* 2002). We also list other reported physiological responses beyond measures of growth or tissue [K] as illustrative examples of alternate plant dynamics involving K (Table 1).

Of the 50 tree studies, 22 of 32 studies (69%) that examined growth showed positive responses induced by the availability of K. Of these growth studies, 18 were fertilized exclusively with K or contained a separate K manipulation component, and of these studies, 14 of the 18 (78%) measured positive growth responses (Table 1). The remaining studies were fertilized with K and other limiting nutrients, such as nitrogen and phosphorus, in factorial experiments. In these studies, a significant effect of the combined fertilization with an impact greater than the treatment minus K was treated as a significant K effect. Twenty-nine of the 38 studies (76%) that measured changes in plant tissue [K] showed a positive increase in K (Table 1). Of the 20 studies that simultaneously examined changes in both growth and tissue [K], 18 studies (90%) showed some response in one of the two categories, and 11 of the 20 studies (55%) showed a positive response in both categories (Table 1). Twenty-six of the 32 conifer studies (81%) and 14 of the 16 broad-leaved studies (88%) showed a positive growth or increase in tissue [K] response to K manipulations (Table 1). Twenty-nine of the 50 studies were done on adult trees in the field, of which

17 focused on tree growth and 24 examined [K] in plant tissues. Ten of the 17 adult tree growth studies (59%) and 15 of the 24 tissue studies (63%) showed effects of K. Among the adult and sapling tree studies, eight were exclusively fertilized with K or heavily fertilized with K in addition to other nutrients, all eight studies showed positive growth (Heiberg *et al.* 1964 Kawana *et al.* 1969, Comerford *et al.* 1980, Shepard & Mitchell 1990, Ouimet & Fortin 1992, Wallander & Wickman 1999, Moore *et al.* 2000, Gleeson & Good 2003). None of the 50 studies reviewed indicated a negative effect of K on growth or tissue concentration when compared with a control, although there were some effects of K on other nutrient dynamics (e.g. inhibition of magnesium uptake – Lea *et al.* 1980; Table 1). Nineteen studies measured or noted other physiological responses related to K. For example, various fertilizations caused a decrease in chlorosis (van den Driessche & Ponsford 1995), a decrease in putrescine production (Sarjala & Kaunisto 1993), and an increase in root phenolic concentration (Shaw *et al.* 1998). We found that the measured secondary effects of K nutrition were positive in most studies with the exception of two studies, which found that K availability interfered with root uptake of magnesium (Lea *et al.* 1980; Sun & Payn 1999).

The increase in tissue concentrations of K could also be a reflection of plant 'luxury' consumption of these nutrients (van den Driessche 1974; Sterner & Elser 2002). However, Leigh & Wyn Jones (1984) have shown that plants typically maintain high concentrations of K in their vacuoles to supply K to the cytoplasm. Depletion of K within the vacuole leads to reductions in relative growth rate as a function of decreased cytoplasmic K concentrations. This phenomenon has been shown in agricultural studies and provides an hypothesis to be tested in tree species. Given a plant's need to maintain such high concentrations of K in the vacuole without concomitant increases in growth, suggests to us that the increased uptake and storage of K when available, indicates a form of limitation. These K manipulation studies reviewed here suggest that tree nutrition and growth have a strong likelihood of being enhanced by K if it were supplied at higher rates than currently occurs in forests.

We also conducted a meta-analysis using studies of K fertilization on tree species to obtain a quantitative measure of the effect size of the phenomenon across these studies. Meta-analysis synthesizes these results from multiple studies indexed by a measure of the magnitude of the effect in that experiment through a standardized difference in the means, or the 'effect size', expressed on a common scale across studies (Hedges & Olkin 1985). Effect size is calculated using the means, sample sizes, standard deviations of the control and treatment groups, which are combined to calculate an effect size index for each study and a grand effect size index for all studies in the meta-analysis (Hedges

& Olkin 1985). The use of meta-analysis has been applied in ecology to various topics, from plant competition studies (Gurevitch *et al.* 1992) to evaluating experimental soil warming on soil respiration and net nitrogen mineralization (Rustad *et al.* 2001). We found 11 of the 38 papers reviewed in Table 1 were strictly limited to K fertilization treatments and provided sufficient statistical information for the meta-analysis. We identified 16 separate, comparative treatment studies in which there were six measured differences in growth and 11 measured differences in tissue concentration (see Appendix). The differences in the magnitude among studies in the measured effect of K on growth and increases in tissue concentration can be seen in the Forrest plot (Fig. 1). Effect sizes greater than zero indicate a significant effect of the measured phenomenon, in our case whether there was significant impact on growth or tissue concentrations. The meta-analysis yielded a significant overall effect size of K treatments on growth (0.71, $P < 0.005$), tissue concentration (0.50, $P < 0.005$), and overall studies (0.56, $P < 0.001$, see Appendix). The results of the meta-analysis were consistent with the majority of observations of the effects of K on plant growth and physiology from the full list of studies provided in Table 1, and lends further

support that K plays an important role in forest primary productivity.

Potassium output at the Watershed Scale

The biotic control over hydrologic loss of a nutrient in stream water from watersheds has served as a basis for understanding factors influencing nutrient limitation and dynamics in terrestrial ecosystems (Vitousek 1977; Likens & Bormann 1995). Seasonal patterns have been well-documented for nitrate-N, usually the dominant form of N in stream water and a critical limiting nutrient in terrestrial systems (Fenn *et al.* 1998). Some Temperate Zone watersheds of North America and Europe have shown that the amount of nitrate (NO_3^-) leaving watersheds in streams diminishes during growing seasons and becomes elevated during non-growing seasons (e.g. Vitousek 1977; Likens & Bormann 1995; Williams *et al.* 1996; Chapman *et al.* 2001; Kaushal & Lewis 2003). This finding suggests that vegetation and soils are responsible for biotic retention or possibly release of NO_3^- within the watershed during the growing season (Aber *et al.* 1989, 1998; Hedin *et al.* 1995), and the subsequent senescence of leaves from deciduous

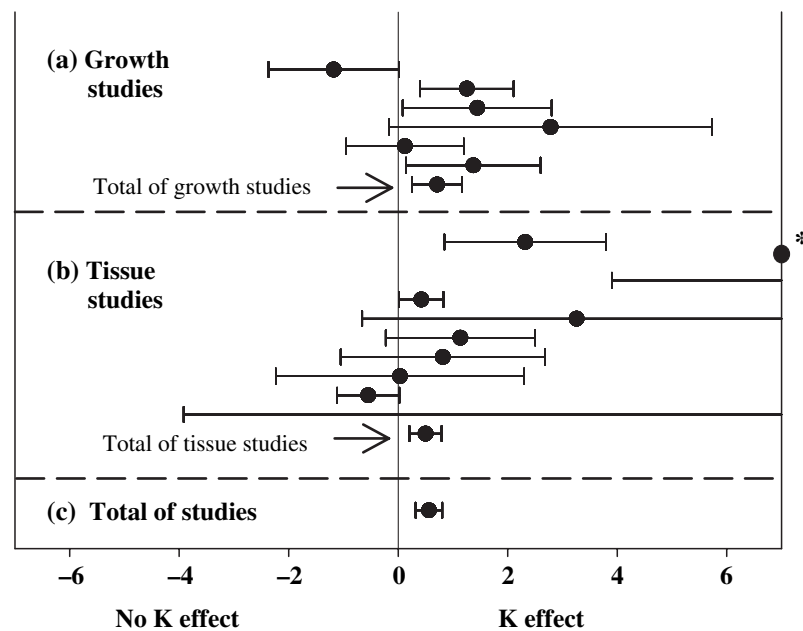


Figure 1 Forrest plot of the meta-analysis of plant growth and tissue concentration response to K fertilization studies. The meta-analysis covered 11 papers across 16 individually measured studies. Studies repeated in a response category measured two distinct response traits (e.g. stem diameter *and* plant height) and were subsequently classified as separate studies. Details of the individual study's statistics, in order from top to bottom of figure, can be found in the Appendix. Each data point corresponds to the reported effect size of each study with 95% confidence intervals. The effect size index in this review was the standardized difference, [(the mean of the treatment – mean of control)/standard deviation]. A point estimate of zero or less indicates a lack of a significant effect, values greater than zero indicates a significant positive effect (i.e. increased growth) of K on the given response variable. Two studies are marked with an asterisk (*) on the right-hand side of the graph indicating a very large effect size.

trees leads to the release of NO_3^- during other portions of the year (Likens & Bormann 1995).

We tested the biotic-watershed nutrient-control hypothesis for K in two ways. Specifically, we considered patterns of K in hydrologic discharge from a representative cross-section of the literature and from several long-term data sets. Since NO_3^- concentrations in stream water are largely controlled by the biota, i.e. rather than by abiotic processes such as weathering or hydrological flows, we assumed that a positive correlation between NO_3^- and K in stream water would support our hypothesis. We restricted our review of watershed monitoring studies to those that reported NO_3^- and K concentrations in streamwater on a month-by-month basis over the course of at least 1 year in minimally disturbed watersheds only, even if other watershed data were available from disturbed watersheds (Uhl & Jordan 1984; Schaefer *et al.* 2000; Kunimatsu *et al.* 2001). We acknowledge that these criteria limited the number of studies that we could include for this review, but it provided examples from some well-studied ecosystems located around the world. We report data from 10 watersheds at six different sites, one watershed in Japan, one in Brazil, two in Venezuela, three in Puerto Rico, and three in New Hampshire USA (Fig. 2). Of the 10 watersheds in this study, we found that six showed significant correlations ($P < 0.05$) between $\log[\text{NO}_3\text{-N}]$ and $\log[\text{K}]$ (Fig. 2). Data from one study, Forti *et al.* (2000), showed a significant negative correlation between NO_3^- and K, and the large range of

concentrations reported for these nutrients in stream water from this watershed suggests that this system is unlikely to be limited by either nutrient (Fig. 2).

We also report similar K and $\text{NO}_3\text{-N}$ relationships for five watersheds that were monitored for several consecutive years (Fig. 3a). These watersheds represent a wide range of forest types in the Americas; see Table 2 for descriptions of the watersheds. As expected, these longer data sets exhibit substantially more scatter than shown in Fig. 2, but all correlations were positive and all the North American sites had significant regression slopes ($P < 0.05$, Fig. 3). Interestingly, these data show a general increase in the slope of the $\log[\text{NO}_3\text{-N}]\text{-}\log[\text{K}]$ relationship. In contrast, the other base cations, sodium (Fig. 3b), magnesium (Fig. 3c), and calcium (Fig. 3d), do not exhibit ubiquitous positive (or negative) correlations with NO_3^- concentrations (Fig. 3, Table 3). We interpret these relationships to indicate that K is uniquely controlled in forest ecosystems relative to the other cations in watershed discharge, and that K and NO_3^- likely have similar mechanisms controlling their concentrations in stream water.

We also looked at annual patterns of K in stream water for the four, long-term data sets with at least 5 years of data (Fig. 4) and found marked intra-annual trends in three. Explanations for some seasonal patterns are logical, e.g. leaf fall at Hubbard Brook constitutes a major flux of K to the forest soils and streams (Fig. 4a), and others are not obvious, e.g. H.J. Andrews (Fig. 4c). We speculate that the

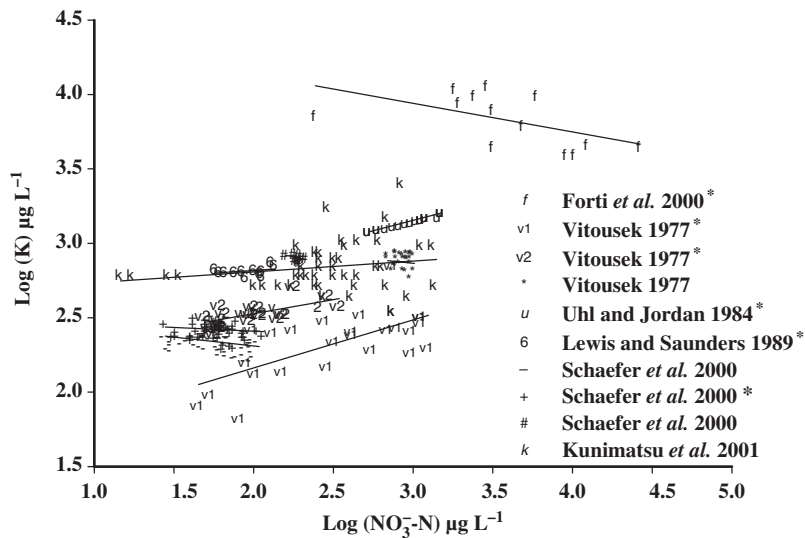


Figure 2 Summary of literature review for nitrogen and potassium forested watershed/streamwater output. The review consisted of 10 individual watersheds within five published papers. Since the concentration values typically ranged from 25 to 27 000 $\mu\text{g N}$ or K L^{-1} , data were log-transformed for this figure. Individual studies are denoted on the right-hand side of the graph and are designated as having a significant N–K discharge relationship by an asterisk following the reference (* a significant correlation at $P < 0.05$). Of these 10 studies, six were found to have significant discharge relationships between N and K. In one case (Forti *et al.* 2000), large amounts of discharge for both K and N showed a strong negative relationship.

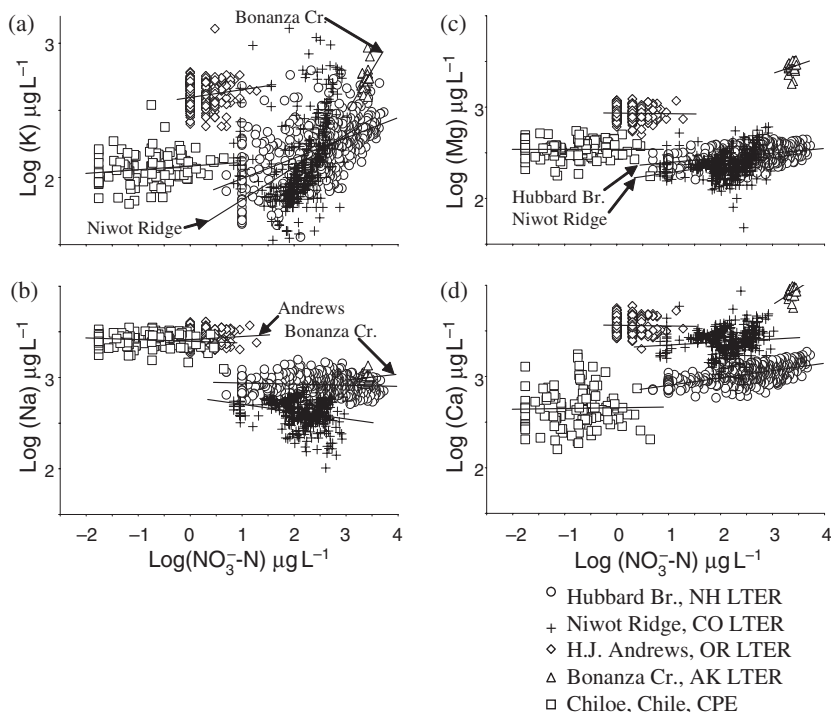


Figure 3 Summary of multi-year N and cation concentrations in stream water from ‘undisturbed’ watersheds representing a wide range of conditions in the Americas; four LTER sites representing the Northeastern USA (Hubbard Brook, circles), the Western-Alpine USA (Niwot Ridge, crosses), the Pacific North-western USA (H.J. Andrews, diamonds), and Alaska (Bonanza Creek, triangles), and a site in Southern Chile (squares) that receives very little atmospheric pollution. The slopes of the linear regressions (lines) and the associated *P*-values are in Table 3. The LTER data were acquired from the LTER Internet sites (similar data were unavailable for other LTERs) and the Chiloe data were from the Cordillera de Piuchué Ecosystem Study (CPES) via Lars Hedin. Some regression lines are labelled to help distinguish among specific sites with overlapping data points.

decrease in streamwater concentrations of K at Hubbard Brook and Niwot Ridge (Figs 4a,b, respectively) are due to biological uptake, resulting in patterns similar to NO_3^- (e.g. Likens *et al.* 1994; Castro & Morgan 2000; Schaefer *et al.* 2000). The Chile site, one of the least disturbed in the Americas, showed weaker seasonal patterns although the concentration spike in 1997 (Fig. 4d) coincided with the longest drought during the study, which may have constituted a substantial disturbance to the system. The patterns at H.J. Andrews (Fig. 4c) are pronounced although difficult to interpret, in part, because this site has distinct wet and dry seasons, which correspond in phase with growth/senescence patterns during which K uptake and release would be anticipated. Regardless of explanations, the patterns in Fig. 4 are intriguing both within watersheds and in comparisons between systems.

We tested whether the K patterns could be explained by hydrology alone by correlating stream cation concentrations with stream discharge, Q , for all five long-term sites. Using a hyperbolic regression (Fig. 5), we found that K generally correlated the weakest of the cations at any single site (Table 4). The one exception was sodium at Bonanza Cr., which had a slightly lower correlation than K with Q . Interestingly, all cations, including K, correlated strongly with Q at H.J. Andrews relative to the other sites (Table 4). Chemicals that are largely generated within a watershed, e.g. via weathering, will often exhibit a ‘dilution response’ (e.g. Fig. 5a) to increased stream discharge (Salmon *et al.* 2001).

We expect to observe this dilution behaviour mitigation of nutrients for which a relatively substantial fraction is biotically cycled. Indeed, K often shows no response to stream discharge (e.g. Fig. 5b) even though its intra-watershed distribution is commonly similar to the other cations (e.g. Salmon *et al.* 2001). It should be noted that the correlation between stream water concentration and Q for any particular cation varies greatly among watersheds (Table 4), which emphasizes the differences among sites. We conclude from this analysis that hydrology imposes a weak control on K availability and transport within a forest watershed and is generally weaker than for other cations.

The ecological importance of K in forest ecosystems

While K has been acknowledged as a critical nutrient for the growth and maintenance of plants, its retention at the watershed scale and importance in stimulating primary production has been less emphasized in the ecological literature as compared with N. Based on three lines of evidence presented in this review, we suggest that K may play a much more important role in forest ecosystems than expected. Overall, we found (1) the majority of tree species surveyed in the literature are likely to have a significant positive growth response to increased availability of K; (2) similar and strong linear relationships exist between N and K in hydrologic output in streams from forested watersheds, globally; and (3) there are distinct long-term

Table 2 Watershed characteristics

	Hubbard Brook LTER	Niwot Ridge LTER	H.J. Andrews LTER	Bonanaza Creek LTER	Chiloe, Chile CPES
Location	New Hampshire	Colorado	Oregon	Alaska	Southern Chile
Latitude/longitude (degree)	44 N/72 W	40 N/105 W	44 N/122 W	65 N/148 W	42 S/74 W
Area (ha)	13.2	8	60.3	520	1.2
Elevation (m)	549–792	>3,380	530–1070	315–738	650–700
Description	Northern Hardwood	Alpine-Tundra Forest	Pacific NW Conifer	High latitude	Temperate rainforest (minimum impact)
Sampling interval and period of record used	Monthly 6/63–12/98* Weekly 1993–2003	Weekly† 5/85–3/03	Bi-weekly 6/81–5/01	Bi-weekly 11/85–3/87	Bi-weekly 3/94–10/99
Watershed/site designator	W6	Martinelli	GSWS02	Caribou Cr. Trib. C2	CP2
Principle investigators responsible for data	Gene Likens Institute of Ecosystem Studies	Nel Caine INSTAAR University of Colorado Boulder	Sherri Johnson USDA Forest Service Pacific NW Research Station	Scott Ray University of Alaska Fairbanks (MSci 1988)	Lars O. Hedin Ecology and Evolution of Biology Princeton University

*Monthly data are flow-weighted averages of weekly samples.

†During the ice-free period of the year only

seasonal patterns in K for some streams across North America.

The review of fertilization studies suggests that trees in many forests respond positively to increases in K availability (69% of fertilization studies reviewed and an effect size of 0.56 from the meta-analysis) indicating a potential lack in the relative or absolute amount of K in soils needed for optimal growth. The results of our review are consistent with other recent syntheses of limiting nutrients to plants (Knecht & Göransson 2004) and global distributions of elements in soils (Jobbágy & Jackson 2001). These studies point to the relative importance of P and K in terrestrial ecosystem primary productivity as they are strongly cycled by plants relative to other nutrients, and their concentrations in the uppermost layers of the soil horizons are likely a result of this strong biotic control (Jobbágy & Jackson 2001). Demand for K at an ecosystem level may be relatively high because of the large number of cellular and physiological activities in which K plays a major role: maintaining intracellular osmotic balance, enzyme activation, protein synthesis and transport, photosynthesis, cell extension, stomatal regulation, seismonastic movements, phloem transport, and cation-anion balance (Evans & Sorger 1966; Marschner 1995; Maathuis & Sanders 1996).

Nutrient limitation in plant communities is often operationally defined as the requirement of a single nutrient necessary to stimulate an increase in production of biomass. Recent work has shown, however, that there can be substantial variation in the nutrient demands and relative proportions of essential nutrients at the species level (Sternier & Elser 2002; Eviner 2004; Knecht & Göransson 2004). Results from the present review and synthesis suggest that multiple elements, including K, may also co-limit tree growth in forests systems. We speculate that plant species may actually vary in their resource demands for N, P, and K based on their stoichiometric requirements, and the relative and absolute abundance of N, P, and K in soils may influence plant community composition in addition to growth (Sternier & Elser 2002; Knecht & Göransson 2004).

Conceptual extension of nutrient limitation to co-limitation has some precedent in the terrestrial ecological literature (e.g. Fahey *et al.* 1998; Bedford *et al.* 1999; Knecht & Göransson 2004; Vitousek 2004), and has been widely accepted in the agricultural literature (see chapters in Kilmer *et al.* 1968). Comparative work has shown that fertilization with N alone and combinations of N, P, K and other base cations can have differential effects on aboveground and belowground processes within forest ecosystems (Franklin *et al.* 2003, Jönsson & Nihlgård 2004). Quantification of the fluxes and internal cycling of multiple nutrients together may lead to a more complete view of the influence of limiting nutrients on patterns and processes in forest ecosystems (Sternier & Elser 2002; Knecht & Göransson 2004).

Table 3 Regression slopes of log[NO₃-N] vs. log[cation] concentrations in stream water (*P*-values)

	Hubbard Br. LTER* (<i>n</i> = 417)	Niwot Ridge LTER (<i>n</i> = 320)	H.J. Andrews LTER (<i>n</i> = 317)	Bonanza Cr. LTER (<i>n</i> = 34)	Chiloe, Chile CPES (<i>n</i> = 112) (±2)
K ⁺	0.15 (<0.001)	0.24 (<0.001)	0.06 (0.007)	0.65 (0.018)	0.03 (0.169)
Na ⁺	-0.01 (<0.001)	-0.72 (<0.001)	0.03 (0.094)	0.63 (0.629)	-0.87 (0.182)
Mg ²⁺	0.05 (<0.001)	0.08 (<0.001)	-0.006 (0.725)	0.19 (0.402)	-0.0002 (1.000)
Ca ²⁺	0.08 (<0.001)	0.03 (0.087)	-0.007 (0.737)	0.36 (0.068)	0.06 (0.814)

*Monthly flow-weighted averages of weekly samples (1963–1998) were used for Hubbard Br. because these data were most easily accessible for NO₃-N.

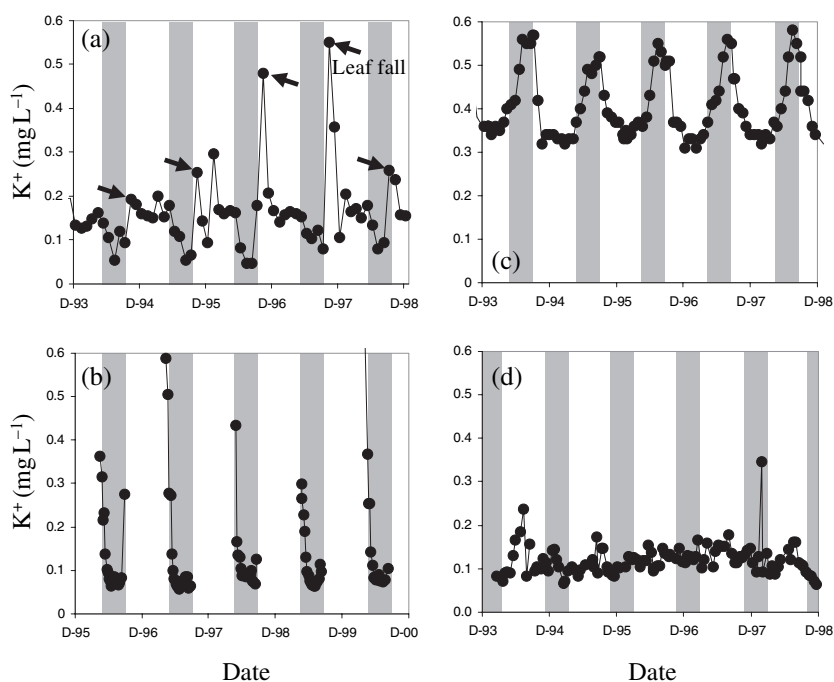


Figure 4 Examples of seasonal patterns of K streamwater concentrations over five consecutive years for three LTER sites: (a) Hubbard Brook w/weekly samples, (b) Niwot Ridge w/weekly samples, and (c) H.J. Andrews w/weekly samples and (d) a site in Southern Chile w/bi-weekly samples. The gray bars indicate the approximate growing-season, which, for the Northern Hemisphere, (a)–(c), = May to September, Southern Hemisphere, (d), = November to March. Bonanza Creek was not included here because the period of record was too short to discern conclusively the presence or absence of seasonal patterns. In (a), the arrows indicate estimated period of leaf fall and the 3 concentrations peaks above 1.0 mg L⁻¹ are, in chronological order, 1.54, 1.81, and 1.06 mg L⁻¹.

In addition to the observed effects of K on plant growth and physiology, results from the present review also reveal a surprising similarity in patterns between N and K in many streams in forest watersheds, which suggests that there may be parallel demand for these nutrients in forest watersheds. In some watersheds, the similar patterns of K dynamics in streams may be largely explained by the large fluxes of K associated with plant uptake and litterfall on a seasonal basis. Previous work has also suggested the importance of biotic control of K at the watershed scale by terrestrial vegetation (in a manner similar to N) when explaining intra-annual patterns in its dynamics in surface waters of minimally disturbed watersheds (Hamilton & Lewis 1987; Likens *et al.* 1994; Likens & Bormann 1995; Salmon *et al.* 2001) and streams draining human-dominated watersheds (Williams *et al.* 2005). A strong biotic demand for K is clearly evident from its rapid increase in stream water following major forest disturbances such as hurricanes and

logging and decreased uptake by plants (Johnson *et al.* 1982; Likens *et al.* 1994; Lamontagne *et al.* 2000; Schaefer *et al.* 2000). Plants and microbes may use similar strategies in acquiring K involving recycling of nutrients from organic matter in upper soil horizons, or assimilating K directly from the weathering products of primary minerals, which can be facilitated through mycorrhizal associations (Waller & Wickman 1999). Potassium may also be leached from soils following decreased uptake by plants and from exchangeable pools in soils on a seasonal basis similar to NO₃ (Jönsson & Nihlgård 2004). In this review, seasonal patterns of K in some streams of North America and differences in temporal patterns with all other base cations (including sodium, which is mono-valent) suggest that the role of K in forest ecosystems is unique, and has closer similarity in its dynamics with N than other base cations. We acknowledge that proximal causes for K retention and underlying mechanisms are still not well known, and detailed

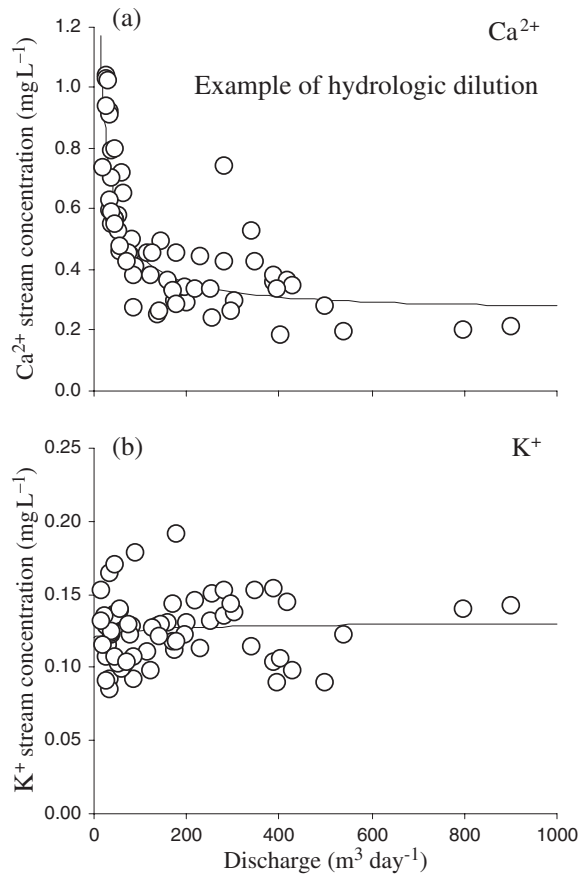


Figure 5 Examples of (a) dilution behaviour of base cations with increasing stream discharge, in this case Ca^{2+} and (b) the commonly observed hydrologically independent behaviour of K^+ in stream discharge. Both examples are from at the Southern Chile site (Salmon *et al.* 2001). The lines are best-fit hyperbolic functions: $C = C_o \left[\frac{1}{1 + \beta Q} \right] + C_f$, where C is the cation concentration, Q is stream discharge, b is a fitting parameter, C_o and C_f are ‘end-members’ or concentration limits corresponding to $Q = 0$ and $Q \rightarrow \infty$, respectively.

K mass balance studies of K are currently rare in the literature (e.g. Likens *et al.* 1994), although many studies have measured K in soils, soil water, and streams (e.g. Brady & Weil 2001; Jobbágy & Jackson 2001; Salmon *et al.* 2001; Vitousek 2004). In general, elucidating and quantifying changes in the supply and demand of K in forests could complement the relatively large amount of existing and ongoing work, which has investigated patterns for N in forests and helped clarify its relative importance and the interactions among key nutrients in regulating the dynamics of plant communities and watershed nutrient loss.

Unraveling the role of K in forest ecosystems

Many forests in Europe and North America have a sustained history of harvesting trees for fuel, fertilizers, and glass manufacture, removing considerable amounts of K stored in biomass (Mohme 1929; Hall 1948; Barker *et al.* 1956; Pisani 1985; Cummings 2002). What impact this removal has had on the long-term availability of K in the subsequent reforestation of the past 100 years is open to speculation, but is likely to have slowed the return of available pools of K for forest growth as has been shown for more modern forests (Likens *et al.* 1970). Other limiting nutrients (N and P) have been added to forests through atmospheric deposition (Likens & Bormann 1995; Vitousek *et al.* 1997; Fenn *et al.* 1998) and through historical changes in land use (Compton & Boone 2000) without concomitant additions for K, which also may affect the ecological significance of K in forests in the future. Nitrogen might be the primary limiting nutrient in many forests, but the relative importance of K as a co-limiting nutrient may increase as other nutrients increase in supply. In this case, changes in multiple and coupled factors in forest dynamics, theoretically, may give rise to a state change in the cycling of K, which has been observed for other base cations such as calcium (Johnson *et al.* 1985; Huntington *et al.* 2000).

Table 4 R^2 values for hyperbolic function of discharge* vs. cation concentrations in stream water (P -values)

	Hubbard Br. LTER† ($n = 784$)	Niwot Ridge LTER† ($n = 270$) (± 2)	H.J. Andrews LTER† ($n = 408$) (± 2)	Bonanza Cr. LTER ($n = 34$)	Chiloe, Chile CPES ($n = 112$) (± 2)
K^+	0.08 (<0.001)	0.03 (0.002)	0.50 (<0.001)	0.13 (0.031)	0.01 (0.158)
Na^+	0.72 (<0.001)	0.25 (<0.001)	0.79 (<0.001)	0.03 (0.301)	0.24 (<0.001)
Mg^{2+}	0.37 (<0.001)	0.22 (<0.001)	0.68 (<0.001)	0.55 (<0.001)	0.12 (0.004)
Ca^{2+}	0.16 (<0.001)	0.22 (<0.001)	0.65 (<0.001)	0.23 (0.004)	0.70 (<0.001)

*Hyperbolic function of discharge is $1/(1 + \beta Q)$ where Q is stream discharge and β is a fitting constant (e.g. Salmon *et al.* 2001). Best-fits were determined by minimizing the sum-of-squares.

†The low P -values may be an artefact of the large sample sizes; we recommend using the relative R^2 values to assess the strength of the correlations for these systems.

Based on the demonstrated importance of K from the information compiled in this review and potential changes in its future cycling and uptake, we propose further areas of study. Fertilization with K in factorially designed field experiments (along with other co-limiting nutrients), and complimentary tracer studies using rubidium-86 (Jones *et al.* 1987), could lead to direct quantification of mechanisms influencing biotic control on K and changes to aboveground and belowground communities in forests. Rubidium, which is an analogue of K, shows similarities in its uptake kinetics (Jones *et al.* 1987) and may be used as an environmental tracer that allows quantifications of rates of K incorporation and flux from different pools in forests. Combined tracer and fertilization approaches may help explain why K is cycled differently than the other base cations, which has been previously observed across studies in different systems (Hamilton & Lewis 1987; Likens *et al.* 1994; Salmon *et al.* 2001), and how added K may stimulate biomass production in trees in nutrient poor soils amended with other nutrients. Characterization of stoichiometric plasticity (N : P : K requirements) at the plant species level and competition experiments across resource gradients could unravel the role of K in influencing the growth, survival, competition and structuring of plant communities (*sensu* Tilman *et al.* 1999), and possibly, microbial communities (*sensu* Wallander & Wickman 1999). In any case, there are many directions for future research on K: its interactions with other biogeochemical cycles, how its ecological significance may change with widespread anthropogenic disturbances such as acid rain, forest harvesting, and increased N deposition, and its general integration into our knowledge of forest ecosystem ecology.

CONCLUSION

This review provides a first attempt to synthesize information from a sampling of the global literature on K, stretching from individual plant studies to long-term watershed data in order to evaluate the overall importance of K in forest ecosystems. We have shown that K fertilization may stimulate primary productivity in different forests, and our effort is one of the first to identify a strong relationship between N and K concentrations in many streams. Our work also identifies contrasting long-term seasonal patterns in K loss from forest biomes throughout North America, which have been previously undocumented except for the north-eastern USA, the underlying mechanisms still remain unclear, however. We stress that this review is not comprehensive in its scope, although we have tried to analyse and present many different examples from the published and unpublished data on the effects and dynamics of K in trees and streams. Our objective is to stimulate thought and

inclusion of this understudied element into mainstream ecological research and to emphasize consideration of importance of K among the other recognized critical nutrients. Including K in studies of forest ecosystems may be essential in gaining a broader understanding of the demonstrated nutrient requirements of many trees, competition between species across natural and altered nutrient gradients, and how multiple biogeochemical cycles can be coupled to influence the dynamics of forest productivity and nutrient loss from watersheds.

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APPENDIX

Meta-analysis table of K effects on growth and tissue concentration. Meta-analysis output was generated by the program *Comprehensive Meta Analysis V1.0.23* (© Biostat, Inc. 1999)

Response variable	Citation	Treat, <i>n</i>	Control, <i>n</i>	Total, <i>n</i>	Effect size	Lower CI	Upper CI	<i>P</i> -value
Growth	Bradbury & Malcolm (1977)	8	8	16	-1.178	-2.368	0.011	0.026
Growth	Hanley & Fenner (1997)	12	17	29	1.254	0.399	2.108	0.002
Growth	Holopainen & Nygren (1989)	7	7	14	1.443	0.084	2.802	0.014
Growth	Ouimet & Fortin (1992)	4	4	8	2.782	-0.168	5.731	0.004
Growth	Triboulot <i>et al.</i> (1997)	8	8	16	0.122	-0.952	1.196	0.800
Growth	Triboulot <i>et al.</i> (1997)	8	8	16	1.372	0.144	2.601	0.012
Growth		47	52	99	0.709	0.257	1.160	0.002
Tissue concentration	Bradbury & Malcolm (1977)	8	8	16	2.321	0.845	3.796	0.000
Tissue concentration	Ericsson & Kähr (1993)	40	40	80	27.836	23.321	32.351	0.000
Tissue concentration	Holopainen & Nygren (1989)	8	8	16	7.243	3.903	10.583	0.000
Tissue concentration	Moore <i>et al.</i> (2000)	49	49	98	0.421	0.015	0.826	0.038
Tissue concentration	Nowak <i>et al.</i> (1991)	3	4	7	3.257	-0.656	7.170	0.004
Tissue concentration	Nowak <i>et al.</i> (1991)	11	4	15	1.136	-0.229	2.501	0.059
Tissue concentration	Ouimet & Fortin (1992)	4	4	8	0.814	-1.052	2.680	0.234
Tissue concentration	Salih & Andersson (1999)	3	3	6	0.033	-2.235	2.300	0.963
Tissue concentration	Shaw <i>et al.</i> (1998)	26	26	52	-0.549	-1.117	0.020	0.050
Tissue concentration	Wilmot <i>et al.</i> (1996)	3	3	6	10.153	-3.919	24.226	0.000
Tissue concentration		155	149	304	0.499	0.206	0.791	0.001
Combined		202	201	403	0.561	0.317	0.806	0.000