Forest Ecology and Management 376 (2016) 126–134

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Alternative field fertilization techniques to promote restoration of leguminous *Acacia koa* on contrasting tropical sites

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ARTICLE INFO

Article history:
Received 13 April 2016
Received in revised form 4 June 2016
Accepted 6 June 2016

Keywords:
Controlled-release fertilizer
Nitrogen
Nutrient management
Outplanting
Phosphorus
Tropical forest restoration

ABSTRACT

Field fertilization can promote early growth and survival of planted trees on degraded pastures and agricultural lands where low soil fertility and high herbaceous competition inhibit regeneration success. Controlled-release fertilizers (CRF) may improve the effectiveness of fertilization relative to that of immediately available fertilizers (IAF) because CRF gradually release nutrients directly to the root zone, thereby limiting nutrient losses. Despite past research in boreal and temperate landscapes, few studies have tested the efficacy of similar applications in tropical systems where year-round high temperatures can increase release rates of CRF and intensity of competing vegetation. On two contrasting sites on the Island of Hawaii, USA, we evaluated early growth and survival responses of koa (*Acacia koa* Gray), a fast-growing legume, using ten treatments: a control, four IAF formulations, and five rates of polymer-coated CRF (15N-9P-12K; 15–75 g). At Pahala, a productive site, we detected no significant growth, survival, or foliar nitrogen (N) or phosphorous (P) responses to the fertilizer treatments. At Volcano, a rockier and cooler site on younger soil, height increased by 36–49% for the highest performing CRF and IAF relative to the control; diameter likewise increased by 55–92%. Growth responses appeared to be a result of P fertilization rather than N. The highest performing IAF had a reduced survival rate relative to the lowest CRF (46% vs. 83%). Although total nutrient application rates were much lower for CRF, our results suggest that on tropical restoration sites, CRF may promote seedling performance at least equally to that of IAF. There is a need to more carefully evaluate the effects of site-specific interactions that may determine field fertilizer responses, across a range of genera and functional groups.

1. Introduction

Newly planted forest tree seedlings can benefit from field fertilization in both restoration and plantation settings. Fertilization may amplify the effects of other silvicultural inputs, such as herbaceous control (Sloan and Jacobs, 2013) and site preparation, leading to increased early growth and survival. Positive outcomes from field fertilization are dependent on climate, soils, and the species fertilized and responses have been mixed in temperate (Bendfeldt et al., 2001; Fox et al., 2007; Jacobs et al., 2005), boreal (Brand, 1991; Sloan and Jacobs, 2013; Sloan et al., 2016), and tropical regions (Lawrence, 2003; Schönau and Herbert, 1989).

Fertilizer dosage and chemical formulation influence the effectiveness of the application. Growth of forest trees is most commonly limited by nitrogen (N) or phosphorous (P). Fertilizer that provides P on an N-limited site, or vice versa, may produce negligible results, as in the case many *Eucalyptus* spp. (Schönau and Herbert, 1989), where response to a given nutrient is species and site specific. Similar effects occur in loblolly pine (*Pinus taeda* L.), in which P is limiting and an effective addition at planting on wet sites in the southern USA but ineffective on many other sites where both N and P are limiting (Fox et al., 2007). Similar effects occur in N-fixing seedlings and mature trees (Binkley et al., 2003; Otsamo et al., 1995; Scowcroft and Silva, 2005; Scowcroft et al., 2007), but a lack of correlation between available soil P resources and growth of legumes in Costa Rica suggests inconsistency in responses across species (Baribault et al., 2012). *Acacia* spp., for example, differ in their preference for nitrate versus ammonium and nodulation response to P fertilization (Sun et al., 1992; Pfautsch et al., 2009), suggesting the importance of species-specific fertilization applications.

In addition to the importance of dosage and formulation, fertilizer type can also determine the effectiveness of the application. The two most common fertilizer types for field plantings are controlled-release fertilizers (CRF) and immediately available

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http://dx.doi.org/10.1016/j.foreco.2016.06.012
0378-1127/

fertilizers (IAF). CRF provide a constant source of nutrition to outplanted seedlings over an extended period (Jacobs et al., 2005), determined by the release rate of a given CRF, which can vary from 3 to 18 months. With polymer-coated CRF, water diffuses through a semi-permeable membrane and releases nutrients (Goertz, 1993). Although water is the initial conduit for nutrient release, soil temperature is the mechanism controlling release rates; higher soil temperatures result in faster release rates in polymer-coated CRF (Kochba et al., 1990). This system may result in an efficient delivery system of nutrients to outplanted seedlings compared to IAF, with reduced nutrient loss out of the system or to competing vegetation (Sloan and Jacobs, 2013). Recent work (Sloan et al., 2016), however, suggests that a high proportion of applied N in both CRF and IAF is lost from the system and planted trees recover only a small proportion. Nevertheless, CRF may maintain or increase growth and survival of planted trees at lower total fertilization rates than IAF (Sloan et al., 2016), which is subject to high rates of nutrient loss through volatilization, leaching, and non-target uptake by competing vegetation following broadcast application (Chang et al., 1996; Imo and Timmer, 1998; Ramsey et al., 2003; Sloan and Jacobs, 2013; Staples et al., 1999). Leached N and P from broadcast fertilizers can also contaminate local water supplies (Binkley et al., 1999; Foley et al., 2005).

Tropical forests have experienced high rates of deforestation (ITTO, 2002), affecting the world's poor particularly hard (Lamb et al., 2005). Reforestation and restoration programs on degraded tropical landscapes can help to alleviate these losses, and silvicultural advances may help to ensure the effectiveness of these efforts. Despite positive research results using CRF in temperate and boreal regions, these fertilizers have not been tested extensively in the tropics where warm temperatures persist year-round, potentially accelerating release rates and confounding ability to transfer fertilizer prescriptions from other biomes.

Hawaii, in particular, has experienced high rates of forest degradation and deforestation, having lost more than half of its native forest to non-native systems (Gon et al., 2006). As such, Hawaii has been proposed as a laboratory for the implementation of innovations in restoration technologies (Friday et al., 2015). Restoration plantings usually rely on koa (*Acacia koa* Gray), one of two canopy level trees across most climate types in Hawaii (Gagne and Cuddihy, 1990), which has great cultural (Whistler, 2009) and economic (Scowcroft et al., 2010) significance and status as one of the most important native trees to Hawaii. After centuries of degradation following the introduction of goats (*Capra hircus*) in 1778, domestic sheep (*Ovis aries*) in 1791, and cattle (*Bos taurus*) in 1793 (Ziegler, 2002) and extraction of timber from native forests (Woodcock, 2003), the value of koa has increased and put additional pressure on naturally regenerated koa stands to satisfy demand for furniture and musical instruments, among other uses (Friday, 2011; Scowcroft et al., 2010; Yanagida et al., 2004). Efforts to reforest upper-elevation areas are further motivated by the importance of providing habitat to endangered birds threatened by the spread of avian malaria (*Plasmodium relictum*) as the climate warms (Rock et al., 2012).

Koa's extensive native range provides a setting where fertilizers can be tested on contrasting sites to identify the advantages of dosages, formulations, and delivery mechanisms. Koa is a shade intolerant, pioneer species (Walters and Bartholomew, 1984; Walters and Bartholomew, 1990; Baker et al., 2009) that occupies a dominant canopy position in forests. Koa uses a heteroblastic growth habit to regenerate in both open fields and large canopy gaps, in which younger true leaves maximize light capture while mature, horizontally oriented phyllodes improve drought tolerance and maintain maximum photosynthetic rates (Craven et al., 2010; Pasquet-Kok et al., 2010). It grows in forests where elevation ranges from around sea level to 2000 masl (Gagne and Cuddihy, 1990), mean annual minimum temperature ranges from less than −1 °C to over 4 °C, and climate types are categorized from xeric to wet (Baker et al., 2009). Hawaiian soils across koa's range are diverse. Soil age and weathering of volcanic soils create a succession of nutrient limitations from N on younger soils to P on older soils, a pantropical trend (Harrington et al., 2001; Vitousek and Farrington, 1997). On a mix of young soils from 2 to 15 ka, however, Pearson and Vitousek (2001) found that annual growth rates of 6- to 20-year-old koa did not increase with N fertilization, instead arguing that P likely functioned as the primary limiting nutrient. This contrasted with results of Vitousek and Farrington (1997), however, who found that N limited growth of *Metrosideros polymorpha* Gaud. on young soils and P, on older soils. The discrepancy in findings may have been because *M. polymorpha* is not an N-fixer, but koa is, or because the studied koa were already well established on the site. These results indicate that N-fixation (Dreyfus et al., 1987; Parrotta, 1992; Miyasaka et al., 1993; Pearson and Vitousek, 2001) may be sufficient to provide koa with N, but the findings do not preclude the possibility that seedling N fertilization (Davis et al., 2011; Dumroese et al., 2011, 2009) may prove useful on degraded sites targeted for forest restoration. These results also suggest that P fertilization may be more important than N fertilization. Furthermore, as a result of the diversity of climate types where koa dominates the canopy, optimal fertilization prescriptions for koa plantations likely vary depending on plantation goals, economics, soil fertility, temperature and annual rainfall.

Thus, we installed experiments at two contrasting sites in Hawaii. We asked the following three questions. First, how would a wide variety of fertilization techniques affect early growth and survival of planted koa seedlings? We hypothesized that increasing fertilization would promote growth, until the highest application rates where phytotoxicity would be observed. We also hypothesized that survival would increase with CRF application relative to IAF because CRF provide a more consistent supply of nutrients. Second, can CRF maintain or improve growth and survival relative to IAF in spite of lower overall amount of nutrients delivered? We hypothesized that CRF would maintain growth increases of IAF relative to the control despite lower overall application rates. Finally, will response to fertilization be consistent across two contrasting sites? We hypothesized that growth and survival would be highest at Pahala, but that fertilization would be more important at Volcano because of its relatively lower site quality.

2. Methods

2.1. Site description

Trials were located near Pahala (19.2214°N, 155.4969°W, 616 masl) and Volcano (19.4757°N, 155.3320°W, 1543 masl), Hawaii on land managed by Kamehameha Schools. The Pahala site was used for cultivation of sugar cane through the early 1990s, while the Volcano site was used as pasture through 2002; both sites were in fallow grass cover for a least a decade prior to planting koa. The locations were selected to minimize differences in slope, with both sites at less than 5% slope overall. The Pahala and Volcano sites receive similar amounts of annual rainfall. For the first year of the study during which Pahala was measured, Pahala received 728 mm according to NOAA weather station, Pahala Mauka (19.204°N, 155.480°W; NCDC, 2016). During the same year, a RAWS station at Keaumo (19.474°N, 155.359°W), close to the Volcano site, received 734 mm of rainfall (RAWS, 2016). Total precipitation during the measurement period from January 2013 to August 2014 at Volcano was 1730 mm. Mean annual temperature is lower at Volcano (13.5 °C) than at Pahala

(19.4 °C) (Giambelluca et al., 2013). The Pahala site corresponds to a soil of intermediate age, between 13 and 30 ka (Wolfe and Morris, 1996; Sherrod et al., 2007), and likely to have achieved equilibrium of N and P (Vitousek and Farrington, 1997). The Volcano site is younger, in the range of 1.5–3 ka (Sherrod et al., 2007) and similar to that studied in Pearson and Vitousek (2001). It is, therefore, more likely limited by N than P and has greater potential than the Pahala site to respond to N additions. The Pahala site is located on Alapai hydrous silty clay loam, classified as hydrous, ferrihydritic, isothermic Typic Hydrudands, while the Volcano substrate consists of Kulalio silt loam, classified as medial-skeletal, amorphic, isomesic Eutric Pachic Fulvudands (Soil Survey Staff). Both soil series typically have a depth to bedrock of 150 cm or more, but differ in other key areas. Alapai soils are less rocky with 0–10% rock fragments by volume in the first 150 cm and no important lava rock component in the first 18 cm. The Kulalio soils typically have 50–90% a'a lava rock fragments to the same depth and are characterized as having 5% a'a stones at the surface, 10% a'a stones in the first 0–8 cm, and 30% a'a fragments from 8 to 18 cm depth. They also differ in mean annual soil temperature: the Alapai series has a mean of 16–20 °C and the Kulalio, 12–18 °C.

The two sites received different site preparation. Volcano was planted in rows between 0.75 and 1.5 m tall koa that had been planted the previous year. Site preparation was performed with a bedding plow behind a tractor, driven twice across the planting site resulting in a planting bed about 0.5 m deep. This was performed 14 months prior to planting, during which time applications of fertilizer and herbicide were done manually and mechanically using all-terrain vehicles (ATVs), respectively. Pahala, in contrast, was installed as one contiguous plantation with site preparation performed one 1 month before planting using the same methods as at Volcano.

2.2. Experimental design

The randomized-blocked design consisted of three blocks at Volcano and four blocks at Pahala comprising eight and ten treatments, respectively. The Volcano site consisted of one block and two treatments less than the site at Pahala because of a labor crew error. An area within each koa plantation was selected for its homogeneity of slope and substrate. At Volcano, the trial was established across six rows in a rectangular area, with each row containing four treatments. At Pahala, the trial was established across 20 rows with two treatments per row. At both sites, between rows spacing was approximately 4 m and between seedling spacing, 2 m. The Volcano experiment was established on 17 January 2013 while the Pahala experiment was established on 18 April 2013. Table 2 provides a summary of fertilizer treatments. At both sites, Osmocote 15-9-12 (Scott's MiracleGro, Marysville, OH, USA), at an estimated 12–14 month release rate assuming constant soil temperature of 22 °C, was applied at five treatment rates varying from 15 g through 75 g per seedling in increasing increments of 15 g. In addition to N, P, and potassium (K), the CRF included micronutrients at the following concentrations: magnesium (1.3%), sulfur (5.9%), boron (0.02%), copper (0.05%), iron (0.46%), manganese (0.06%), molybdenum (0.02%), and zinc (0.05%). At Pahala, the trial also included four IAFs: two rates of 10-30-10, one 11-52-0 (monoammonium phosphate or MAP) treatment, and a 0-45-0 (triple super phosphate or TSP) treatment, with doses of these latter two non-CRF formulations calibrated to deliver equivalent P mass (Table 2). The higher 10-30-10 treatment represented the standard operating procedure for commercial koa plantations on Kamehameha Schools land; the lower treatment was half of the standard rate. At Volcano, the two rates of 10-30-10 were omitted because of installation problems. We included fertilizers with both N and P to compare the effectiveness of CRF relative to IAF applications in operational use (10-30-10 IAF), and to test the importance of N and P fertilization of a legume on contrasting sites. The extensive array of fertilizers and broad range of N and P application rates were selected to elucidate the mechanisms by which fertilizers influence koa growth.

In the CRF treatments, applied N varied from a minimum of 2.26 g per seedling to a maximum of 11.25 g. For the same treatments, the range of P per seedling was 1.35–6.75 g, and the range of K per seedling was 1.80–9.00 g. The operational-based treatments contained considerably higher levels of all elements: 16.80 g N and K per seedling and 50.40 g P per seedling. The MAP treatment was designed to deliver comparable P (50.96 g per seedling), which corresponded to 10.78 g N. Although the TSP treatment contained no N or K, P levels (50.85 g) were comparable to the operational treatment.

CRF treatments were applied by a dibble method in which fertilizer was applied equally in three holes at a depth of 10 cm near the seedling root system, with up to 30 g CRF applied to each hole depending on the treatment. These CRF application holes were filled in with at least 1 cm of soil covering the fertilizer material. IAF were administered as a crown application, evenly distributed in a radius of 20 cm around the base of each seedling.

2.3. Measurements

Soil at each site was characterized for pH, P, K, N, soil organic matter (SOM; calculated as total carbon multiplied by 1.72), and texture (Table 1). A composite soil sample of twenty subsamples at Pahala and fifteen at Volcano was analyzed at the University of Hawaii at Manoa Agricultural Diagnostic Service Center (Honolulu, HI). All samples were randomly collected on 13 August 2015 within control blocks using a soil probe to a depth of 20 cm. Because both soils were Andisols, the soils were not air dried before the analysis. Total carbon and total nitrogen were determined by dry combustion (Soil Survey Staff, 2004). Extractable phosphorous was determined using the Modified Truog procedure (Ayers and Hagihara, 1952). Textural analysis followed Kettler et al. (2001).

In addition to baseline measurements following planting, root collar diameter (RCD, mm), diameter at breast height (DBH, 1.4 m above ground), height (cm) and survival were measured at three census dates. At Pahala, the censuses occurred 3, 6 and 12 months after planting. At Volcano, where growth rates were slower, the censuses occurred 3, 6, and 20 months after planting. Whereas the final diameter measurement at Pahala was the DBH, the final measurement at Volcano was RCD in order to keep consistent measurements and allow for growth calculations. Diameter measurements were taken with a Vernier caliper (General Tools & Instruments, Secaucus, NJ, USA). For forked trees, height was measured for the taller fork.

2.4. Foliar nutrient analyses

Six months after installation, sub-samples of leaves from the upper one-third of seedlings were collected for each treatment within each block at both sites. At least ten leaves were collected and combined to form one composite sample for each treatment within a block. The same was done for phyllodes at Pahala; phyllodes were not present on seedlings at Volcano at the time of collection. The combined samples were air-dried to a constant mass at 18.3 °C before grinding them with a Wiley Mill using a 20-mesh screen. The samples were submitted to A & L Great Lakes Laboratories (For Wayne, IN, USA) for foliar nutrient analyses. Foliar N concentrations were obtained by combustion using the Dumas procedure (AOAC 968.06) in a LECO nitrogen analyzer (LECO Corp.,

Table 1
Summary of mean (±SE) soil nutrient content and texture at Volcano and Pahala. Results from composite soil samples (15 subsamples at Volcano, 20 subsamples at Pahala). An asterisk beside column headers indicates significance of ANOVA test ($P < 0.05$).

Site	pH*	P (ppm)	K (ppm)	N (%)*	SOM (%)*	Sand (%)	Silt (%)*	Clay (%)
Volcano	5.23 (0.03)	15.00 (2.08)	67.33 (9.13)	0.81 (0.03)	19.49 (1.15)	34.00 (1.30)	64.58 (1.31)	1.42 (0.67)
Pahala	5.88 (0.11)	9.93 (3.45)	68.25 (16.51)	0.50 (0.04)	11.44 (0.79)	18.10 (5.32)	81.77 (5.34)	0.12 (0.06)

Table 2
Per-seedling rates by treatment for fertilizer mass and nutrient delivered. Note that the CRF application included other macro- and micro-nutrients.

Fertilizer treatment (NPK)	Code	g plant^{-1}	N (g plant^{-1})	P (g plant^{-1})	K (g plant^{-1})
Control	CTRL	0	0.00	0.00	0.00
10-30-10	2SOP	168	16.80	50.40	16.80
10-30-10	1SOP	84	8.40	25.20	8.40
11-52-0	MAP	98	10.78	50.96	0.00
0-45-0	TSP	113	0.00	50.85	0.00
15-9-12	15gCRF	15	2.25	1.35	1.80
15-9-12	30gCRF	30	4.50	2.70	3.60
15-9-12	45gCRF	45	6.75	4.05	5.40
15-9-12	60gCRF	60	9.00	5.40	7.20
15-9-12	75gCRF	75	11.25	6.75	9.00

St. Joseph, MI, USA). After digesting other plant samples in nitric + pechloric acids (AOAC 935.13), other nutrient analyses were conducted using inductively coupled argon plasma analysis (AOAC 985.01). All results are presented as concentrations.

2.5. Statistical analyses

All analyses were performed using R Software (R.C. Team, 2014). Data from Pahala and Volcano were analyzed separately. Soil data were analyzed as a one-way ANOVA. Survival data at Pahala were analyzed as a binomial distribution (Wilson and Hardy, 2002) using a Generalized Linear Model (GLM) with a logit link function (Venables and Ripley, 2013). The GLM model included two factors, Treatment and Block, without interactions because the interaction was not significant. Survival data at Volcano were analyzed using a Generalized Linear Mixed-Effect Model with a binomial response (Bates et al., 2014). Treatment was treated as a main effect. The random effect was constructed to model a separate effect for each treatment within each block because other tests had demonstrated an interaction effect between Treatment and Block at Volcano. Height, RHG, and diameter at both Pahala and Volcano were analyzed using the R Package, lme4 (Bates et al., 2014), for General Linear Mixed-Effect models, where Treatment was a main effect and the random effect modeled a separate effect for each treatment within Block to account for interaction between the two. The analysis of height at Volcano included baseline heights as a covariate in the model because an ANOVA of baseline heights showed significant differences ($P < 0.001$). When treatment effects were significant ($P < 0.05$) in the ANOVA, Post-hoc pairwise comparisons were done using the Multcomp Package in R (Hothorn et al., 2008) to run Tukey's Studentized Range tests to compare treatment means. Foliar analyses, where composite tissue samples were collected for leaves and phyllodes, were analyzed as one-way ANOVAs.

3. Results

Soils differed significantly between sites for N ($P = 0.0026$), SOM ($P = 0.0018$), and silt ($P = 0.0437$), but did not differ for P ($P = 0.305$), K ($P = 0.967$), sand ($P = 0.0552$), or clay ($P = 0.069$).

Survival at Pahala across treatments averaged 95.8% after one year and fertilization did not significantly affect survival ($P = 0.569$ for treatment and $P = 0.711$ for block, Fig. 1). Survival at Volcano was significantly affected by the fertilization treatment ($P = 0.0193$). The only significant difference among the treatments was between the 15 g CRF and TSP treatments, which had survival rates of 83% and 47%, respectively (Fig. 1).

At Pahala, neither absolute height growth nor relative height growth (RHG) were significantly affected by fertilization treatments ($P = 0.1247$ and $P = 0.1537$, respectively; Figs. 2 and 3). As with height growth at Pahala, DBH was not significantly affected by fertilization treatments ($P = 0.1539$; Fig. 4). At Volcano, absolute height and RHG were significantly affected by fertilization treatment ($P = 0.0068$ and $P = 0.0457$, respectively; Figs. 2 and 3). MAP, TSP, 45 g CRF, and 75 g CRF had significantly higher absolute heights than the control treatment after 20 months, the latter three of which were also significantly higher than the 15 CR as well. The RHG of TSP was significantly higher than the 15 g CRF, 30 g CRF and 60 g CRF treatments after 20 months.

At Volcano, absolute RCD of treatments after twenty months was significantly affected by fertilization treatments ($P = 0.049$, Fig. 4). The TSP treatment's RCD was larger than the control, 15 g

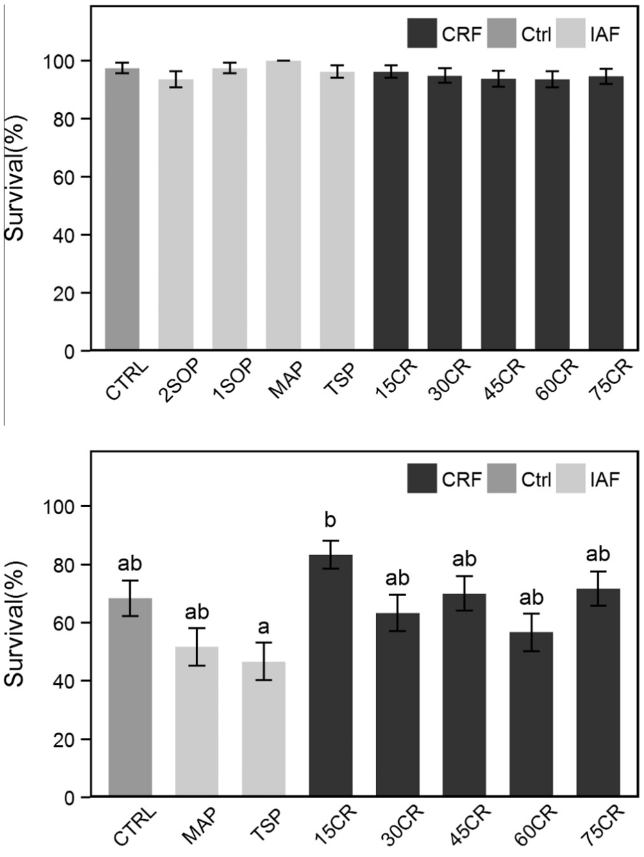

Fig. 1. Mean (±SE) survival from Pahala (top) and Volcano (bottom) by treatment. No significant differences were found at Pahala. Letters above error bars correspond to Tukey HSD groups. If no letters are present, no significant differences were found. Treatment codes are CTRL (Control), 2SOP (10-30-10 168 g), 1SOP (10-30-10 64 g), MAP (10-52-0), TSP (0-45-0) and the five CRF treatments from 15 g (15CR) to 75 g (75CR). Note that Pahala has two extra treatments: 2SOP and 1SOP.

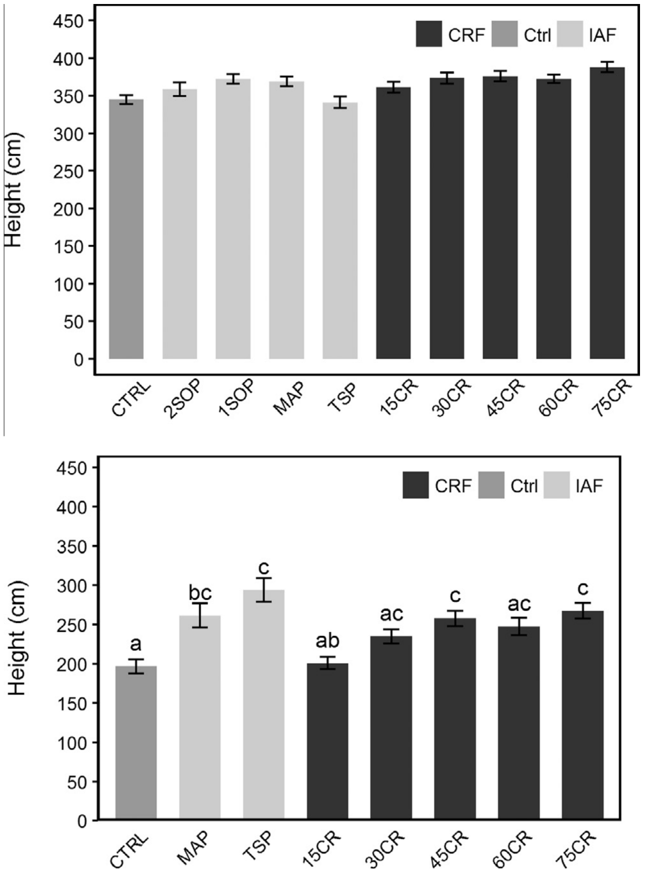

Fig. 2. Mean (±SE) absolute height (cm) of the Pahala (top) and Volcano (bottom) site by treatment. No significant differences were found at Pahala. Letters above error bars correspond to Tukey HSD groups. If no letters are present, no significant differences were found. Treatment codes are CTRL (Control), 2SOP (10-30-10 168 g), 1SOP (10-30-10 64 g), MAP (10-52-0), TSP (0-45-0) and the five CRF treatments from 15 g (15CR) to 75 g (75CR). Note that Pahala has two extra treatments: 2SOP and 1SOP.

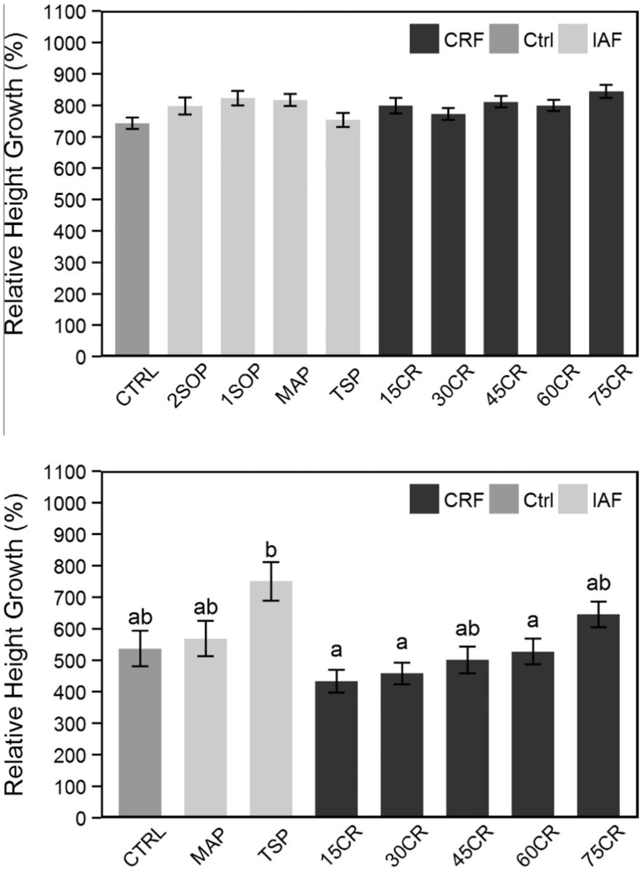

Fig. 3. Mean (±SE) relative height growth at Pahala (top) and Volcano (bottom). No significant differences were found at Pahala. Letters above error bars correspond to Tukey HSD groups. If no letters are present, no significant differences were found. Treatment codes are CTRL (Control), 2SOP (10-30-10 168 g), 1SOP (10-30-10 64 g), MAP (10-52-0), TSP (0-45-0) and the five CRF treatments from 15 g (15CR) to 75 g (75CR). Note that Pahala has two extra treatments: 2SOP and 1SOP.

CRF, 30 g CRF, and 60 g CRF treatments after 20 months. The RCDs in the 45 g, 60 g and 75 g CRF treatments were all larger than the control.

At Pahala, foliar concentrations of N and K were significantly affected by fertilization treatments (P = 0.0294 and P = 0.0004, respectively; Table 3). Pairwise comparisons, however, were not significant for N. The 75 g CRF treatment had higher K concentration than the control, 10-30-10 at 84 g, 11-52-0 and 0-45-0 after six months. All of the CRF treatments and the 10-30-10 at 168 g had higher foliar K concentrations than the 11-52-0 treatment. Concentration of P in leaves at Pahala was not significantly affected by fertilization (P = 0.4707). Phyllode N and P concentrations at Pahala were not significantly affected by fertilization treatments (P = 0.4646 and P = 0.1639, respectively), but concentration of K was significantly affected (P = 0.0039), whereby concentration of K in the 30 g CRF treatment was significantly higher than that of the control and 11-52-0 treatments. The 45 g CRF and 10-30-10 at 168 g treatments were higher than the control.

At Volcano, foliar concentrations of N, P, and K in leaves were significantly affected by fertilization treatment (P = 0.0378, P = 0.0018, and P < 0.001, respectively). Pairwise comparisons for N, however, were not significant. Foliar P in the 11-52-0 and 0-45-0 treatments was significantly higher than those of the control and 15 g CRF treatments after six months. Foliar K in the 30 g CRF was significantly higher than foliar K in the 10-30-10 at 64 g, 11-52-0, and 0-45-0 treatments. The 45 g, 60 g, and 70 g CRF treatments also resulted in higher foliar K concentrations than 0-45-0 and 11-52-0 treatments. Foliar K concentration in the 11-52-0 treatment was significantly lower than all other treatments.

4. Discussion

These experiments on contrasting sites in a tropical environment showed a mix of neutral and positive responses to fertilization, depending upon dosage and site. Similar to results at the Volcano site, most studies on nutrient limitation of seedlings in the tropics have reported positive responses to nutrient additions (Lawrence, 2003), indicating a need to overcome nutrient deficiencies to increase growth during establishment. Studies finding neutral responses to fertilization of tropical legumes have suggested that responses are associated with evolution of these species to grow in infertile soils (Veenendaal et al., 1996) or because soil symbionts were lacking (Baraloto et al., 2006).

In our case, seedlings were planted within koa's native range, where all required soil symbionts were likely present. Interestingly, koa responded to fertilization at the more fertile site, Volcano, but growth and survival were not improved at the site with lower soil fertility, Pahala. Possibly, the Pahala site's soil and climate were optimized and observed growth rates approached the upper limit for koa. For example, Daehler et al. (1999) found an average height of 1.1 m for 8-month-old koa from the Island of Hawaii, close to the growth rate for the control at the Volcano site but about one-third that of the control at the Pahala site.

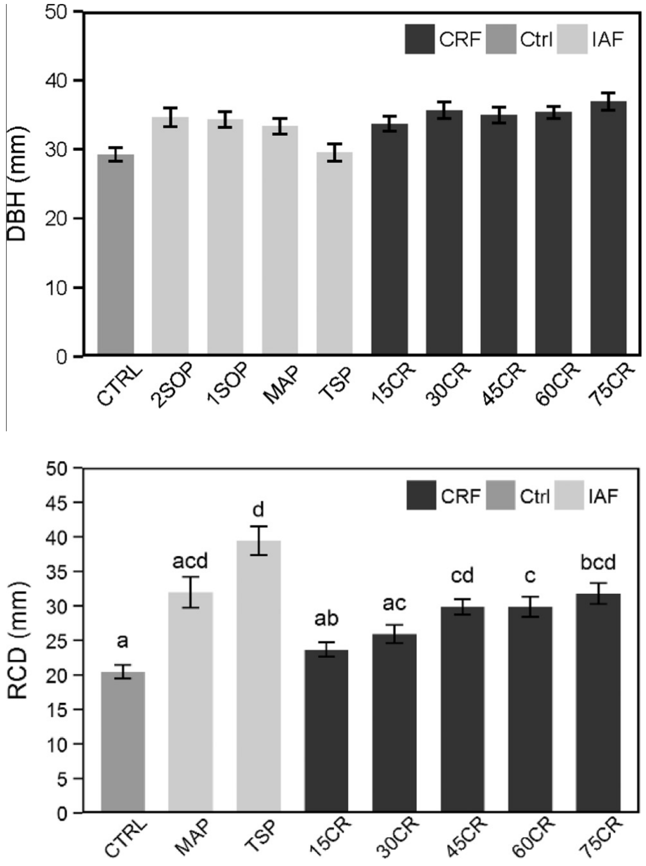

Fig. 4. Mean (±SE) DBH (mm) at Pahala (top) after one year and RCD (mm) at Volcano (bottom) after twenty months. No significant differences were found at Pahala. Letters above error bars correspond to Tukey HSD groups. If no letters are present, no significant differences were found. Treatment codes are CTRL (Control), 2SOP (10-30-10 168 g), 1SOP (10-30-10 64 g), MAP (10-52-0), TSP (0-45-0) and the five CRF treatments from 15 g (15CR) to 75 g (75CR). Note that Pahala has two extra treatments: 2SOP and 1SOP.

Table 3

Mean N, P, and K concentrations (±SE) for leaves and phyllodes at Pahala and Volcano at six months. Letters indicate Tukey's HSD groups ($P < 0.05$). Treatments listed are control (CTRL), 10-30-10 at 168 g (2SOP) and 84 g (1SOP), 11-52-0 (MAP), 0-45-0 (TSP), and CRF from 15 g (15CR) to 75 g (75CR).

Site and type	Treatment	N (%)	P (%)	K (%)
Pahala leaves	CTRL	2.99 (0.10) a	0.11 (0.01) a	1.16 (0.08) ab
	2SOP	3.13 (0.21) a	0.13 (0.00) a	1.34 (0.04) bc
	1SOP	2.58 (0.17) a	0.11 (0.01) a	1.08 (0.03) ab
	MAP	2.60 (0.06) a	0.12 (0.01) a	0.89 (0.09) a
	TSP	2.99 (0.09) a	0.14 (0.02) a	1.20 (0.07) ab
	15CR	2.55 (0.01) a	0.11 (0.00) a	1.27 (0.03) bc
	30CR	2.71 (0.10) a	0.14 (0.01) a	1.30 (0.05) bc
	45CR	2.93 (0.17) a	0.12 (0.01) a	1.32 (0.12) bc
	60CR	2.94 (0.21) a	0.12 (0.01) a	1.16 (0.04) ac
	75CR	3.13 (0.16) a	0.13 (0.02) a	1.46 (0.09) c
Pahala phyllodes	CTRL	2.56 (0.08) a	0.11 (0.02) a	1.12 (0.06) a
	2SOP	3.19 (0.27) a	0.17 (0.02) a	1.59 (0.07) bc
	1SOP	2.78 (0.26) a	0.18 (0.03) a	1.49 (0.07) ac
	MAP	2.69 (0.16) a	0.17 (0.01) a	1.18 (0.05) ab
	TSP	2.64 (0.15) a	0.14 (0.02) a	1.33 (0.03) ac
	15CR	2.39 (0.09) a	0.12 (0.01) a	1.41 (0.08) ac
	30CR	2.80 (0.13) a	0.19 (0.01) a	1.64 (0.08) c
	45CR	3.02 (0.38) a	0.17 (0.03) a	1.59 (0.13) bc
	60CR	2.87 (0.31) a	0.14 (0.03) a	1.37 (0.18) ac
	75CR	3.04 (0.43) a	0.16 (0.01) a	1.57 (0.10) ac
Volcano leaves	CTRL	2.89 (0.16) a	0.08 (0.01) a	1.17 (0.08) bd
	MAP	2.96 (0.32) a	0.14 (0.02) b	0.63 (0.10) a
	TSP	3.09 (0.09) a	0.17 (0.01) b	0.92 (0.14) ab
	15CR	2.97 (0.08) a	0.08 (0.01) a	1.22 (0.06) bd
	30CR	3.42 (0.15) a	0.09 (0.01) ab	1.52 (0.01) d
	45CR	3.41 (0.27) a	0.10 (0.01) ab	1.39 (0.06) cd
	60CR	3.77 (0.09) a	0.10 (0.00) ab	1.48 (0.02) cd
	75CR	3.75 (0.22) a	0.10 (0.01) ab	1.43 (0.07) cd

Relatively little research has compared the efficacy of CRF versus IAF during regeneration establishment. This has been particularly true for tropical species. The only other studies comparing survival and growth response to CRF and IAF application were performed on boreal tar sands restoration sites with *Populus tremuloides* Michx and *Picea glauca* (Moench) Voss in Canada (Sloan and Jacobs, 2013; Sloan et al., 2016). Despite differences in climate, soils, and species, results were similar to those at the Volcano site in our experiment in that the IAF treatments supplied 5–10 times more total N, but recovery of applied N and growth were equal or better for CRF treatments. Importantly, Sloan and Jacobs (2013) attributed growth differences between IAF and CRF to the nearly quadrupled herbaceous competition in the IAF relative to the CRF and control plots. Although this trend of increased herbaceous competition for IAF was not observed in Sloan et al. (2016), the growth responses to fertilization were similar to that of Sloan and Jacobs (2013) and our study, in which herbaceous competition was not measured because it was, treated effectively using site preparation. Nevertheless, where fertilizer responses were detected at Volcano, CRF maintained growth at all but the lowest application rate and increased or maintained survival relative to IAF despite much lower overall application rates (e.g., the MAP treatment supplied 2.4× N and 18.8× P relative to the 30 g CRF treatment).

Trees that vary in ability to fix N may respond differently to fertilization on the same site (Otsamo et al., 1995). Our results from Pahala, where no fertilizer effect was noted either in survival or growth, suggest that nutrition was not a limitation to koa growth due to high inherent site quality and the absence of herbaceous competition. In fact, it is difficult to identify a limitation to growth and survival at the Pahala site with data from the present study. It is possible that in the absence of weed control, the CRF may have outperformed the IAF because of increased herbaceous competition in the IAF treatments (Sloan and Jacobs, 2013). This is supported by a recent study examining koa performance in Hawaii in which herbaceous control during site preparation 30 days prior to planting resulted in 40–50% taller trees after 30 months (Pinto et al., 2015).

Regardless of fertilizer type, the majority of applied fertilizer nutrients are not taken up by target plants (Sloan et al., 2016), but CRF exhibits a reduction in total nutrient loss from the system relative to IAF. At Volcano, both IAF and CRF promoted increased growth relative to the control, but CRF, even at the highest rates, maintained these gains in growth rates despite lower overall application rates. Specifically, the 75 g CRF treatment produced the same height and RCD performance as the TSP and MAP treatments at Volcano, despite an application rate of only 4% more N than the MAP treatment and 87% less P to the seedlings compared to both the MAP and TSP treatments. The results at the Volcano site lead us to conclude that, in agreement with our second hypothesis, CRF represent a more effective delivery system of nutrients, a trend previously noted in boreal systems (Hangs et al., 2003; Sloan and Jacobs, 2013; Sloan et al., 2016) and now established at a tropical site.

Although not directly tested, this study also supports previous findings that P fertilization is more important than N fertilization for koa and related N-fixer species. In *Acacia melanoxylon* R. Br., which is closely related to koa (Robinson and Harris, 2000), Pinkard (2003) found that P fertilization had a greater effect on stem growth than fertilization with N or an N and P combination. In our study, the additional N in the MAP and 75 g CRF treatments was probably inconsequential because N has not been shown to be a likely limiting nutrient for koa (Ares and Fownes, 2001; Pearson and Vitousek, 2001), whereas P, both in TSP and other forms, has been shown to stimulate growth in koa in both seedlings (Scowcroft and Silva, 2005) and mature stands (Scowcroft et al., 2007). Foliar analyses in our study suggest the same effect, where no differences in N concentration were observed among any treatments, but both MAP and TSP resulted in P concentrations no different from CRF treatments above 15 g at Volcano and significantly higher than the control and 15 g CRF treatment (Table 3). Thus, the CRF treatments at 30 g and above had foliar P concentrations similar to the MAP and TSP treatments, despite much lower overall P application rates and the tendency for lower release rates of P from CRF compared to other nutrients (Haase et al., 2007). Similar foliar P concentrations and growth in response to fertilization suggest that P was limiting at Volcano; and CRF treatments above 15 g were as effective as the IAF treatments despite much lower application rates. These results also suggest that future trials with N-fixing trees should concentrate on CRF formulations higher in P relative to N.

Climate and soil differences likely contributed to reduced growth rates and survival at Volcano relative to Pahala. Despite slightly more fertile soil (Table 1), the Volcano site was colder, had rockier soil, and was inter-planted within a one-year old koa plantation. The Volcano site's proximity to the active Kilauea crater may have also put it in the path of higher frequency vog emissions (http://weather.hawaii.edu/vmap/), made up of sulfur dioxide (SO_2) gas and sulfate (SO_4) aerosols (Sutton et al., 1997), which have been shown to damage koa (Skolmen, 1990). The Kulalio soil at Volcano, with 50–90% rock fragments in the first 150 cm, represents a harsher growing medium than that found at Pahala on Alapai soil, which averages 0–10% rock fragments to the same depth. The increased rockiness at Volcano could have resulted in less root access to nutrients and increased filtration rates and drainage of rainfall at Volcano relative to Pahala, leading to increased water stress despite similar rainfall regimes. At Volcano, moreover, where koa was planted in rows as at the Pahala site, some seedlings may have been planted on poor quality microsites, increasing mortality.

Differences in site preparation may have also contributed to reduced performance at Volcano. The Volcano site, in contrast to the Pahala site where site preparation and planting occurred during a single year, received twice as many passes with a tractor and bedding plow and ground-based (ATV) herbicide application the year preceding planting, which may lead to reduced productivity (Stone and Elioff, 1998) from compacted soil and lowered porosity (Grigal, 2000; Shepperd, 1993). These in turn could have limited water availability and root growth (Alvarez and Steinbach, 2009).

These complicating site factors, involving likely interactions between site preparation, stressors (e.g., vog), soil factors, and climate, make it difficult to identify precise causes of disparity in performance at Volcano and Pahala. This underscores the necessity of further testing to optimize fertilization protocols for tropical N-fixing trees. Studies in other biomes have identified fertilization rates where phytotoxicity was induced; the immediate delivery of high amounts of nutrients to the root zone of planted trees can exacerbate stress and increase mortality from drought events (Graciano et al., 2005; Jacobs et al., 2004; Jacobs and Timmer, 2005). As our study did not yield these results, future trials testing higher rates, or more frequent applications, may better identify limiting factors on difficult restoration sites for koa and other tropical species.

Our results question the importance and economic returns of fertilization of koa and (perhaps) other N-fixing legumes in the tropics. Compared to the control, an average relative height growth increase of 31%, 36%, and 49% was observed from the 45CR, 75CR, and TSP treatment, respectively (Fig. 2). These growth advantages correspond to a total height difference of about 60–100 cm at Volcano after 20 months, but materials and labor costs associated with fertilization can be significant. A hypothetical cost analysis of fertilizers used at Volcano and Pahala sites is shown in Table 4. Based on an estimated labor cost of $ 250 ha^{-1}, and low and high-end estimated total establishment costs of $6200 and $11,000 ha^{-1}, respectively, materials cost 3.4–6.1% of the total establishment budget for a planting application of 10-30-10 fertilizer, and 5.7–10.1% when labor costs are included. Thus, up to a 10% cost savings could be realized by eliminating such application. For more expensive projects (i.e., difficult site access, extensive needs for site preparation, high seedling costs, and scale), fertilization represents a lower percentage of the overall establishment cost but omitting fertilization could provide significant savings in absolute terms. For example, a high-cost project on 10 ha with two scheduled applications of 10-30-10 at the standard rate could save approximately $12,500 by foregoing the application. Nevertheless, the disparity between the two sites in responses also indicates that gains from fertilizer applications will differ widely across sites of varying soil types and climate.

Table 4
Hypothetical cost analysis of fertilizers used at Volcano and Pahala sites. Product costs ($) are from 2013 on Hawaii and cost ha^{-1} is based on 1815 seedlings ha^{-1}.

Fertilizer type	Unit weight (kg)	Price ($)	Price kg^{-1} ($)	Price g^{-1} ($)
Product costs				
15-9-12	22.68	105.75	4.66	0.004663
11-52-0	22.68	35.50	1.57	0.001565
0-45-0	22.68	33.50	1.48	0.001477
10-30-10	22.68	28.00	1.23	0.001235
Fertilizer type	Dose (g plant^{-1})	Cost plant^{-1} ($)	Cost ha^{-1} ($)	
Establishment costs				
Control	0	0.00	0.00	
10-30-10	168	0.21	376.44	
10-30-10	84	0.10	188.22	
11-52-0	98	0.15	278.41	
0-45-0	113	0.17	302.94	
15-9-12	15	0.07	126.94	
15-9-12	30	0.14	253.88	
15-9-12	45	0.21	380.83	
15-9-12	60	0.28	507.77	
15-9-12	75	0.35	634.71	

Acknowledgements

Funding support was provided by the Tropical Hardwood Tree Improvement and Regeneration Center and the Fred M. van Eck Forest Foundation for Purdue University. Kamehameha Schools provided access to these research sites. The authors wish to thank Kamakani Dancil and Nicholas Koch for valuable assistance with this project. Two anonymous reviewers provided helpful comments that improved the manuscript.

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