

Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest

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Abstract. We maintained a factorial nitrogen (N), phosphorus (P), and potassium (K) addition experiment for 11 years in a humid lowland forest growing on a relatively fertile soil in Panama to evaluate potential nutrient limitation of tree growth rates, fine-litter production, and fine-root biomass. We replicated the eight factorial treatments four times using 32 plots of 40 × 40 m each. The addition of K was associated with significant decreases in stand-level fine-root biomass and, in a companion study of seedlings, decreases in allocation to roots and increases in height growth rates. The addition of K and N together was associated with significant increases in growth rates of saplings and poles (1–10 cm in diameter at breast height) and a further marginally significant decrease in stand-level fine-root biomass. The addition of P was associated with a marginally significant ($P = 0.058$) increase in fine-litter production that was consistent across all litter fractions. Our experiment provides evidence that N, P, and K all limit forest plants growing on a relatively fertile soil in the lowland tropics, with the strongest evidence for limitation by K among seedlings, saplings, and poles.

Key words: Barro Colorado Nature Monument, Panama; fertilization; fine litter; fine roots; nitrogen; nutrient limitation; phosphorus; potassium; tree growth; tropics.

INTRODUCTION

Fertilizers that combine nitrogen (N), phosphorus (P), and potassium (K) are routinely required to maintain agricultural productivity. The role of nutrient limitation is less certain in natural ecosystems for at least two reasons. First, nutrients are recycled through decomposition rather than being removed in harvests. Second, most wild plants tolerate lower nutrient supplies than do most agricultural species. In natural ecosystems, nutrients are supplied by weathering rock, atmospheric deposition, and, in the case of N, biological fixation. All ecosystems lose nutrients through gaseous emission, leaching to groundwater, and overland export to streams and rivers. The potential for nutrient limitation in wild plants reflects the ability of plants to adjust to the local balance of nutrient supply and loss.

The balance of nutrient supply and loss changes as soils age and, in the case of N, with latitude (Walker and

Syers 1976, Vitousek 1984, Vitousek and Sanford 1986, Hedin et al. 2009, Vitousek et al. 2010). Weathering bedrock is the primary source of P and K, and their availability tends to decline as soils age (Walker and Syers 1976, Hedin et al. 2003). In regions of active geological uplift, ongoing erosion continues to supply rock-derived nutrients (Porder et al. 2007). Elsewhere as soils age, long-distance transport in dust and precipitation becomes the principal source of rock-derived nutrients. In contrast, N is largely absent from igneous and metamorphic rock, its primary sources are biological fixation and atmospheric deposition, and its supply initially increases in young soils, reaches maximum levels in moderately weathered soils, and declines in some highly weathered soils as other nutrients come to limit biological N fixation (Vitousek 2004, Lambers et al. 2008, Barron et al. 2009). Some lowland tropical forests sustain levels of N cycling, N losses, N:P ratios in leaves and fine litter, and C:P ratios in fine litter that far exceed levels observed in temperate and boreal forests (Vitousek 1984, McGroddy et al. 2004). A latitudinal gradient in soil age contributes to this trend, with lower N and greater P availability on younger soils initiated by repeated glacial cycles and the widespread deposition of

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glacial dust at higher latitudes (Vitousek and Sanford 1986). In addition, N fixation by heterotrophic bacteria and epiphytes that are decoupled from soil N supplies and up-regulation of biological N fixation by abundant legumes should disturbance reduce N availability are hypothesized to sustain high N losses from N-rich tropical forests (Hedin et al. 2009). For these reasons, supplies of N, P, and K are all likely to be relatively high in N-rich, lowland tropical forests growing in regions of active geological uplift.

Plants adjust to local nutrient availability through changes in species composition, phenotypic plasticity, and adaptation. As an example of changes in species composition, tree species characterized by dense wood and low foliar nutrient concentrations dominate forests on nutrient-poor soils in the geologically stable eastern and central Amazon and tend to be replaced by tree species characterized by lighter wood and larger foliar nutrient concentrations on richer soils influenced by the rapidly eroding Andes in the western Amazon (Fyllas et al. 2009, Patiño et al. 2009). As an example of a likely mix of phenotypic plasticity and local adaptation, widespread Amazonian species tend to have denser wood and lower foliar nutrient concentrations when growing on poorer soils (Fyllas et al. 2009, Patiño et al. 2009). Collectively, these adjustments mediate the potential limitation of primary production by nutrients and are likely to lead to simultaneous limitation by multiple nutrients. Simultaneous limitation can arise through physiological responses that maintain homeostasis at the level of individual plants, limitation of different species by different nutrients at the level of plant communities, and positive feedbacks among nutrient supply rates at the level of ecosystems (Vitousek et al. 2010).

Recent meta-analyses of fertilization experiments are broadly consistent with the hypothesis that multiple nutrients limit plant growth in natural communities. A meta-analysis of 38 potassium fertilization experiments involving 26 forest tree species demonstrates that K addition tends to increase growth rates (69% of studies) and tissue K concentrations (76%; Tripler et al. 2006). A meta-analysis of 126 terrestrial N fertilization experiments demonstrates that N is equally likely to limit aboveground net primary production at all latitudes (LeBauer and Treseder 2008). Finally, a meta-analysis of 173 terrestrial studies that included independent manipulations of N and P or factorial manipulation of N and P demonstrates that N and P tend to co-limit plant biomass or plant productivity (Elser et al. 2007).

Unfortunately, lowland tropical forests are underrepresented in these meta-analyses. There has not been a single K fertilization experiment in a tropical forest. Just five P fertilization experiments and four N fertilization experiments have evaluated community-level responses in lowland tropical forests. Most of these experiments took place in young secondary forests, where reduced organic matter pools limit nutrient availability and rapid

increases in plant biomass sustain high nutrient demand (Campo and Vazquez-Yanes 2004, Davidson et al. 2004). The only fertilization experiments conducted in old-growth, lowland tropical forests are a four-year factorial manipulation of N and P on a relatively infertile soil in Borneo (Mirmanto et al. 1999) and a two-year manipulation of P on a relatively infertile soil in Cameroon (Newbery et al. 2002). We lack a single fertilization experiment that has lasted more than four years in a lowland tropical forest.

For these reasons, we initiated a chronic NPK factorial fertilization experiment in an old-growth tropical forest in the lowlands of Panama in 1998. Here, we report the first 10 to 11 years of responses for fine-root biomass, fine-litter production, and tree growth rates. We evaluate radial growth responses of saplings, poles, and larger trees separately because they experience contrasting light levels, and light availability is likely to limit potential responses to fertilization in shaded plants. We expected the strongest responses for P and K addition in this N-rich forest and for progressively larger trees that experience progressively higher light levels.

METHODS

Study site

The 38.4-ha study site (9°06'31" N, 79°50'37" W) is located on the mainland in the Barro Colorado Nature Monument in the Republic of Panama (Appendix A: Fig. A1). Tree species composition and stature (canopy heights up to 40 m) are characteristic of very old (>200 yr), secondary forest. Aerial photographs confirm the presence of tall forest at the site in 1927 (S. J. Wright, *personal observation*).

Table 1 summarizes concentrations of N, P, and K in bedrock and fine litter and in plant available forms in surface soils (0–10 cm depth) in our control plots. The bedrock is an 85-m thick Miocene basalt (Stewart et al. 1980) and is relatively rich in P (Table 1). Elevation grades from 25 m in the southwest to 61 m in the northeast corner of the study site (Appendix A: Fig. A1). In the FAO classification, the soils are Endogleyic Cambisols and Acric Nitisols in the lower and upper parts of the landscape, respectively (Koehler et al. 2009, who accidentally reverse the position of the soil types). These soil types are widespread in Mesoamerica (IUSS Working Group WRB 2006). Plant available soil nutrient concentrations are representative of forest soils in central Panama (B. L. Turner, *unpublished data*), and soil K concentrations are representative of Mesoamerica (Barthold et al. 2008). Total P and total reserve base concentrations are 600 mg/kg and 97 mmol_c/kg, respectively, for the upper 30 cm of soil (J. B. Yavitt, *unpublished data*). Total P and reserve base concentrations are smaller for >92% and 60% of 63 Amazonian sites (Fyllas et al. 2009), respectively. Soils at the study site are relatively fertile for the lowland tropics.

TABLE 1. Nutrient status in bedrock, fine litter, and surface soils of the study site in the Barro Colorado Nature Monument, Panama.

Element	Bedrock (ppm) [†]	Input in litter (kg·ha ⁻¹ ·yr ⁻¹) [‡]	Concentration in control soils (mg element/kg dry soil) [§]
K	3410	57	84–131
N		180	5.3–5.6 nitrate; 6.2–15.5 ammonium
P	1600	11	1.4–2.2

[†] Mean value for Miocene basalts in the Panama Canal area (C. Jaramillo, *unpublished data*).

[‡] Measured for forest 3 km from our site on Barro Colorado Island (Yavitt et al. 2004).

[§] For samples stored at 2–4°C for 24–48 h and extracted in 2 mol/L KCl for ammonium and nitrate, Mehlich III for the smaller K and P values, Bray 1 for the larger P value, and 1 mol/L NH₄Cl for the larger K value (Yavitt et al. 2009, Sayer and Tanner 2010).

Experimental design

We replicated the eight treatments of a 2 × 2 × 2 factorial NPK experiment four times. We placed the four replicates perpendicular to the 36-m topographic gradient because soil properties (Yavitt et al. 2009) and tree distributions (S. J. Wright, *unpublished data*) parallel the gradient. Within each replicate, we blocked the N, P, K, and NPK treatments vs. the NP, NK, PK, and control treatments (Appendix A: Fig. A1). This balanced, incomplete-block design minimizes uncontrolled error associated with spatial variation, enables evaluation of main effects and two-way interactions, but limits power to evaluate the three-way interaction (Winer 1971). The 32 experimental plots each measured 40 × 40 m. The minimum distance between plots was 40 m, excepting two plots separated by 20 m and a 3 m deep streambed (Appendix A: Fig. A1).

Beginning in 1998, we added fertilizer by hand in four equal doses each wet season with 6–8 weeks between applications (15–30 May, 1–15 July, 1–15 September, and 15–30 October). Nitrogen was added as coated urea ((NH₂)₂CO), P as triple superphosphate (Ca(H₂PO₄)₂·H₂O), and K as potassium chloride (KCl). Annual doses were 125 kg N·ha⁻¹·yr⁻¹, 50 kg P·ha⁻¹·yr⁻¹, and 50 kg K·ha⁻¹·yr⁻¹, which equals 69%, 470%, and 88% of annual inputs from fine litter at a nearby site (3 km), respectively (Table 1). Similar large additions of P relative to annual litter inputs are standard practice in forestry and in previous tropical nutrient addition experiments (Tanner et al. 1992, Mirmanto et al. 1999, Fisher and Binkley 2000) because many soils, including soils at our site, sequester large amounts of added P in forms that are inaccessible to plants (Yavitt et al. 2010). After nine years, N addition had reduced soil pH and base saturation and increased nitrate leaching, N-oxide emissions, and aluminum saturation (Corre et al. 2010).

Tree growth

We measured diameter at breast height (dbh) or just above buttresses for all free-standing woody plants with dbh > 10 cm in the central 30 × 30 m and with dbh ≥ 1 cm in the central 20 × 30 m of each 40 × 40 m plot in 1997, 2000, and 2008 (see Plate 1). All measured trees were > 5 m from the nearest plot boundary. For

analyses of relative growth rates (RGR), we excluded trees with multiple stems, broken stems, and buttresses or other deformities whose growth prevented measurements at the same height in consecutive censuses. The 9551 trees that remained included those that first recruited to the 1-cm dbh minimum size threshold and those that died between 2000 and 2008. We calculated RGR for 1997–2000 and 2000–2008 as $RGR_{i-f} = \log(\text{dbh}_f/\text{dbh}_i)/((\text{DC}_f - \text{DC}_i)/365)$, where DC represents day of century and the subscripts *i* and *f* represent initial and final values, respectively. We performed separate analyses for four tree size classes (1.0 cm ≤ dbh ≤ 2.4 cm, 2.5 cm ≤ dbh ≤ 4.9 cm, 5.0 cm ≤ dbh ≤ 9.9 cm, and dbh ≥ 10 cm) to isolate trees with contrasting levels of shading and to control size-related variation in RGR. Response variables were mean RGR for each plot, census interval, and size class. The median (minimum) number of trees used to calculate RGR for each plot and census interval was 75 (36), 47 (19), 23 (10), and 19 (7) for the smallest to largest size classes, respectively.

Fine-root biomass

We collected soil to 10 cm depth from four (six in 2009) random locations in the central 20 × 20 m of each plot with a 5 cm diameter split-sleeve core in April 2000, November 2008, and April 2009. We washed soils through a 0.5-mm sieve leaving roots and coarse sand. We oven-dried fine (<2 mm diameter) and coarse (2–5 mm) roots to constant mass at 60°C. We performed separate analyses for 0–5 and 5–10 cm depths and for fine roots only because many cores lacked coarse roots. Response variables were mean dry mass for each plot, year, and depth.

Fine-litter production

We randomly located three litter traps in the central 30 × 30 m of each plot on 1 July 1998. The minimum distance between traps was 10 m. Each trap had an effective surface area of 0.58 m² composed of an open bag of 1-mm mesh window screen raised 80 cm above the ground on a PVC frame. We collected litter once each month following the methods of Proctor (1983), oven-dried litter to constant mass at 60°C, and, beginning in November 1998, weighed leaves, wood, reproductive material, and other fine litter or “dust”

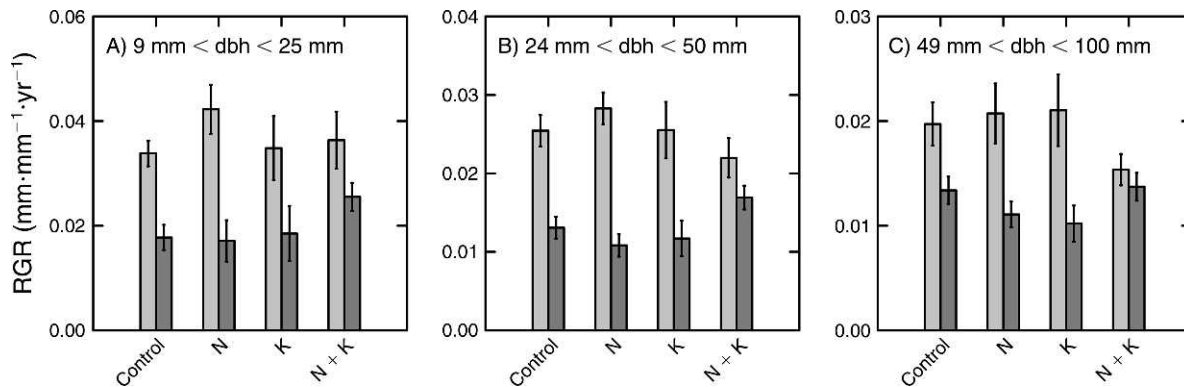


FIG. 1. Tree growth responses to nitrogen (N) and potassium (K) addition for three subcanopy size classes. Each panel illustrates a significant $N \times K \times$ census interaction ($F_{1,18} = 5.45, 8.34,$ and 6.82 ; $P = 0.031, 0.010,$ and 0.018 in panels (A), (B), and (C), respectively). Relative growth rates (RGR) declined significantly from 1997–2000 (light bars) to 2000–2008 (dark bars) for each size class. N plus K addition ameliorated the decline for all three size classes. The full experiment included eight factorial N, K, and phosphorus (P) treatments. P addition had no significant effects on RGR, and the four P addition treatments (P, N + P, K + P, and N + K + P) are pooled with the appropriate treatment without P (control, N, K, and N + K, respectively). Thus, bars represent RGR (mean \pm SE) for eight plots. Above each panel are the diameter at breast height (dbh) limits for the tree size class.

separately. The response variable was mean dry mass production ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) for each plot and year. Years extended from 1 November to 31 October.

Aboveground net primary production (ANPP)

We summed fine-litter and wood production to estimate ANPP. To estimate wood production, we estimated the aboveground biomass (AGB) of each tree at each census (1997, 2000, and 2008) using its dbh, wood density ($\text{g dry mass}/\text{cm}^3$ fresh volume) determined for each species (Wright et al. 2010), and the “best predictive equation” for tropical moist forest from Chave et al. (2005). Mean wood density was substituted for six rare species that lacked a wood density measurement. Stand-level wood production equaled the sum of $\text{AGB}_f - \text{AGB}_i$ for trees that survived from census i to census f and the AGB of trees that recruited during the census interval. The response variable was dry mass production of wood plus fine litter ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) for each plot and year.

Analyses

We performed repeated-measures analyses of variance (ANOVA) for each response variable to control spatial variation among plots and to evaluate temporal variation. Between-subject (henceforth, between-plot) effects evaluate responses over the entire experiment. Within-subject (henceforth, within-plot) effects evaluate variation among years and interactions among treatments and year. A nutrient response that lagged behind the initial addition of nutrients might be insignificant over the entire experiment but lead to a significant treatment \times year interaction. Such lags characterize tree responses to fertilization (Tanner et al. 1992). Repeated-measures ANOVA assumes compound symmetry of the variance-covariance matrix if there are more than two repeated measures. We therefore used the conservative

Greenhouse-Geisser correction for violations of the compound symmetry assumption to evaluate the significance of all within-plot effects for fine-root biomass and fine-litter production, which had three and 11 repeated measures, respectively. All analyses were performed with SYSTAT 11.0 (Richmond, California, USA).

RESULTS

Tree growth

Tree growth rates decreased through time (Figs. 1 and 2). $\text{RGR}_{2000-2008}$ was significantly smaller than $\text{RGR}_{1997-2000}$ for all four tree size classes ($F_{1,18} > 15.0$, $P < 0.001$; Appendix B: Tables B1–B4).

A single consistent response to nutrient addition characterized the three smaller size classes (Fig. 1). The $N \times K \times$ year interaction was significant for each of these size classes ($F_{1,18} = 6.82, 8.34,$ and 5.45 ; $P = 0.018, 0.010,$ and 0.031 ; Appendix B: Tables B2, B3, and B4, respectively). The combined N + K treatment ameliorated the temporal decline in RGR. The pattern of similar growth rates for control, N, K, and combined N + K treatments in the first interval and larger growth rates for the combined N + K treatment in the second interval indicates a positive lagged response to the combined N + K treatment (Fig. 1).

The response of large trees ($\text{dbh} > 10$ cm) to nutrient addition was more complicated (Fig. 2; Appendix B: Table B1). The between-plot, $N \times K$ interaction was marginally significant (Appendix B: Table B1; $F_{1,18} = 4.41$, $P = 0.050$) because RGR was similar for the control and combined N + K treatments but larger for the N and K treatments (Fig. 2B).

The $P \times$ year interaction was also significant for large trees (Fig. 2C; $F_{1,18} = 7.95$, $P = 0.011$; Appendix B: Table B1); however, the pattern of growth rates underlying this interaction is inconsistent with a positive response to P addition. Added P appears to have depressed

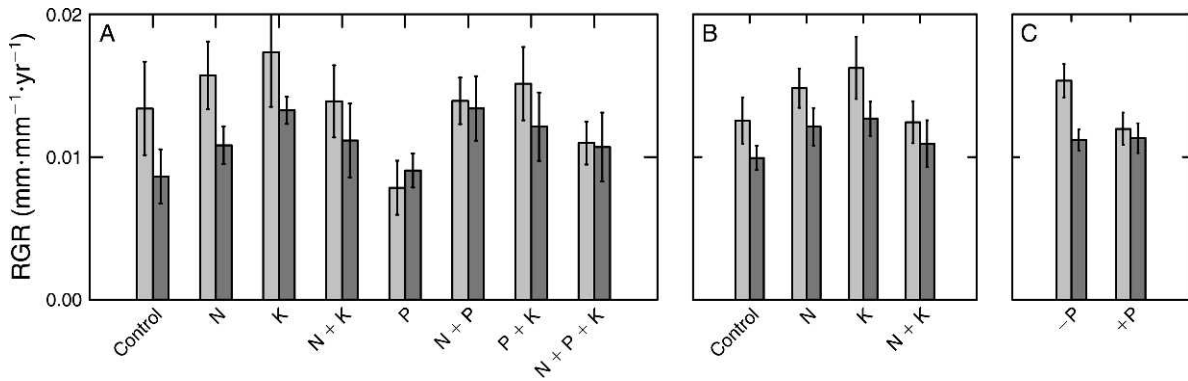


FIG. 2. Growth responses of large trees (>10 cm dbh) to phosphorus (P), nitrogen (N), and potassium (K) addition. Relative growth rates (RGR) declined significantly from 1997–2000 (light bars) to 2000–2008 (dark bars). Panel (A) presents the eight treatments in the full factorial NPK design, and bars represent RGR (mean \pm SE) for four plots. Panel (B) presents the marginally significant $N \times K$ interaction ($F_{1,18} = 4.41$, $P = 0.050$). The P addition treatments (P, N + P, K + P, and N + K + P) are pooled with the appropriate treatment without P (control, N, K, and N + K, respectively), and bars represent RGR (mean \pm SE) for eight plots. Panel (C) presents the significant $P \times$ census interaction ($F_{1,18} = 7.95$, $P = 0.011$). The four P addition treatments (P, N + P, K + P, and N + K + P) are pooled, the four treatments without P (control, N, K, and N + K) are pooled, and bars represent RGR (mean \pm SE) for 16 plots.

RGR_{1997–2000} and to have had no effect on RGR_{2000–2008} (Fig. 2C). The arrangement of treatments in Fig. 2A also illustrates the effect of added P. The control, N, K, and combined N + K treatments are arranged from left to right first without and then with added P (Fig. 2A). Added P did not increase tree growth rates.

Fine-root biomass

Fine-root biomass in surface soils (0–5 cm depth) varied significantly with K addition. The addition of K was associated with a significant reduction in fine-root biomass (Fig. 3A; $F_{1,18} = 9.69$, $P = 0.006$; Appendix B: Table B5). The $N \times K \times$ year interaction was also marginally significant ($F_{2,36} = 3.22$, $P = 0.064$; Appendix B: Table B5), with fine-root biomass in surface soils reduced in one year with N addition alone, in two years with K addition alone, and in all three years with combined NK addition (Fig. 3B). Fine-root biomass in subsurface soils (5–10 cm depth) was unaffected by nutrient additions (Appendix B: Table B6).

Fine-root biomass also varied significantly among years. Fine-root biomass was approximately twice as large in April 2000 as in November 2008 and April 2009 (Fig. 3B; Appendix B: Tables B5 and B6). Similar large temporal variation in fine-root biomass has been observed previously in a nearby forest (Cavelier et al. 1999).

Fine-litter production

There was a marginally significant increase in fine-litter production with P addition (Fig. 4A; $F_{10,180} = 4.10$, $P = 0.058$; Appendix B: Table B7). We also examined the four fractions that comprise fine-litter production separately (Fig. 4B–E). The mean level of production was larger where P was added and smaller where P was not added for 39 of the 44 combinations of year and

litter fraction (Fig. 4B–E). Two of the five exceptions were for the first year of the experiment (Fig. 4D–E). The three remaining exceptions were for reproductive structures (Fig. 4C). Reproductive output varies widely in space and time in central Panama (Wright et al. 2005). As an example, the coefficient of variation (SD/mean) of annual production (averaged over the 32 experimental plots) was 250% to 500% greater for reproductive structures (0.203) than for total fine litter (0.040), leaf litter (0.055), or small branches (0.080). It is not surprising that the spatial and temporal variation in reproductive output sometimes overwhelmed the effect of added P. The consistent increase in the three remaining fractions of fine-litter production after the first year of P addition (30 out of 30; Fig. 4B, D, and E) suggests that the marginally significant effect of P addition on total fine-litter production is real.

Aboveground net primary production (ANPP)

ANPP averaged 14.7 ± 4.0 Mg·ha⁻¹·yr⁻¹ (mean \pm SD). This included 11.4 ± 3.2 and 4.2 ± 2.7 Mg·ha⁻¹·yr⁻¹ of fine-litter and wood production, respectively. There were no significant effects of nutrient treatments for ANPP (Appendix B: Table B8); however, we have little confidence in our plot-level estimates of wood production and hence ANPP. Our plot-level estimates of wood production were highly variable. As an example, the overall coefficient of variation (SD/mean) for plots was 0.64 and 0.28 for wood and fine-litter production, respectively. We believe our plots are too small to estimate wood production accurately because just 3% of the trees larger than 10 cm dbh account for 50% of the aboveground biomass (Muller-Landau et al. 2006) and a similar percentage of wood production in mature forests in central Panama. Our effective plot size was just 0.09 ha because trees were not

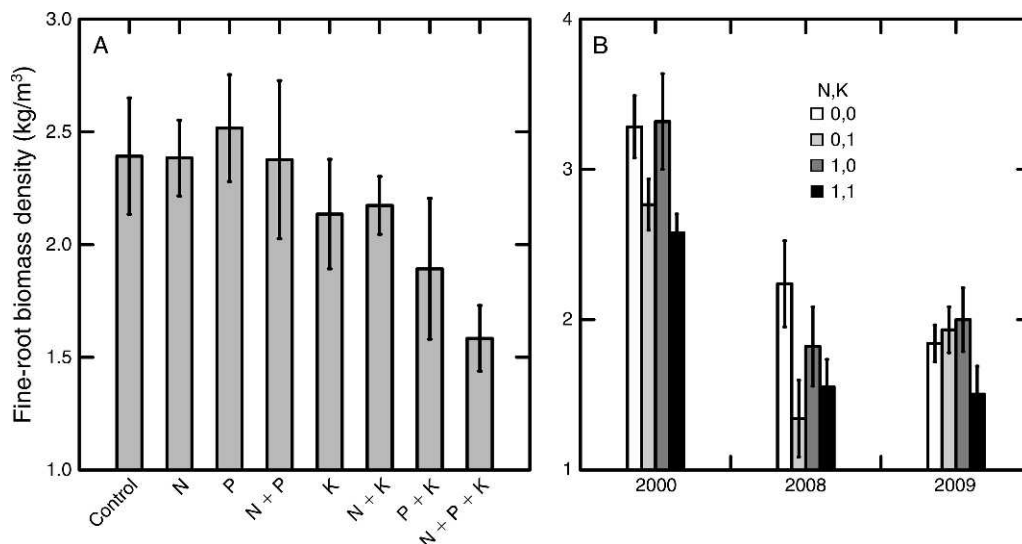


FIG. 3. Fine-root biomass responses to nutrient addition for surface soils (0–5 cm depth). Panel (A) presents the eight treatments in the factorial NPK design. The four treatments with K addition are to the right to illustrate the significant effect of K addition ($F_{1,18} = 9.69$, $P = 0.006$). Bars represent values (mean \pm SE) for four plots and three years. Panel (B) isolates the marginally significant $N \times K \times \text{year}$ interaction ($F_{2,36} = 3.22$, $P = 0.064$). The inset key matches the shading of the bars with the four factorial combinations of N and K, where 1's and 0's represent plots where N or K were added or not added, respectively. P addition had no significant effects on fine-root biomass, and the four P addition treatments (P, N + P, K + P, and N + K + P) are pooled with the appropriate treatment without P (control, N, K, and N + K, respectively). Bars represent values (mean \pm SE) for eight plots in panel (B).

measured in a 5-m fertilized buffer. A plot of 0.09 ha might or might not contain a large tree, and this ensured highly variable plot-level estimates of wood production. We do not mention ANPP again.

DISCUSSION

The addition of N, P, and K increased concentrations of the same nutrient in soils, leaves, and fine litter in an old-growth, lowland tropical forest growing on a relatively fertile soil in Panama (Table 2). Experimental increases in tissue concentrations might represent luxury consumption or might enable additional plant responses if nutrients limit plant function. We evaluated community-level responses to nutrient addition including fine-root biomass, fine-litter production, and tree growth rates.

Relative growth rates (RGR) declined significantly during the 11-year study (Figs. 1 and 2; Appendix B: Tables B1–B4). This is the fourth tropical forest for which a decadal trend toward slower tree growth rates has been observed (Feeley et al. 2007, Clark et al. 2010). Possible mechanisms include rising temperatures and temperature-dependent respiration rates and/or temperature-dependent photosynthetic rates, increasing abundance of competing woody vines, increasing competition among trees in the final stages of secondary succession, natural decadal climate variation, and cumulative effects of trampling (Wright 2010). Regardless of its cause, slowing tree growth rates affect the interpretation of responses to nutrient addition. A positive response to nutrient addition that lags behind the initial application

of nutrients might be expressed as a relatively small decline in RGR and not as an increase in RGR. We performed repeated-measures analyses with repeated measures on census intervals to evaluate temporal variation in each response variable and possible lagged responses to nutrient addition.

Responses to phosphorus addition

It is widely hypothesized that P limits primary production on highly weathered tropical soils (see *Introduction*; Vitousek 1984, Lambers et al. 2008, Hedin et al. 2009). Six P fertilization experiments have now been conducted in lowland tropical forests. Three of the six took place in young secondary forests (Campo and Vazquez-Yanes 2004, Davidson et al. 2004), where relatively small organic matter pools limit nutrient availability, rapid biomass accumulation provides a strong nutrient sink, and nutrient limitation is to be expected regardless of soil weathering status. Not surprisingly, tree growth rates and/or fine-litter production increased after 3–4 years of P addition in these 4-, 12-, and 60-year-old secondary forests (Campo and Vazquez-Yanes 2004, Davidson et al. 2004).

The three remaining P addition experiments took place in old-growth forests and provide an opportunity to evaluate the hypothesis that P limits tree growth and fine-litter production in mature lowland, tropical forests. The three experiments took place on soils with total P concentrations of 80 mg P/kg (upper 10 cm; Mirmanto et al. 1999), 277 mg P/kg (average of upper 5 cm and 15–20 cm; Newbery et al. 2002), and 484 mg P/kg (upper 15

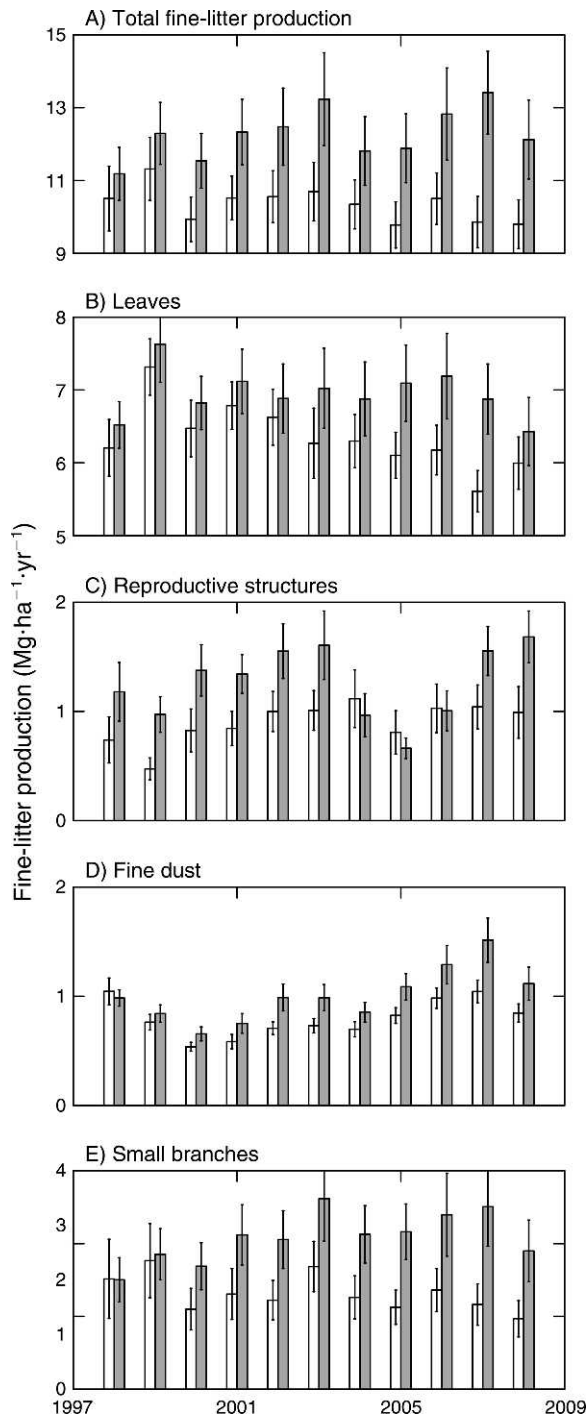


FIG. 4. Responses to phosphorus (P) addition for total fine-litter production (panel A, $F_{1,18} = 4.10$, $P = 0.058$) and its four fractions (panels B–E) over 11 years. Solid and open bars represent pooled treatments with and without added P, respectively. The four litter fractions are (B) leaves, (C) reproductive structures, (D) fine material or dust, and (E) twigs and small branches. The addition of N and K had no significant effects. Therefore, the four P addition treatments (P, N + P, K + P, and N + K + P) are pooled, the four treatments without P (control, N, K, and N + K) are pooled, and each bar represents production (mean \pm SE) for 16 plots.

cm, see *Results*; Yavitt et al. 2010). P addition had no significant effect on tree growth at any of these sites. At the low-P site, fine-litter production averaged 25% greater with P addition than in controls just 8–20 months after the first P application (Mirmanto et al. 1999). At the intermediate-P site, there was no significant effect on fine-litter production; however, fine litter was measured for just one month \sim 2.5 years after the initial P application and 0.5 years after the final P application (Newbery et al. 2002). Finally at our high-P site, fine-litter production averaged 25% greater with P addition than in controls for years eight through 11 after the first P application (Fig. 4A). The obvious conclusion is that more and longer P fertilization experiments will be required before generalization is possible. In the meantime, the evidence that P limits fine-litter production at a P-poor site in Borneo and a relatively P-rich site in Panama suggests that P is likely to limit plant production in many tropical forests.

Responses to nitrogen addition

It is widely hypothesized that N is available in excess of plant demand in lowland tropical forest soils (see *Introduction*; Vitousek 1984, Hedin et al. 2009). LeBauer and Treseder (2008) rejected this hypothesis and concluded that N limitation was equally strong for temperate and tropical forests. Their conclusion is based on a meta-analysis of N addition experiments that included 15 tropical forest experiments; however, just four of these 15 experiments took place in the lowlands. The remaining 11 experiments took place in montane forests. The N cycles and C:N ratios of fine litter in montane tropical forests are similar to those in temperate forests (Vitousek 1984, Tanner et al. 1998, Hedin et al. 2009). Montane forests should therefore be excluded to evaluate the hypothesis that N is available in excess of plant demand in lowland tropical forests. In addition, three of the four lowland experiments evaluated by LeBauer and Treseder (2008) were conducted in

TABLE 2. Increases (%) with nutrient addition in concentrations of the added nutrient for soils, fine litter, and sun-exposed canopy leaves.

Element	Increase with addition of same nutrient (%)		
	Soil [†]	Fine litter [‡]	Canopy leaves [§]
K	24	16	18
N	47	7	5
P	34	27	38

[†] For samples stored at 2–4°C for 24–48 h and extracted in 2 mol/L KCl for ammonium and nitrate, Bray's P1 solution for P, and 1 mol/L NH₄Cl for K. The value for N refers to nitrate; ammonium was unaffected (Koehler et al. 2009, Yavitt et al. 2010).

[‡] Kaspari et al. (2008).

[§] Mean value for one individual of each of three species for each 40 × 40 m plot. The increase for N is only marginally significant ($P = 0.087$).

young secondary forests, where nutrient limitation is expected as previously discussed (see *Discussion: Responses to phosphorus addition*).

Just two N fertilization experiments have evaluated community-level responses in old-growth, lowland tropical forests (Mirmanto et al. 1999; see *Results*). Fine-litter production increased significantly with N addition just 8–20 months after the first N application in Borneo (Mirmanto et al. 1999). In contrast in our experiment, N alone had no significant effects on fine-root biomass, fine-litter production, and tree growth rates; however, the combined addition of N and K was associated with a significant increase in the growth rates of the three smaller size classes of trees (Fig. 1) and a marginally significant reduction in fine-root biomass (Fig. 3B).

Co-limitation by N and K is indicated, especially for sapling and pole-sized trees. Thus, the two experiments conducted in mature, lowland tropical forests suggest limitation by N (Mirmanto et al. 1999) or co-limitation by N and K (see *Results*). The hypothesis that N is available in excess of plant demand in mature lowland tropical forests is not supported.

Responses to potassium addition

In contrast to N and P, the possibility that K might limit tropical forest plants has been entirely overlooked and there are no prior K addition experiments from lowland tropical forests to compare with our results (Tripler et al. 2006). This is surprising because K, like P, is derived from rock and monovalent K^+ ions are particularly prone to leaching losses in the humid tropics (Veldkamp et al. 1990, Hedin et al. 2003). In our experiment, K addition decreased fine-root biomass (Fig. 3A), increased fine-root turnover (Yavitt et al. 2010), decreased seedling allocation to roots, increased seedling height growth rates (L. Santiago, *unpublished data*), and when combined with N addition increased growth rates of smaller trees (Fig. 1). Limitation by K is clearly indicated. The possibility that K might limit plants in tropical forests deserves greater attention.

The mechanism linking K addition to root dynamics is unclear. In the laboratory, K-deficient plants are unable to increase allocation to root growth because K^+ is required to load sucrose into the phloem, and K deficiency impedes sucrose export from leaves to support increased allocation to roots (Hermans et al. 2006). Nonetheless, the addition of K was associated with strong and consistent changes in root dynamics in our experiment. These included significant decreases in seedling allocation to roots (L. Santiago, *unpublished data*) and in stand-level fine-root biomass detected with both root cores and minirhizotrons (Fig. 3A; Yavitt et al. 2010). Allocation shifted away from roots with K addition. The discrepancy with laboratory experiments (Hermans et al. 2006) suggests unknown links between root allocation and K availability.



PLATE 1. Most mature tropical forests include a small number of very large trees. These largest trees make disproportionate contributions to stand-level wood production, and their rarity introduces large variation in wood production among our experimental plots. Three technicians are required to measure the diameter of the largest trees above buttresses and other deformities of the lower trunk. The photograph shows a canopy emergent *Cavanillesia platanifolia* (Bonpl.) Kunth being measured above the swollen lower trunk characteristic of many species in the family Bombacaceae. Photo credit: Marcos Guerra, STRI.

CONCLUSIONS

After 11 years of chronic nutrient addition, our experiment provides evidence for co-limitation of plants growing on a relatively fertile lowland tropical forest soil by N, P, and K. The addition of K reduced fine-root biomass at the community level, reduced allocation to roots in seedlings, and increased seedling height growth rates. The simultaneous addition of K plus N increased growth rates of small saplings and pole-sized trees. And, the addition of P increased fine-litter production, which is dominated by large trees and lianas. Thus, there is also a suggestion that different nutrients limit different forest strata and/or plants of different sizes.

Clearly many more fertilization experiments must be conducted in mature, lowland tropical forests before the hypothesis that P limits primary production while N is available in excess of plant demand on moderately to

highly weathered tropical soils can be fully evaluated (Vitousek 1984, Vitousek and Sanford 1986, Hedin et al. 2009). In the meantime, the three fertilization experiments that evaluated community-level responses in mature, lowland tropical forests (Mirmanto et al. 1999, Newbery et al. 2002; see *Results*) suggest that N ($N = 2$ out of two experiments), P ($N = 2$ out of three experiments), and a second rock-derived nutrient, K ($N = 1$; see *Results*) limit plant growth and/or fine-litter production. These results and long-standing observations that nutrients other than N, P, and K influence plant function and plant distributions in lowland tropical forests (e.g., Baillie et al. 1987, Cuevas and Medina 1988) suggest that the full range of nutrients that might limit plants in lowland tropical forests should now be considered.

ACKNOWLEDGMENTS

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APPENDIX A

Maps showing the location of the study site, its topography, and locations of each experimental plot (*Ecological Archives* E092-136-A1).

APPENDIX B

ANOVA tables for the factorial, incomplete block design for the eight response variables analyzed in this article (*Ecological Archives* E092-136-A2).

SUPPLEMENT

All data sets analyzed in this article (*Ecological Archives* E092-136-S1).

Ecological Archives E092-136-A1

S. Joseph Wright, Joseph B. Yavitt, Nina Wurzburger, Benjamin L. Turner, Edmund V. J. Tanner, Emma J. Sayer, Louis S. Santiago, Michael Kaspari, Lars O. Hedin, Kyle E. Harms, Milton N. Garcia, and Marife D. Corre. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, and litter production in a lowland tropical forest. *Ecology* 92:1616–1625.

Appendix A. Maps showing the location of the study site, its topography and locations of each experimental plot.

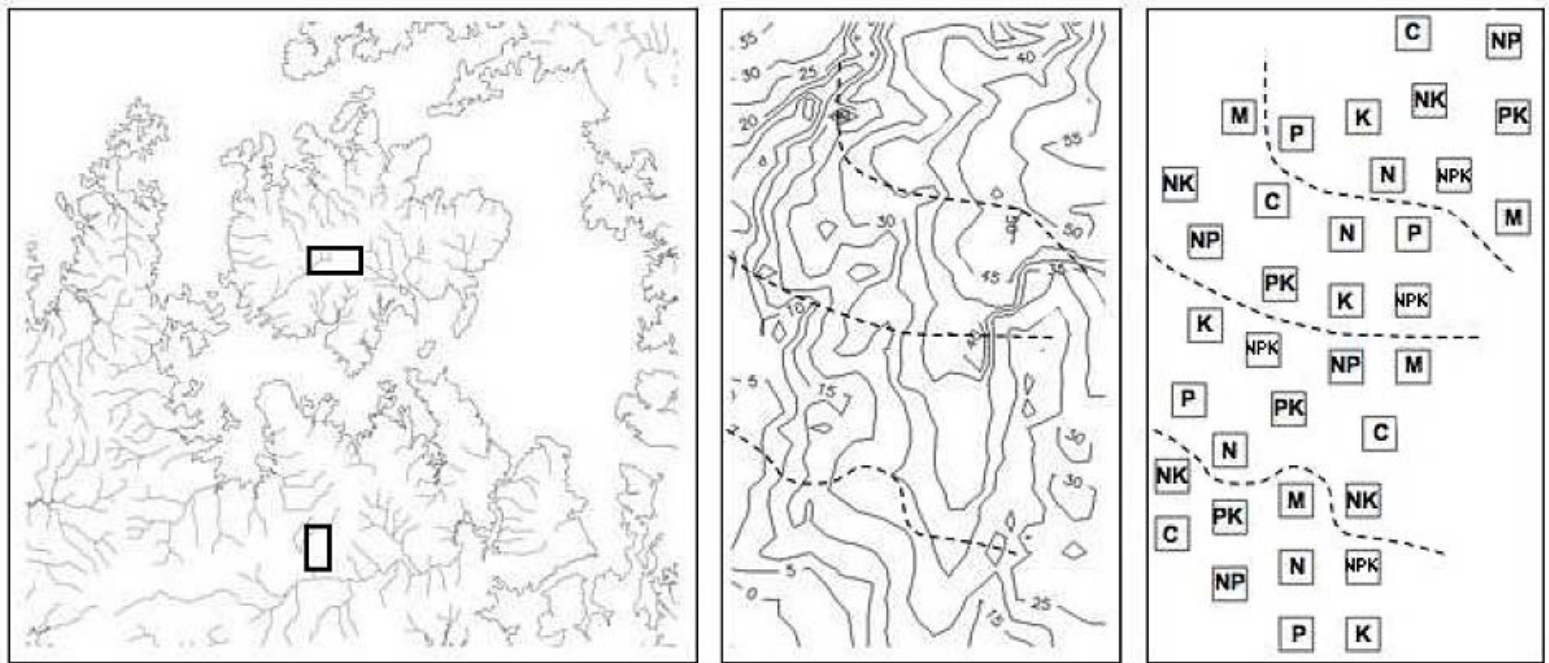


FIG. A1. Maps of the study area. The left panel shows the region. White represents Gatun Lake. The large island is Barro Colorado Island (BCI). The northern rectangle is the Forest Dynamics Plot (1000 m by 500 m) on BCI. The southern rectangle is the fertilization site (480 m by 800 m) on the Gigante Peninsula in the Barro Colorado Nature Monument. The central panel shows the topography of the fertilization site. The right panel shows the placement of treatments. The dashed lines separate four replicates of the full factorial N-P-K experiment. Treatments are represented by the combination of nutrients added (N, P, and/or K), by C for controls and by M for micronutrients. The micronutrient treatment is not addressed here.

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Ecological Archives E092-136-A2

S. Joseph Wright, Joseph B. Yavitt, Nina Wurzbürger, Benjamin L. Turner, Edmund V. J. Tanner, Emma J. Sayer, Louis S. Santiago, Michael Kaspari, Lars O. Hedin, Kyle E. Harms, Milton N. Garcia, and Marife D. Corre. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, and litter production in a lowland tropical forest. *Ecology* 92:1616–1625.

Appendix B. ANOVA tables for the factorial, incomplete block design for the eight response variables analyzed in this article.

TABLE B1. ANOVA for relative growth rates ($\text{RGR} \times 100$) of trees with initial $\text{DBH} \geq 10$ cm.

Between Plots

Source	SS	df	MS	F	P
Between blocks					
Rep	0.341	3	0.114	0.295	0.828
Block(Rep)	0.639	4	0.160	0.415	0.795
Within blocks					
N	0.036	1	0.036	0.093	0.764
P	0.306	1	0.306	0.796	0.384
K	0.346	1	0.346	0.899	0.356
N*P	0.087	1	0.087	0.227	0.640
N*K	1.698	1	1.698	4.411	0.050
P*K	0.014	1	0.014	0.037	0.849
Error	6.929	18	0.385		

Within Plots

Source	SS	df	MS	F	P
Between blocks					
Year*Rep	0.555	3	0.185	3.059	0.055
Yr*Block(Rep)	0.556	4	0.139	2.300	0.098
Within blocks					
Year	0.908	1	0.908	15.030	0.001
Year*N	0.012	1	0.012	0.200	0.660
Year*P	0.480	1	0.480	7.945	0.011
Year*K	0.003	1	0.003	0.055	0.817
Year*N*P	0.000	1	0.000	0.002	0.967
Year*N*K	0.088	1	0.088	1.461	0.242
Year*P*K	0.116	1	0.116	1.925	0.182
Error	1.088	18	0.060		

TABLE B2. ANOVA for relative growth rates (RGR \times 100) of trees with initial DBH between 5.0 and 9.9 cm.

Between Plots

Source	SS	df	MS	F	P
Between blocks					
Rep	0.901	3	0.300	0.695	0.567
Block(Rep)	1.384	4	0.346	0.801	0.540
Within blocks					
N	0.017	1	0.017	0.040	0.844
P	0.000	1	0.000	0.000	0.996
K	0.060	1	0.060	0.139	0.714
N*P	0.342	1	0.342	0.793	0.385
N*K	0.090	1	0.090	0.209	0.653
P*K	0.945	1	0.945	2.190	0.156
Error	7.773	18	0.432		

Within Plots

Source	SS	df	MS	F	P
Between blocks					
Year*Rep	1.088	3	0.363	1.523	0.243
Yr*Block(Rep)	3.997	4	0.999	4.195	0.014
Within blocks					
Year	7.960	1	7.960	33.416	0.000
Year*N	0.321	1	0.321	1.348	0.261
Year*P	0.103	1	0.103	0.431	0.520
Year*K	0.108	1	0.108	0.455	0.509
Year*N*P	0.001	1	0.001	0.006	0.940
Year*N*K	1.624	1	1.624	6.819	0.018
Year*P*K	0.974	1	0.974	4.091	0.058
Error	4.288	18	0.238		

TABLE B3. ANOVA for relative growth rates ($RGR \times 100$) of trees with initial DBH between 2.5 and 4.9 cm.

Between Plots

Source	SS	df	MS	F	P
Among blocks					
Rep	1.284	3	0.428	0.775	0.523
Block(Rep)	3.826	4	0.956	1.733	0.187
Within blocks					
N	0.000	1	0.000	0.000	0.995
P	0.025	1	0.025	0.045	0.835
K	0.140	1	0.140	0.254	0.620
N*P	0.102	1	0.102	0.185	0.673
N*K	0.111	1	0.111	0.201	0.660
P*K	0.342	1	0.342	0.620	0.441
Error	9.936	18	0.552		

Within Plots

Source	SS	df	MS	F	P
Among blocks					
Year*Rep	0.444	3	0.148	0.649	0.594
Yr*Block(Rep)	2.387	4	0.597	2.614	0.070
Within blocks					
Year	23.746	1	23.746	104.01	0.000
Year*N	0.139	1	0.139	0.608	0.446
Year*P	0.053	1	0.053	0.234	0.635
Year*K	1.210	1	1.210	5.301	0.033
Year*N*P	0.727	1	0.727	3.186	0.091
Year*N*K	1.903	1	1.903	8.335	0.010
Year*P*K	0.024	1	0.024	0.106	0.749
Error	4.110	18	0.228		

TABLE B4. ANOVA for relative growth rates ($RGR \times 100$) of trees with initial DBH between 1.0 and 2.4 cm.

Among Plots					
Source	SS	df	MS	F	P
Among blocks					
Rep	10.572	3	3.524	1.718	0.199
Block(Rep)	13.454	4	3.364	1.640	0.208
Within blocks					
N	2.996	1	2.996	1.460	0.242
P	0.189	1	0.189	0.092	0.765
K	0.283	1	0.283	0.138	0.714
N*P	3.428	1	3.428	1.671	0.212
N*K	0.001	1	0.001	0.000	0.984
P*K	1.354	1	1.354	0.660	0.427
Error	36.924	18	2.051		
Within Plots					
Source	SS	df	MS	F	P
Among blocks					
Year*Rep	1.906	3	0.635	1.326	0.297
Yr*Block(Rep)	7.323	4	1.831	3.823	0.020
Within blocks					
Year	44.677	1	44.677	93.294	0.000
Year*N	0.267	1	0.267	0.559	0.465
Year*P	0.527	1	0.527	1.101	0.308
Year*K	1.568	1	1.568	3.275	0.087
Year*N*P	0.802	1	0.802	1.675	0.212
Year*N*K	2.607	1	2.607	5.445	0.031
Year*P*K	0.129	1	0.129	0.270	0.610
Error	8.620	18	0.479		

TABLE B5. ANOVA for fine root biomass density in surface soils (0 to 5 cm depth). G-G represents within subjects *P* values after implementing the Greenhouse-Geisser correction for violations of the compound symmetry assumption of repeated measures ANOVA.

Among Plots

Source	SS	df	MS	F	P
Among blocks					
Rep	0.904	3	0.301	0.549	0.655
Block(rep)	1.027	4	0.257	0.468	0.759
Within blocks					
N	0.263	1	0.263	0.479	0.498
P	0.767	1	0.767	1.396	0.253
K	5.319	1	5.319	9.687	0.006
N*P	0.343	1	0.343	0.625	0.440
N*K	0.022	1	0.022	0.040	0.843
P*K	1.351	1	1.351	2.460	0.134
Error	9.884	18	0.549		

Within Plots

Source	SS	df	MS	F	P	G-G
Between blocks						
Year*Rep	5.157	6	0.859	3.545	0.007	0.013
Year*Block(rep)	1.875	8	0.234	0.967	0.477	0.469
Within blocks						
Year	31.142	2	15.571	64.222	0.000	0.000
Year*N	0.014	2	0.007	0.029	0.972	0.949
Year*P	0.212	2	0.106	0.437	0.650	0.608
Year*K	0.876	2	0.438	1.806	0.179	0.187
Year*N*P	0.122	2	0.061	0.251	0.780	0.732
Year*N*K	1.559	2	0.780	3.215	0.052	0.064
Year*P*K	0.816	2	0.408	1.683	0.200	0.206
Error	8.728	36	0.242			

TABLE B6. ANOVA for fine root biomass density in subsurface soils (5 to 10 cm depth). G-G represents within subjects *P* values after implementing the Greenhouse-Geisser correction for violations of the compound symmetry assumption of repeated measures ANOVA.

Among Plots						
Source	SS	df	MS	F	P	
Among blocks						
Rep	0.763	3	0.254	1.464	0.258	
Block(rep)	0.480	4	0.120	0.691	0.608	
Within blocks						
N	0.094	1	0.094	0.541	0.471	
P	0.049	1	0.049	0.281	0.603	
K	0.206	1	0.206	1.184	0.291	
N*P	0.574	1	0.574	3.305	0.086	
N*K	0.192	1	0.192	1.106	0.307	
P*K	0.294	1	0.294	1.693	0.210	
Error	3.127	18	0.174			
Within Plots						
Source	SS	df	MS	F	P	G-G
Among blocks						
Year*Rep	1.362	6	0.227	2.188	0.067	0.085
Year*Block(rep)	0.536	8	0.067	0.646	0.734	0.702
Within blocks						
Year	13.134	2	6.567	63.301	0.000	0.000
Year*N	0.226	2	0.113	1.089	0.347	0.337
Year*P	0.013	2	0.006	0.061	0.941	0.907
Year*K	0.167	2	0.084	0.805	0.455	0.432
Year*N*P	0.254	2	0.127	1.225	0.306	0.301
Year*N*K	0.141	2	0.070	0.679	0.513	0.483
Year*P*K	0.129	2	0.065	0.622	0.542	0.510
Error	3.735	36	0.104			

TABLE B7. ANOVA for fine litter production. G-G represents within subjects *P* values after implementing the Greenhouse-Geisser correction for violations of the compound symmetry assumption of repeated measures ANOVA.

Among Plots

Source	SS	df	MS	F	P
Among blocks					
Rep	1127.29	3	375.763	4.663	0.014
Block (rep)	211.54	4	52.885	0.656	0.630
Within blocks					
N	141.71	1	141.708	1.758	0.201
P	330.44	1	330.436	4.100	0.058
K	50.336	1	50.336	0.625	0.440
N*P	101.22	1	101.216	1.256	0.277
N*K	0.934	1	0.934	0.012	0.915
P*K	10.92	1	10.922	0.136	0.717
Error	1450.60	18	80.589		

Within Plots

Source	SS	df	MS	F	P	G-G
Among blocks						
Year*Rep	105.32	30	3.511	1.009	0.461	0.446
Yr*Block(rep)	84.672	40	2.117	0.608	0.968	0.837
Within blocks						
Year	60.979	10	6.098	1.753	0.072	0.163
Year*N	66.715	10	6.672	1.918	0.045	0.133
Year*P	49.261	10	4.926	1.416	0.176	0.246
Year*K	44.964	10	4.496	1.292	0.238	0.285
Year*N*P	20.026	10	2.003	0.576	0.833	0.646
Year*N*K	15.867	10	1.587	0.456	0.916	0.728
Year*P*K	14.219	10	1.422	0.409	0.941	0.762
Error	626.241	180	3.479			

TABLE B8. ANOVA for above-ground net primary production.

Among Plots

Source	SS	df	MS	F	P
Among blocks					
REP	271.210	3	90.403	3.459	0.038
BLOCK(REP)	63.379	4	15.845	0.606	0.663
Within blocks					
N	3.992	1	3.992	0.153	0.701
P	14.234	1	14.234	0.545	0.470
K	16.256	1	16.256	0.622	0.441
N*P	83.396	1	83.396	3.191	0.091
N*K	41.033	1	41.033	1.570	0.226
P*K	8.443	1	8.443	0.323	0.577
Error	470.379	18	26.132		

Within Plots

Source	SS	df	MS	F	P
Among blocks					
Year*Rep	10.792	3	3.597	0.655	0.590
Yr*Block(rep)	8.864	4	2.216	0.404	0.803
Within blocks					
Year	8.204	1	8.204	1.495	0.237
Year*N	10.671	1	10.671	1.944	0.180
Year*P	9.049	1	9.049	1.649	0.215
Year*K	10.880	1	10.880	1.982	0.176
Year*N*P	2.726	1	2.726	0.497	0.490
Year*N*K	0.432	1	0.432	0.079	0.782
Year*P*K	0.623	1	0.623	0.114	0.740
Error	98.805	18	5.489		

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S. Joseph Wright, Joseph B. Yavitt, Nina Wurzburger, Benjamin L. Turner, Edmund V. J. Tanner, Emma J. Sayer, Louis S. Santiago, Michael Kaspari, Lars O. Hedin, Kyle E. Harms, Milton N. Garcia, and Marife D. Corre. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, and litter production in a lowland tropical forest. *Ecology* 92:1616–1625.

Supplement

**All data sets analyzed in this article.
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File list

[Data.txt](#)

Description

The data.txt file is a tab-delimited ascii file. It contains all response variables presented in this article. The first row contains the capitalized variable names used in column definitions below.

Column definitions:

1. PLOT – An integer to identify the 32 experimental plots
2. N – A value of 1 (one) identifies an N addition plot. A value of 0 (zero) identifies a plot that did not receive added N.
3. P – A value of 1 (one) identifies a P addition plot. A value of 0 (zero) identifies a plot that did not receive added P.

4. K – A value of 1 (one) identifies a K addition plot. A value of 0 (zero) identifies a plot that did not receive added K.
5. BLOCK – An integer to identify the two blocks within each replicate. In the balanced, incomplete blocks design, one block in each replicate includes the treatments +N, +P, +K and +NPK and the second block in each replicate includes the treatments CONTROL, +NP, +NK and +PK. Values are 0 (zero) or 1 (one).
6. REP - An integer to identify the four replicates of the factorial NPK experiment.
7. RGR14_25 – The relative growth rate between 1997 and 2000 for saplings with DBH between 10 and 24 mm DBH in 1997.
8. RGR46_25 – The relative growth rate between 2000 and 2008 for saplings with DBH between 10 and 24 mm DBH in 2000.
9. RGR14_50 – The relative growth rate between 1997 and 2000 for saplings with DBH between 25 and 49 mm DBH in 1997.
10. RGR46_50 – The relative growth rate between 2000 and 2008 for saplings with DBH between 25 and 49 mm DBH in 2000.
11. RGR14_100 – The relative growth rate between 1997 and 2000 for saplings with DBH between 50 and 99 mm DBH in 1997.
12. RGR46_100 – The relative growth rate between 2000 and 2008 for saplings with DBH between 50 and 99 mm DBH in 2000.
13. RGR14_CAN – The relative growth rate between 1997 and 2000 for saplings with DBH greater than 99 mm DBH in 1997.
14. RGR46_CAN – The relative growth rate between 2000 and 2008 for saplings with DBH greater than 99 mm DBH in 2000.
15. ANPP9800 – Above-ground net primary production between 1998 and 2000. ANPP is the sum of wood and fine litter production. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
16. ANPP0008 – Above-ground net primary production between 2000 and 2008. ANPP is the sum of wood and fine litter production. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
17. F2000_5CM – Fine root biomass between 0 and 5 cm depth in April 2000. Fine roots are < 2 mm in diameter. Units are kg m^{-3} .
18. C2000_5CM – Coarse root biomass between 0 and 5 cm depth in April 2000. Coarse root diameters are between 2 and 5 mm. Units are kg m^{-3} . These data were not analyzed due to the large numbers of zeros, but are included here to facilitate comparison with other studies.
19. F2008_5CM – Fine root biomass between 0 and 5 cm depth in November 2008. Fine roots are < 2 mm in diameter. Units are kg m^{-3} .
20. C2008_5CM – Coarse root biomass between 0 and 5 cm depth in November 2008. Coarse root diameters are between 2 and 5 mm. Units are kg m^{-3} . These data were not analyzed due to the large numbers of zeros, but are included here to facilitate comparison with other studies.

21. F2009_5CM – Fine root biomass between 0 and 5 cm depth in April 2009. Fine roots are < 2 mm in diameter. Units are kg m^{-3} .
22. C2009_5CM – Coarse root biomass between 0 and 5 cm depth in April 2009. Coarse root diameters are between 2 and 5 mm. Units are kg m^{-3} . These data were not analyzed due to the large numbers of zeros, but are included here to facilitate comparison with other studies.
23. F2000_10CM – Fine root biomass between 5 and 10 cm depth in April 2000. Fine roots are < 2 mm in diameter. Units are kg m^{-3} .
24. C2000_10CM – Coarse root biomass between 5 and 10 cm depth in April 2000. Coarse root diameters are between 2 and 5 mm. Units are kg m^{-3} . These data were not analyzed due to the large numbers of zeros, but are included here to facilitate comparison with other studies.
25. F2008_10CM – Fine root biomass between 5 and 10 cm depth in November 2008. Fine roots are < 2 mm in diameter. Units are kg m^{-3} .
26. C2008_10CM – Coarse root biomass between 5 and 10 cm depth in November 2008. Coarse root diameters are between 2 and 5 mm. Units are kg m^{-3} . These data were not analyzed due to the large numbers of zeros, but are included here to facilitate comparison with other studies.
27. F2009_10CM – Fine root biomass between 5 and 10 cm depth in April 2009. Fine roots are < 2 mm in diameter. Units are kg m^{-3} .
28. C2009_10CM – Coarse root biomass between 5 and 10 cm depth in April 2000. Coarse root diameters are between 2 and 5 mm. Units are kg m^{-3} . These data were not analyzed due to the large numbers of zeros, but are included here to facilitate comparison with other studies.
29. L_1998 – Leaf litter production in 1998. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
30. F_1998 – Production of reproductive structures in 1998. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
31. B_1998 – Small branch (< 2 cm in diameter) production in 1998. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
32. D_1998 – Production of frass, dust and other small particles in 1998. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
33. T_1998 – Total fine litter production in 1998. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
34. L_1999 – Leaf litter production in 1999. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
35. F_1999 – Production of reproductive structures in 1999. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
36. B_1999 – Small branch (< 2 cm in diameter) production in 1999. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
37. D_1999 – Production of frass, dust and other small particles in 1999. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
38. T_1999 – Total fine litter production in 1999. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
39. L_2000 – Leaf litter production in 2000. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
40. F_2000 – Production of reproductive structures in 2000. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.

41. B_2000 – Small branch (< 2 cm in diameter) production in 2000. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
42. D_2000 – Production of frass, dust and other small particles in 2000. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
43. T_2000 – Total fine litter production in 2000. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
44. L_2001 – Leaf litter production in 2001. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
45. F_2001 – Production of reproductive structures in 2001. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
46. B_2001 – Small branch (< 2 cm in diameter) production in 2001. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
47. D_2001 – Production of frass, dust and other small particles in 2001. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
48. T_2001 – Total fine litter production in 2001. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
49. L_2002 – Leaf litter production in 2002. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
50. F_2002 – Production of reproductive structures in 2002. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
51. B_2002 – Small branch (< 2 cm in diameter) production in 2002. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
52. D_2002 – Production of frass, dust and other small particles in 2002. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
53. T_2002 – Total fine litter production in 2002. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
54. L_2003 – Leaf litter production in 2003. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
55. F_2003 – Production of reproductive structures in 2003. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
56. B_2003 – Small branch (< 2 cm in diameter) production in 2003. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
57. D_2003 – Production of frass, dust and other small particles in 2003. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
58. T_2003 – Total fine litter production in 2003. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
59. L_2004 – Leaf litter production in 2004. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
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63. T_2004 – Total fine litter production in 2004. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
64. L_2005 – Leaf litter production in 2005. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.
65. F_2005 – Production of reproductive structures in 2005. Units are $\text{Mg ha}^{-1} \text{ yr}^{-1}$.

66. B_2005 – Small branch (< 2 cm in diameter) production in 2005. Units are Mg ha⁻¹ yr⁻¹.
67. D_2005 – Production of frass, dust and other small particles in 2005. Units are Mg ha⁻¹ yr⁻¹.
68. T_2005 – Total fine litter production in 2005. Units are Mg ha⁻¹ yr⁻¹.
69. L_2006 – Leaf litter production in 2006. Units are Mg ha⁻¹ yr⁻¹.
70. F_2006 – Production of reproductive structures in 2006. Units are Mg ha⁻¹ yr⁻¹.
71. B_2006 – Small branch (< 2 cm in diameter) production in 2006. Units are Mg ha⁻¹ yr⁻¹.
72. D_2006 – Production of frass, dust and other small particles in 2006. Units are Mg ha⁻¹ yr⁻¹.
73. T_2006 – Total fine litter production in 2006. Units are Mg ha⁻¹ yr⁻¹.
74. L_2007 – Leaf litter production in 2007. Units are Mg ha⁻¹ yr⁻¹.
75. F_2007 – Production of reproductive structures in 2007. Units are Mg ha⁻¹ yr⁻¹.
76. B_2007 – Small branch (< 2 cm in diameter) production in 2007. Units are Mg ha⁻¹ yr⁻¹.
77. D_2007 – Production of frass, dust and other small particles in 2007. Units are Mg ha⁻¹ yr⁻¹.
78. T_2007 – Total fine litter production in 2007. Units are Mg ha⁻¹ yr⁻¹.
79. L_2008 – Leaf litter production in 2008. Units are Mg ha⁻¹ yr⁻¹.
80. F_2008 – Production of reproductive structures in 2008. Units are Mg ha⁻¹ yr⁻¹.
81. B_2008 – Small branch (< 2 cm in diameter) production in 2008. Units are Mg ha⁻¹ yr⁻¹.
82. D_2008 – Production of frass, dust and other small particles in 2008. Units are Mg ha⁻¹ yr⁻¹.
83. T_2008 – Total fine litter production in 2008. Units are Mg ha⁻¹ yr⁻¹.

There are no missing values.

Check sum values are:

Column 1 (PLOT): Sum equals 586.

Column 5 (BLOCK): Sum equals 48.

Column 7 (RGR14_25): Sum equals 1.168.

Column 83 (T_2008): Sum equals 350.839.

PLOT	N	P	K	BLOCK	REP	RGR14_25	RGR46_25	RGR14_50	RGR46_50																																																																									
RGR14_100	RGR46_100	RGR14_CAN	RGR46_CAN	ANPP9800	ANPP0008	F2000_5CM	C2000_5CM	F2008_5CM	C2008_5CM	F2009_5CM	C2009_5CM	F2000_10CM	C2000_10CM	F2008_10CM	C2008_10CM	F2009_10CM	C2009_10CM	L_1998	F_1998	B_1998	D_1998	T_1998	L_1999	F_1999	B_1999	D_1999	T_1999	L_2000	F_2000	B_2000	D_2000	T_2000	L_2001	F_2001	B_2001	D_2001	T_2001	L_2002	F_2002	B_2002	D_2002	T_2002	L_2003	F_2003	B_2003	D_2003	T_2003	L_2004	F_2004	B_2004	D_2004	T_2004	L_2005	F_2005	B_2005	D_2005	T_2005	L_2006	F_2006	B_2006	D_2006	T_2006	L_2007	F_2007	B_2007	D_2007	T_2007	L_2008	F_2008	B_2008	D_2008	T_2008										
1	0	1	0	1	1	0.035164324	0.013183721	0.026243962	0.011219047	0.027392462	0.015613347	0.009461194	0.011089997	9.067166738	9.678984704	2.670486376	2.290807232	2.215261862	0.391647568	2.298276887	1.130464307	1.269773364	1.397911892	0.835752483	0.405398523	0.572447161	0.958152958	5.135524798	0.265859285	1.243944637	0.734140715	7.379469435	5.739907728	0.505190311	1.5455594	0.557093426	8.347750865	4.674740484	0.403690888	1.106689735	0.446943483	6.632064591	5.355824683	0.548442907	2.240484429	0.448096886	8.592848904	5.380622837	0.621683968	2.612456747	0.637254902	9.252018454	5.028835063	0.561130334	0.950980392	0.465397924	7.006343714	4.698961938	0.511534025	1.134371396	0.452710496	6.797577855	5.113033449	0.230680507	0.933679354	0.476355248	6.747981546	5.893886967	0.334486736	0.914071511	0.633794694	7.776239908	5.175893887	0.316608997	0.982122261	0.652249135	7.126874279	4.807093426	0.411188005	1.144175317	0.485294118	6.847750865
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3	1	1	0	2	1	0.03988521	0.01025097	0.023637633	0.009848843	0.023966362	0.007217186	0.01149687	0.012686202	15.08136518	19.41125582	3.337662338	2.973771327	2.947797301	0.440539852	2.360071301	0.906035141	1.944232238	1.280621339	0.549868432	0.134453782	0.21101774	0.750021221	8.355536332	0.955882353	2.551038062	1.252595156	13.1150519	10.56401384	0.137543253	3.826989619	0.882352941	15.41089965	9.147058824	0.367647059	4.771626298	1.243944637	15.53027682	9.368512111	0.960207612	3.64100346	1.154844291	15.12456747	10.50432526	1.331314879	6.251730104	1.866782007	19.95415225	10.02941176	0.94550173	5.616782007	1.704152249	18.29584775	10.95069204	0.823529412	4.701557093	1.435986159	17.91176471	10.64100346	0.98615917	4.027681661	1.577854671	17.0683391	11.66349481	0.612456747	3.765570934	2.198961938	18.24048443	9.882352941	1.356401384	5.458477509	3.225778547	19.92301038	10.07352941	3.793252595	5.737024221	2.592560554	22.19636678
4	1	0	0	1	1	0.030127966	0.006776646	0.021320476	0.006992031	0.015517366	0.008667509	0.010680565	0.00739397	12.34021252	16.02361213	2.94881589	0.443340973	1.672184025	0.38927086	2.629827689	1.279687633	1.335115865	0.29284441	1.021305492	0.266530855	0.204566675	0.622697564	4.987024221	0.098615917	1.594290657	0.75432526	7.434256055	7.448961938	0.269896194	2.637543253	0.651384083	11.00778547	7.003460208	0.284602076	1.856401384	0.477508651	9.621972318	7.10467128	0.475778547	1.939446367	0.466262976	9.98615917	7.276816609	0.758650519	2.09083045	0.603806228	10.73010381	7.126297578	1.098615917	2.767301038	0.810553633	11.80276817	7.630622837	0.299307958	2.465397924	0.678200692	11.07352941	7.470588235	0.39532872	2.74567474	0.647923875	11.25951557	7.770761246	0.646193772	2.292387543	0.76384083	11.47318339	6.571799308									

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0.834775087	11.46193772					
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0.014941278	0.014360356	0.01095048	13.40999877	11.29758844	2.346829641	0 1.361684068
0.05432476	1.823444529	0.985485103	1.606060606	2.823784059	1.18037518	0.489262372 0
0.119174943	6.642445213	0.692618224	2.577854671	0.647058824	10.55997693	7.235294118
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0.511534025	7.178200692	5.61822376	0.405420992	0.505767013	0.364475202	6.893886967
6 0 0	0 2 1	0.039640018	0.023759381	0.034864676	0.015434838	0.018591942
0.008304398	0.006769896	0.004563185	9.002030485	9.812050666	3.387827858	0.392666157
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0.478662053	0.780853518	0.398500577	6.433679354	6.540369089	0.764129181	1.103806228
0.493079585	8.901384083	6.272202999	0.946943483	1.602652826	0.60899654	9.430795848
5.265282584	0.691464821	1.787197232	0.429065744	8.173010381	5.314878893	1.937716263
1.625720877	0.459630911	9.320645905	6.137254902	0.584198385	2.543829296	0.69088812
9.956170704	4.419261822	1.248558247	1.250288351	0.60438293	7.371395617	4.139561707
2.132064591	1.698385236	0.427912341	8.389273356	4.023068051	0.853517878	0.674163783
0.412918108	5.96366782					
7 0 1	1 2 1	0.047526912	0.010623798	0.0444662	0.013797533	0.028718471
0.004249543	0.00900551	0.006452238	14.04005277	13.53994279	3.450725745	1.10236822
1.800016976	2.06094559	2.195059842	0.890077243	1.489177489	0.685714286	0.94915542
0.280451575	0 0.197266786	5.42733564	1.376297578	1.936851211	0.964532872	9.705017301
8.907439446	0.665224913	1.642733564	0.781141869	11.99653979	6.875432526	1.365051903
2.977508651	0.660899654	11.87889273	7.043252595	1.325259516	1.503460208	0.623702422
10.49567474	6.487889273	0.778546713	2.298442907	0.785467128	10.35034602	7.139273356
0.402249135	2.698096886	1.53200692	11.7716263	6.884083045	0.118512111	2.106401384
0.732698962	9.841695502	8.061418685	0.418685121	2.662629758	1.514705882	12.43252595
7.972318339	0.435121107	2.468858131	1.469723183	11.57612457	6.857266436	0.592560554
2.954152249	1.62283737	12.02681661	7.302768166	2.107266436	2.78200692	1.278546713
13.47058824						
9 1 0	1 1 2	0.054761745	0.028595687	0.029204437	0.014806536	0.016688598
0.010026327	0.007575684	0.005221726	14.14607653	13.81604305	2.913674561	0.976063153
1.996095408	0.860198625	2.192343604	1.157117392	1.20091673	1.199643494	1.20091673
0.531364061	0.308123249	0.314234785	4.971741638	3.253171857	1.841407151	0.877739331
10.94405998	6.602076125	0.970011534	3.715974625	0.555074971	11.84313725	5.555940023
2.941176471	2.352941176	0.513264129	11.3633218	6.662629758	1.734717416	2.514417532
0.638985006	11.55074971	5.982122261	1.802768166	2.250288351	0.833333333	10.86851211
5.909457901	2.742214533	2.299307958	0.666666667	11.61764706	5.956170704	1.619953864
2.367358708	0.935409458	10.80968858	6.53633218	2.06343714	2.865051903	1.293540946
12.62572088	6.280853518	1.464244521	3.040369089	0.953863899	11.73875433	5.469146482
1.817474048	2.735294118	1.171568627	11.19925029	5.059400231	2.186851211	1.670703576
0.689734717	9.606689735					
10 1 0	1 2 1	0.050611345	0.034688142	0.026722859	0.021409092	0.014422586
0.015322396	0.01517893	0.017774679	11.49384607	12.64829018	2.909600204	1.377132671
1.842458195	0.715898481	2.105593753	0.872930991	0.876496053	1.988031576	1.083269672
0.433070198	0.959171547	0.667855021	5.332756632	1.576124567	2.034602076	1.070357555
10.01384083	5.902537486	0.385813149	2.082468281	0.543829296	8.914648212	4.452133795

0.4544406	1.820645905	0.416955017	7.144175317	4.685121107	0.938869666	2.042675894
0.414071511	8.080738178	5.005767013	0.889273356	2.301614764	0.561130334	8.757785467
5.472318339	1.05449827	2.564302191	0.66349481	9.75461361	4.528258362	0.377739331
1.444059977	0.465397924	6.798154556	5.244521338	0.989042676	1.950980392	0.600346021
8.675317186	5.611880046	0.711649366	3.074971165	1.055363322	10.4538639	4.99538639
0.975201845	1.837370242	1.314878893	9.12283737	8.470011534	0.769896194	2.385813149
1.130334487	12.75605536					
11 1 0	0 2 2	0.038695362	0.008346701	0.031313135	0.0059575	0.038350068
0.011465577	0.02193283	0.011455998	10.07233655	11.74505545	5.164502165	1.222307105
0.687717511	0.445463034	2.287411934	1.283252695	1.475681182	0.392920805	0.838808251
0.32730668	0.350394703	0.238010356	3.784602076	0.08650519	1.115051903	0.491349481
5.477508651	5.801038062	0.25 1.466262976	0.584775087	8.102076125	4.405709343	0.648788927
0.926470588	0.359861592	6.34083045	5.533737024	0.432525952	1.262110727	0.379757785
7.608131488	5.547577855	0.419550173	1.569204152	0.603806228	8.140138408	5.028546713
0.41349481	1.343425606	0.62283737	7.408304498	4.917820069	1.083044983	1.035467128
0.549307958	7.381487889	4.883217993	0.423875433	1.152249135	0.605536332	6.672145329
5.321799308	1.92733564	1.64532872	0.801038062	9.69550173	4.993079585	0.777681661
2.364186851	0.902249135	9.037197232	4.669550173	0.204152249	1.506055363	0.690311419
7.070069204						
12 0 0	0 1 2	0.038058504	0.027802844	0.028286139	0.024072889	0.017741762
0.019651025	0.022362884	0.013631357	10.92527741	11.60283247	4.090909091	0.59714795
2.014090485	0.823189882	1.601731602	0.604532722	1.093710211	1.585943468	0.656650539
0.465665054	0.178592649	0.825736355	6.076701269	0.183967705	1.678777393	0.847750865
8.787197232	5.69550173	0.273356401	1.319492503	0.587081892	7.875432526	5.624567474
0.270472895	1.399653979	0.468858131	7.76355248	5.567474048	0.250288351	1.698961938
0.404267589	7.920991926	4.873702422	0.293540946	1.678777393	0.448096886	7.294117647
4.651095732	0.638985006	1.491349481	0.491349481	7.2727797	5.230103806	0.142445213
1.075547866	0.477508651	6.925605536	5.35467128	0.50461361	1.701845444	0.602652826
8.083044983	5.703575548	0.410611303	2.333333333	0.874855825	9.322376009	6.089388697
0.481545559	2.261822376	0.987312572	9.820069204	5.918685121	0.848904268	1.593425606
0.638985006	9					
13 0 1	1 1 2	0.0254226	0.012365457	0.018988689	0.010230742	0.016824468
0.011146739	0.018973258	0.015435091	15.79181772	16.51676531	2.606315253	2.075375605
0.467192938	0.416942535	1.562855445	0.878363467	1.2179781	0.340208811	0.353790001
0.355996944	0.548680078	0.175027587	5.910034602	0.703575548	1.478662053	0.578431373
8.670703576	5.94982699	1.861014994	1.927912341	0.491349481	10.23010381	6.218569781
1.098615917	1.452710496	0.360438293	9.130334487	6.141868512	1.121107266	1.898500577
0.457900807	9.619377163	5.657439446	1.478085352	1.533448674	0.576701269	9.24567474
5.953575548	2.376009227	1.784025375	0.717128028	10.83073818	4.873125721	1.937716263
2.025951557	0.472318339	9.303344867	5.353517878	0.970588235	2.039792388	0.574394464
8.920991926	5.022491349	1.438292964	1.861591696	0.739331027	9.080161476	4.554209919
3.332179931	1.741637832	0.880622837	10.34832757	4.554209919	2.126874279	1.747404844
0.693194925	9.121683968					
14 0 1	0 2 2	0.032307964	0.006108858	0.028245522	0.011274393	0.014363003
0.008575585	0.011843983	0.009902776	8.913713487	10.09143481	3.048892284	0.987522282
1.113487819	0.356336474	1.868941516	0.834394364	1.429590018	1.255411255	0.49163908
0.323232323	0.563279857	0.497411086	4.191464821	0.816608997	1.069204152	0.585928489
6.663206459	4.411188005	0.647635525	1.038638985	0.422145329	6.519607843	4.095155709
1.30449827	1.467704729	0.367358708	7.234717416	4.457900807	2.276239908	1.208765859
0.295847751	8.238754325	4.617647059	1.579008074	1.257208766	0.725490196	8.179354095
3.991926182	1.132641292	1.443483276	0.489042676	7.057093426	4.447520185	0.955594002
2.065167243	0.396770473	7.865051903	4.789504037	0.604959631	1.346597463	0.611880046
7.308535179	4.576701269	0.62283737	1.037485582	0.635524798	6.87716263	4.316608997
2.176470588	1.602076125	0.721453287	8.816608997	3.855247982	1.220299885	1.445790081

0.606113033	7.12745098									
15	1	1	0	1	2	0.04216416	0.028441679	0.030547119	0.013603058	0.018757534
0.01027616	0.013468702	0.012214748	10.20325846	12.57873251	2.673287497	0.880315763				
1.769629064	0.535777948	1.629063747	1.069688481	1.107715814	1.206773619	0.578049402				
0.077582548	0.492487904	0.428656311	4.717128028	0.866782007	1.577854671	0.686851211				
7.848615917	5.290657439	2.041522491	0.938581315	0.5	8.770761246	4.885813149	0.753460208			
1.187716263	0.390138408	7.217128028	4.780276817	1.657439446	1.629757785	0.461937716				
8.529411765	4.190311419	0.855536332	1.924740484	0.573529412	7.544117647	4.270761246				
0.35899654	0.758650519	0.562283737	5.950692042	4.770761246	0.453287197	2.031141869				
1.083044983	8.277681661	4.896193772	0.369377163	3.327854671	0.75432526	9.30449827				
3.634083045	0.369377163	1.149653979	0.410899654	5.564013841	4.739619377	2.151384083				
1.224913495	0.790657439	8.906574394	4.46366782	1.375432526	0.719723183	0.508650519				
7.067474048										
17	1	1	1	2	2	0.041963635	0.014225557	0.029656936	0.013552931	0.022474418
0.006868836	0.007230368	0.006150836	14.82938045	15.69536414	2.333842628	0	0.915202445			
0.408454291	1.355912062	0.485697309	0.625159155	0.714795009	0.532212885	0.390968509				
0.308462779	0.164502165	7.005190311	1.735870819	2.84083045	1.254901961	12.83679354				
7.373414072	1.687139562	3.621683968	0.9544406	13.6366782	7.214532872	2.192041522				
3.092848904	0.667820069	13.16724337	6.599192618	2.21799308	3.427912341	0.625720877				
12.87081892	6.761822376	2.837370242	2.88177624	0.928489043	13.4094579	6.058823529				
2.44982699	3.14071511	0.925605536	12.57497116	6.238754325	0.735870819	2.233564014				
0.724913495	9.933102653	8.108419839	0.970588235	4.185121107	1.234140715	14.43483276				
6.264705882	1.267877739	5.621972318	1.944348328	15.04267589	6.686851211	2.385813149				
5.779123414	2.509803922	17.3615917	6.8411188	2.76384083	4.064878893	1.317474048				
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18	0	0	1	2	2	0.038406855	0.010369582	0.023970405	0.007225273	0.020403108
0.009185889	0.025930676	0.010793052	11.04247096	10.7094912	3.290807232	0.285459638				
1.918003565	0.382819795	2.629148629	1.328410152	1.284441049	0.605551311	0.541040659				
0.658517953	0.298955946	0	3.961361015	0.14994233	1.688581315	0.555940023	6.355824683			
5.093425606	0.203575548	1.618800461	0.554209919	7.470011534	4.968858131	0.844867359				
1.036908881	0.373702422	7.224336794	4.382929642	0.453863899	0.81372549	0.362168397				
6.012687428	4.32295271	0.565743945	0.644752018	0.385813149	5.919261822	4.303344867				
0.257208766	0.677623991	0.408304498	5.646482122	4.090542099	0.226643599	0.880046136				
0.354094579	5.5455594	3.888696655	0.204152249	0.780853518	0.460207612	5.322376009				
4.664359862	0.431372549	0.734717416	0.553056517	6.383506344	4.149365629	0.364475202				
0.961361015	0.612456747	6.087658593	4.838523645	0.273356401	0.732987313	0.593425606				
6.438292964										
19	0	0	1	1	3	0.014845303	0.012499498	0.013633423	0.006447685	0.00770649
0.008434422	0.012360134	0.012953651	13.13969949	18.5273952	2.875273746	0.676954418				
0.433749257	0.534250064	1.827009592	1.161701044	0.609116374	0.10236822	0.217638571				
0.208131738	0.208810797	0.637806638	5.809688581	1.344290657	2.662629758	0.834775087				
10.65138408	7.121972318	0.438581315	2.064878893	0.852941176	10.4783737	6.978373702				
1.475778547	2.097750865	0.484429066	11.03633218	6.979238754	1.10467128	2.57266436				
0.576124567	11.23269896	6.896193772	1.108131488	2.049307958	0.588235294	10.64186851				
6.635813149	2.120242215	3.136678201	0.721453287	12.61418685	7.164359862	1.498269896				
4.019031142	0.756920415	13.43858131	7.335640138	1.588235294	3.137543253	1.15916955				
13.14273356	5.953287197	1.656574394	3.332179931	1.375432526	11.68858131	6.80017301				
1.402249135	2.862456747	1.458477509	12.5233564	5.385813149	1.043252595	3.057958478				
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20	1	1	1	1	3	0.013298362	0.027453319	0.013572704	0.014325329	0.011342502
0.012300247	0.012051542	0.017287462	21.20650754	22.80513504	2.457601222	0.493251846	1.653509889			
0.25244037	0.948306595	0.194211018	0.60758849	0	0.432560903	0.453102453	0.233766234			
0.231729055	8.746828143	0.29527105	4.142445213	1.400807382	14.58535179	11.02941176	0.389273356			
4.988465975	1.211072664	17.61822376	8.761245675	0.054786621	4.444636678	1.133794694	14.39446367			

9.883506344	0.378892734	5.055940023	1.456747405	16.77508651	9.205882353	0.10438293	3.919838524
1.607843137	14.83794694	10.21683968	0.30911188	4.267589389	1.281430219	16.07497116	10.23154556
0.118800461	3.901960784	1.319492503	15.53143022	10.9106113	0.451557093	3.728373702	1.692618224
16.52941176	11.12975779	0.425028835	5.451557093	2.591695502	19.37024221	10.08823529	1.265282584
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21 0 1	1 2 3	0.040226396	0.027878864	0.029820313	0.019095747	0.037863147	0.013336099
0.019754465	0.016678007	15.7097663	16.64573818	3.019438078	1.403955522	1.649605297	0.745267804
1.841303794	1.161531279	0.957728546	2.562006621	0.484508955	0.384008149	0.801459978	0.208810797
6.594290657	3.37283737	1.857266436	0.896193772	12.72058824	6.528546713	0.269896194	2.095155709
0.680795848	9.574394464	7.051903114	2.673875433	1.69982699	0.440311419	11.86591696	7.201557093
1.0683391	2.031141869	0.461937716	10.76297578	7.976643599	2.644463668	2.596020761	1.065743945
14.28287197	7.575259516	2.801038062	3.057958478	0.626297578	14.06055363	6.471453287	1.296712803
4.302768166	0.621107266	12.62283737	7.349480969	0.625432526	2.98615917	0.821799308	11.67906574
7.403979239	2.227508651	2.737889273	0.923875433	13.30709343	5.842560554	2.570934256	2.846020761
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22 1 1	0 2 3	0.055614522	0.013585283	0.025822246	0.006005088	0.012817632	0.006621897
0.012092713	0.008995253	21.048261	23.19065511	3.438757321	0	2.382480265	0.399966047
2.774297598	0.627620745	1.268143621	0.424497072	0.555131143	0.356336474	0	6.957612457
3.69550173	4.89532872	1.410034602	16.95847751	10.7517301	1.666089965	5.064878893	1.538927336
19.0216263	8.256920415	3.433391003	4.719723183	0.813148789	17.22318339	10.28373702	2.363321799
7.467128028	1.091695502	21.20588235	9.076124567	2.934256055	6.125432526	1.044982699	19.18079585
7.594290657	4.936851211	6.155709343	1.176470588	19.8633218	7.899653979	3.019031142	4.623702422
0.929930796	16.43771626	9.32266436	0.589965398	4.530276817	1.333044983	15.72404844	9.970588235
1.525086505	8.546712803	1.916089965	22.09948097	8.428200692	2.576124567	7.110726644	1.810553633
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23 1 0	0 1 3	0.030332168	0.010634386	0.033953002	0.015174912	0.018166644	0.015823883
0.013887935	0.010639316	10.61793878	11.77376687	3.811900518	2.193022664	1.559460148	0.726254138
1.756557168	0.785671844	0.998981411	0.620066208	1.185128597	1.164756812	0.72421696	0
7.366782007	0.143598616	0.506920415	0.942906574	8.960207612	7.520761246	0.140138408	0.636678201
0.548442907	8.846020761	8.153979239	0.188581315	1.283737024	0.520761246	10.14705882	8.041522491
0.302768166	1.487889273	0.439446367	10.2716263	6.487889273	0.461937716	0.870242215	0.577854671
8.397923875	7.813148789	0.846020761	2.299307958	0.697231834	11.65570934	7.884083045	0.088235294
1.948096886	0.638408304	10.55882353	6.303633218	0.12283737	2.026816609	0.728373702	9.147058824
6.856401384	0.05017301	2.65916955	0.901384083	10.46712803	4.778546713	0.546712803	0.788927336
0.676470588	6.790657439	6.501730104	0.173010381	1.1816609	0.792387543	8.648788927	
24 0 1	0 1 3	0.02244402	0.017824127	0.014050984	0.009899638	0.00462185	0.011119272
0.002971117	0.005616039	15.40852125	18.86995473	3.127832951	0.727272727	3.247941601	0.642220525
2.044834904	0.907902555	1.620066208	0.280112045	1.570494865	0.903149138	0.391477803	0
7.416955017	0.60899654	5.075259516	1.35899654	14.46020761	6.868512111	0.666955017	5.113321799
0.752595156	13.40138408	6.863321799	1.371972318	3.950692042	0.833910035	13.01989619	7.253460208
1.494809689	4.955017301	1.40916955	15.11245675	7.293252595	2.55449827	4.051038062	2.134948097
16.03373702	10.84602076	2.25432526	7.134948097	1.556228374	21.79152249	7.717128028	1.148788927
6.824394464	1.338235294	17.02854671	7.655709343	0.337370242	6.293252595	1.979238754	15.57352941
7.450692042	0.937716263	6.524221453	2.238754325	17.15138408	7.692906574	0.954152249	7.807093426
2.522491349	18.9766436	6.348615917	1.824394464	4.841695502	1.897058824	14.91176471	
26 0 0	0 2 3	0.027484978	0.00913327	0.021839981	0.008403275	0.030626183	0.007828025
0.011469772	0.007457956	15.73613893	13.69002009	2.441303794	0	1.474747475	0.81928529
1.408539173	0.964264494	1.556659027	0.197860963	0.551905611	0.548510313	0	0.29980477
8.192041522	0.423010381	3.185121107	1.247404844	13.04757785	9.441176471	0.32266436	2.364186851
0.753460208	12.88148789	9.191176471	0.567474048	2.272491349	0.664359862	12.69550173	9.285467128
0.430795848	1.966262976	0.631487889	12.31401384	8.301038062	0.452422145	2.598615917	0.85467128
12.2067474	11.76038062	0.62283737	4.156574394	1.035467128	17.57525952	7.855536332	0.165224913
1.997404844	0.602076125	10.62024221	7.522491349	0.198961938	1.493079585	0.900519031	9.942041522
7.311418685	0.288062284	0.973183391	0.788062284	9.360726644	5.367647059	0.484429066	1.500865052

0.742214533	8.095155709	8.570069204	0.517301038	1.214532872	0.878027682	11.1799308			
27 1 0	1 2 3	0.034332175	0.020254015	0.026963403	0.016557761	0.009500131	0.016065836		
0.01306544	0.011424402	14.57000366	13.56040622	2.560988032	0	1.350819116	0.733723793		
1.719887955	0.525252525	0.723707665	1.426788897	0.413547237	0.326797386	0	0	7.837370242	
1.026528258	0.961937716	1.369665513	11.19550173	9.388119954	0.521337947	2.27739331	1.16378316		
13.35063437	7.621683968	0.350634371	1.493079585	0.655132641	10.12053057	8.275663206	1.017301038		
1.521914648	0.599192618	11.41407151	6.950403691	1.012110727	1.403690888	0.955017301	10.32122261		
5.987312572	1.044405998	2.15455594	1.031141869	10.21741638	8.071510957	0.776816609	2.761822376		
1.34544406	12.955594	6.389273356	0.290080738	1.580161476	1.462802768	9.775951557	6.950980392		
0.660322953	1.843713956	1.733564014	11.18858131	7.14071511	1.287485582	2.458189158	1.539792388		
12.42618224	7.359861592	0.747404844	2.428489043	1.319492503	11.85524798				
28 1 0	0 1 4	0.033324186	0.020246149	0.022553317	0.013514199	0.014977607	0.01468141		
0.016333132	0.013790484	15.67481046	18.05237063	2.154570919	0.389355742	2.455818691	0.521347933		
1.475426534	0.306086071	0.79908327	0.664374841	0.559714795	0	0	0	7.5	0.55017301
3.959630911	1.232987313	13.24279123	7.882352941	1.676470588	3.786620531	0.955594002	14.30103806		
5.92733564	2.14994233	3.346020761	0.572087659	11.99538639	6.405420992	2.335063437	3.667243368		
0.5911188	12.9988466	6.916378316	3.212226067	4.02710496	0.841983852	14.99769319	5.756632065		
2.166666667	5.575547866	0.80449827	14.30334487	6.938869666	2.193194925	4.781430219	0.843713956		
14.71107266	6.919261822	2.8183391	4.666666667	1.061707036	15.26989619	7.338811995	3.417820069		
4.903114187	1.519031142	17.19953864	6.746828143	3.155132641	3.905420992	1.460207612	15.26758939		
6.431372549	3.413206459	4.307093426	1.302191465	15.4538639					
29 1 1	1 1 4	0.049991279	0.031874254	0.020422849	0.018116858	0.013491316	0.018465683		
0.010244828	0.00838097	12.38920753	15.7293342	2.032085561	1.401578813	0.943722944	0.024615907		
0.839317545	0.604872252	0.995925643	1.838298956	0.866819455	0.285544521	0.752058399	0		
5.685121107	0.258362168	2.106113033	0.734140715	8.783737024	5.765282584	1.324682814	3.196655133		
0.871395617	11.15801615	5.932525952	2.19550173	1.869088812	0.650519031	10.64763552	5.212802768		
1.052479815	2.539792388	0.719723183	9.524798155	7.008650519	1.329873126	3.398500577	0.862745098		
12.59976932	6.085351788	1.66378316	5.190311419	1.11361015	14.05305652	8.357554787	0.592272203		
3.873702422	1.337370242	14.16089965	6.511245675	1.252018454	4.67704729	1.502595156	13.9083045		
8.418685121	1.401384083	5.016724337	1.528258362	16.3650519	7.908304498	1.514417532	3.528835063		
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30 0 1	0 1 4	0.030476885	0.017733507	0.033397943	0.014460998	0.015512981	0.017699908		
0.007088713	0.009622168	13.71682015	17.10313311	4.010949834	0.851031322	3.05118411	0.472625414		
1.500721501	1.487310076	1.92793481	2.652915712	2.04074357	0.421865716	0.474323063	0.363296834		
7.871972318	0.661476355	1.779123414	1.158016148	11.47058824	10.15628604	1.434832757	2.544982699		
0.899653979	15.03575548	8.718569781	1.50461361	2.914071511	0.683391003	13.82064591	8.889273356		
1.517301038	4.19550173	0.601499423	15.20357555	8.227797001	3.066320646	3.314302191	0.787773933		
15.39619377	8.690311419	2.113033449	4.846597463	0.866205306	16.51614764	9.19088812	1.080161476		
3.761245675	0.964821223	14.97404844	8.9544406	1.456170704	4.578431373	1.021337947	15.99769319		
8.58650519	1.168973472	3.196078431	0.887543253	13.83910035	9.467128028	1.520472895	3.399365629		
1.038062284	15.43252595	7.896770473	1.733564014	2.847174164	0.956747405	13.43425606			
32 0 0	1 1 4	0.063457027	0.052389672	0.030112269	0.023158747	0.023566098	0.019356954		
0.009624237	0.014156596	33.82866313	21.07006707	2.540870894	1.886681946	2.419489008	0.781257958		
1.982004923	0.899414311	1.025974026	0.40565317	0.915202445	0.823529412	0	0	7.089965398	
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19.6366782	9.130622837	0.251730104	4.654844291	1.009515571	15.0467128	7.099480969	0.278546713		
6.522491349	1.480968858	15.38148789	10.74307958	0.292387543	4.009515571	1.071799308	16.11678201		
4.705017301	0.131487889	4.569204152	0.9316609	10.33737024	5.583910035	0.188581315	3.514705882		
1.01816609	10.22750865	4.5	0.17733564	1.546712803	0.551903114	6.775951557	3.770761246		
0.099480969	1.115916955	0.538062284	5.524221453	4.015570934	0.155709343	1.021626298	0.755190311		
5.948096886	4.415224913	0.15916955	0.902249135	0.448096886	5.924740484				
33 0 1	1 2 4	0.037900218	0.009980958	0.028733345	0.007382848	0.022415476	0.011060568		
0.012800069	0.009905106	12.60189808	11.31764832	2.0710466	1.101349631	0.828452593	0.588914354		
1.220609456	0.637297343	0.754978355	1.048943214	0.801799508	0	0	0	6.969723183	0.298442907

2.597750865	0.933391003	10.79930796	7.888408304	0.212802768	2.551038062	1.369377163	12.0216263				
7.019896194	0.14100346	3.040657439	0.632352941	10.83391003	7.424740484	0.152249135	3.264705882				
0.950692042	11.79238754	7.081314879	0.400519031	2.55017301	0.793252595	10.82525952	6.510380623				
0.221453287	2.097750865	0.668685121	9.498269896	6.534602076	0.14532872	2.073529412	0.615916955				
9.369377163	5.359861592	0.142733564	1.885813149	0.743079585	7.993079585	6.003460208	0.288927336				
2.256920415	0.737889273	9.287197232	6.243944637	0.243079585	2.323529412	1.039792388	9.850346021				
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34	1	0	1	2	4	0.021039503	0.01626522	0.016788852	0.011959287	0.019645651	0.015787567
0.019755086	0.010197029	12.2679617	13.11120831	3.063661828	1.29004329	2.377557083	0.733554028				
1.051014345	0.640522876	1.393175452	0.505984212	1.31024531	0.852898735	0	0	5.121107266			
0.475201845	1.28200692	0.765859285	7.644175317	6.490196078	0.824106113	3.168973472	0.697231834				
11.1805075	5.622260669	0.830449827	2.985582468	0.58650519	10.02479815	6.650519031	1.79527105				
2.348327566	0.688581315	11.48269896	6.210495963	1.296424452	2.485005767	0.637831603	10.62975779				
4.513264129	0.925605536	1.621107266	0.505190311	7.565167243	4.382352941	3.188004614	1.457324106				
0.588235294	9.615916955	4.453863899	1.476355248	2.572087659	0.707035755	9.151672434	4.976931949				
0.757208766	3.807958478	0.980968858	10.55651672	4.906574394	1.544982699	3.109573241	0.933679354				
10.49480969	4.598039216	0.74567474	2.546712803	0.82295271	8.728950404						
35	1	1	0	2	4	0.067882137	0.038378214	0.037052949	0.015501777	0.023220903	0.01385195
0.018650066	0.019720762	16.11090557	18.54678957	3.016806723	2.840845429	1.099397335	0.550547492				
1.088532383	0.433239963	0.675324675	0.596553773	0.809948222	0.772939479	0	0	6.699538639			
2.267589389	2.293540946	1.163206459	12.42387543	7.583621684	1.525951557	3.660899654	0.926758939				
13.69723183	6.612456747	1.243367935	2.989042676	0.689158016	11.53402537	7.318915802	2.453863899				
2.746828143	0.756632065	13.27623991	7.148788927	1.951557093	3.851787774	1.130334487	14.08246828				
8.440599769	1.04094579	8.044982699	1.805651672	19.33217993	5.802768166	1.953863899	3.538062284				
0.856401384	12.15109573	5.733564014	0.782583622	2.409457901	1.158592849	10.05420992	6.453863899				
2.747404844	3.182237601	1.250865052	13.6343714	7.404267589	0.73644752	3.459630911	1.438292964				
12.77912341	6.249134948	3.029988466	3.658592849	1.219723183	14.15743945						
36	0	0	0	2	4	0.034610745	0.028550572	0.025694153	0.018537001	0.019386842	0.010594626
0.0129883	0.008907501	19.41963455	15.81899237	3.484593838	0	3.103132162	1.431117902				
1.708174179	0.388252271	0.930990578	0.859943978	0.862745098	0.23223835	0	0	9.143598616			
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16.98788927	6.676470588	0.151384083	4.043252595	0.666089965	11.53719723	7.94550173	0.320069204				
3.845155709	0.752595156	12.8633218	7.984429066	1.421280277	4.324394464	1.23183391	14.96193772				
8.826124567	0.48615917	4.64100346	1.384948097	15.33823529	8.425605536	0.910899654	3.588235294				
1.080449827	14.00519031	8.192906574	0.214532872	1.784602076	0.912629758	11.00432526	8.775951557				
0.672145329	3.455017301	1.570069204	14.47318339	7.638408304	0.478373702	4.673010381	1.958477509				
14.7482699	7.116782007	0.729238754	2.829584775	1.524221453	12.19982699						