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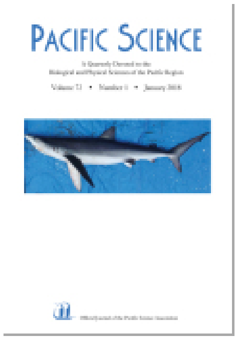

PACIFIC SCIENCE

Enhancing Aboveground Carbon Storage and Invasion Resistance through Restoration: Early Results from a Functional Trait-Based Experiment[1]

Donald D. Rayome,[2,5] *Rebecca Ostertag,*[3] *and Susan Cordell*[4]

Abstract: One of many ecosystem services essential to land management is carbon regulation, but presence of invasive species can influence carbon (C) in undesirable ways. Here we discuss early results of C accumulation from the Liko Nā Pilina hybrid wet forest restoration experiment. The focus of our project is to deliberately increase C storage through a functional trait-based approach to restoration. By choosing plant species mixes with specific functional trait values, a novel ecosystem can be assembled that supports desired ecosystem services such as C regulation. We designed species mixtures based on species rate of C turnover (slow or moderate) and their position in trait space (complementary or redundant functional trait values). New species mixes were planted as four treatments (Slow Redundant, Slow Complementary, Moderate Redundant, and Moderate Complementary), with an additional unmanaged Reference treatment. Our objective was to compare C in aboveground woody biomass using allometric equations to determine which mixture had the greatest potential for site restoration, balancing carbon storage with the eventual goal of creating forests better able to resist establishment by invasion species. Initially, we predicted the Moderate Complementary treatment would have increased C storage. However, we found that the Moderate Redundant treatment had the greatest C storage, largely driven by a few fast-growing species during early development. Even though our short-term results did not support our experimental prediction, these data serve as an important benchmark for contrasting with later results when ecological succession might favor complementary species mixes for sustainable biomass productivity and decreased management efforts.

Rapid changes in the world's ecosystems from human activities (Chapin et al. 2000, Mascaro et al. 2008, Cusack et al. 2016) have resulted in a new era of human-dominated ecosystems: the Anthropocene (Morse et al. 2014, Lugo 2015, Bai et al. 2016). Due to unprecedented levels of human influence, the Anthropocene can be described as an era of ecosystem novelty, or ecosystems existing without analogues in historical or modern reference conditions (Hobbs et al. 2009, Montoya and Raffaelli 2010, Catford et al. 2012). As changing species abundances and successional patterns alter ecosystem func-

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tions and processes, consequences or potential benefits of novelty can be difficult to ascertain (Mascaro et al. 2008, Kueffer et al. 2010, Hulvey et al. 2013). The challenge of managing novel landscapes and understanding their effects requires new strategies that extend beyond recovering historical compositions and processes (Hobbs et al. 2011) and instead focus on resulting ecosystem services (Harborne and Mumby 2011, Hulvey et al. 2013).

One of many ecosystem services essential to land management is carbon regulation (Vitousek, D'Antonio, et al. 1997; Vitousek, Mooney, et al. 1997; Foley et al. 2005). Land managers are likely to be interested in carbon storage from economic and legal standpoints and as a powerful complement to restoration (Huston and Marland 2003, Lubowski et al. 2005, Torres et al. 2010, Evans et al. 2015, Asner et al. 2016). Humans often diminish the capacity of terrestrial ecosystems to store carbon through utilization, degradation, and biological invasion (Ciccarese et al. 2009). As a result, many ecosystems greatly affected by humans tend to release more carbon than they store (Foley et al. 2005, Fargione et al. 2008, Pongratz et al. 2009). However, there are several examples of management activities such as reforestation and ecosystem service restoration that can help to reduce carbon loss (Albrecht and Kandji 2003, Chazdon 2008, Ciccarese et al. 2009).

Rates of carbon accumulation and cycling are strongly influenced by climate such that tropical forests often contain the highest carbon pools (FAO 2010, Raunikar et al. 2010, Payn et al. 2015). Land managers working in tropical ecosystems can use these high rates to their advantage. Hawaiian forests store substantial amounts of carbon, comparing favorably with their global tropical counterparts (Asner et al. 2011, Ostertag et al. 2014) even with proportionally fewer native tree species, and thus present a unique opportunity to examine carbon cycling in a simplified context. Further, species invasions, disease, and other anthropogenic pressures (Hughes and Denslow 2005, Asner et al. 2016, Crow et al. 2016) impact forests on all islands. Resulting novel species compositions, structural alterations, and functional changes inhibit a return to previously known forest types and support a need for carbon management.

One strategy to promote desired levels of carbon accumulation and cycling is to use a functional trait-based approach to assemble plant communities that support desired services such as carbon storage. Functional traits relate to the expression of various morphological, structural, physiological, or chemical traits of organisms. For example, selecting species with a broad range of functional trait expressions may preclude species invasions if the chosen functional traits are already represented in the community (Pokorny et al. 2005, Funk et al. 2008). Because plant functional traits relate to resource capture and processing ability, it is likely that a plant species' position in trait space influences its ability to cycle carbon in ways that affect long-term storage. Complementary assemblages of species in a community are hypothesized to increase ecosystem service variety, species performance, and invasion resistance, and redundant assemblages likely concentrate services (Hooper 1998, Funk et al. 2008). Traits associated with slower C cycling place many natives in a trait space that is at a disadvantage when competing with invasives, especially where traits that promote faster C cycling overlap with traits that promote weediness or inhibit native species recovery (Cardinale et al. 2011). As succession progresses, functional traits that allow a given species to take advantage of fluctuating environmental conditions likely become less influential. Rather, traits that promote successful competition and resource co-opting become more pertinent (Lohbeck et al. 2014), with highly productive or otherwise influential species often driving ecosystem performance measures (Cardinale et al. 2011). Thus reducing interspecific competition through more complementary functional composition (Suding et al. 2008, Hooper and Dukes 2010) becomes important when assessing the trade-offs necessary to meet ecosystem management objectives. However, complementary species mixes may not be advantageous at all stages of restoration because early stages may require species with fast rates of growth that quickly yield suitable microclimatic conditions within a site (Sonnier et al. 2012, Fry et al. 2013, Ostertag et al. 2015).

Functional trait-based restoration has rarely been tested in most forested ecosystems (Lavorel 2013, Ostertag et al. 2015). The Liko Nā Pilina hybrid lowland wet forest restoration experiment addresses functional trait effects in terms of complementary versus redundant experimental plant communities, acknowledging both the need for supporting native species integrity as well as the realities of restoring in areas subject to constant invasion pressure and human use. Carbon is an ecosystem variable readily assessed over a shorter time frame (Ostertag et al. 2009, Cordell et al. 2016). As an experiment, Liko Nā Pilina consists of a reference (invaded forest) and four restoration treatments in which natives were left in place, all nonnative species were cleared, and different mixtures of 10 redundant or complementary species were planted. Noninvasive nonnative species (exotic) were combined with natives to fill ecological roles and aid in guiding site biodiversity toward species assemblages that promote preferred ecosystem functions and services such as slower carbon cycling rates. In this project, we tested how species assemblages store carbon at an early experimental stage, leading to the following hypothesis: The species mixture with a combination of "Moderate" C cycling species and the "Complementary" functional trait species will have the highest C storage capacity as measured by aboveground woody biomass. Such early carbon storage results are an important benchmark for comparison with later successional stages when biotic and abiotic limitations may differ.

MATERIALS AND METHODS

Experimental Design and Study Site

The process of developing treatments in the Liko Nā Pilina experiment is described in Ostertag et al. (2015) and is briefly summarized here. To choose species for the experiment, we investigated 15 functional traits of native and exotic candidate species that could be found living in the lowland wet forest community in East Hawai‘i Island. Species were classified as exotic as opposed to invasive based primarily on the Hawai‘i Weed Risk Assessment score [Daehler et al. 2004 (see www.botany.hawaii.edu/faculty/daehler/wra/)]. To focus on C, we ran a Principal Component Analysis (PCA) on a subset of traits related to C allocation (leaf mass per area, foliar C : N, stem specific gravity, maximum height, stature in the field, and integrated water-use efficiency) to calculate species arrangement in trait space. We identified core species that had sets of traits that can lead to either slow or moderate rates of C turnover (Table 1). Remaining species in each treatment were selected by calculating the centroid of the four core species and then choosing species (based on Euclidean distances) that were either similar (near) in trait expression to the core species (Redundant) or different (far) (Redundant). Four treatment combinations exist: Slow Complementary, Slow Redundant, Moderate Complementary, and Moderate Redundant. Intact invaded reference plots served as a control for comparison.

Lowland [30 m above sea level (a.s.l.)] wet forest portions of the Keaukaha Military Reservation (KMR, 19° 42′ 15″ N, −155° 2′ 40″ W) in Hilo, Hawai‘i, serve as the test location (Ostertag et al. 2015). The site is located on an ‘a‘ā lava flow occurring 750–1,500 yr ago, with annual temperature average 22.7°C (Giambelluca et al. 2014) and average annual rainfall 3,347 mm (Giambelluca et al. 2011). Native canopy but limited native tree regeneration (Cordell et al. 2009) and heavy invasion by nonnative, invasive trees and shrubs characterizes forests at KMR [approximately 45% of basal area (Ostertag et al. 2009)]. Reference treatment plots received no management, but the four experimental treatments were cleared before planting. Experimental nonnative tree species clearing began in late July 2012 and ended in mid-April 2013, and native tree species were left intact. Introduced trees that were at least 50% rooted in a plot or had a tree canopy that

TABLE 1

Species in the Liko Nā Pilina Experiment, Noting Presence of Each Species in the Four Hybrid Community Treatments

Species Code	Species Origin[a]	Scientific Name	Family	Slow Redundant	Moderate Redundant	Slow Complementary	Moderate Complementary	Existing
ALEMOL	E	*Aleurites moluccana*	Euphorbiaceae		X	X		
ANTPLA	N	*Antidesma platyphyllum*	Phyllanthaceae	X				
ARTALT	E	*Artocarpus altilis*	Moraceae		Core		Core	
CALINO	E	*Calophyllum inophyllum*	Clusiaceae	Core		Core		
CIBGLA	N	*Cibotium menziesii/glaucum*	Cibotiaceae	X			X	X
COCNUC	E	*Cocos nucifera*	Arecaceae	X	X			
DIOSAN	N	*Diospyros sandwicensis*	Ebanaceae					X
MANIND	E	*Mangifera indica*	Anacardiaceae	Core		Core	X	
METPOL	N	*Metrosideros polymorpha*	Myrtaceae					X
MORCIT	E	*Morinda citrifolia*	Moraceae			X		
MYRLES	N	*Myrsine lessertiana*	Myrsinaceae		Core		Core	X
PANTEC	N	*Pandanus tectorius*	Pandanaceae	Core	X	Core		X
PERAME	E	*Persea americana*	Lauraceae			X	X	
PIPALB	N	*Pipturus albidus*	Urticaceae		X	X		X
POLHAW	N	*Polyscias hawaiensis*	Araliaceae	X			X	
PRIBEC	N	*Pritchardia beccariana*	Arecaceae	Core	X	Core		
PSYHAW	N	*Psychotria hawaiiensis*	Rubiaceae					X
PSYODO	N	*Psydrax odorata*	Rubiaceae	X	Core		Core	
RHUSAN	N	*Rhus sandwicensis*	Anacardiaceae			X	X	
SAMSAM	E	*Samanea saman*	Fabaceae		Core		Core	
SYZMAL	E	*Syzygium malaccense*	Myrtaceae	X				
TERCAT	E	*Terminalia catappa*	Combretaceae				X	
THEPOP	N	*Thespesia populneoides*	Malvaceae		X	X		

[a] E, exotic; N, native.

Note: Each experimental treatment had four core species that were chosen for either their slow or moderate rates of C turnover, and six additional species that had functional traits that were either redundant or complementary to the core species. Also noted are existing native species not removed from the experimental plots.

fell more than halfway into the buffer zone (2.5 m) were removed. Herbicide (30% Garlon 4 Ultra, mixed with 70% crop oil) was sprayed immediately onto cut stumps to prevent resprouting. Planting density was based on data from other Hawaiian lowland wet forests that have maintained a greater abundance of native species (Zimmerman et al. 2008), as well as the mature plant size. Total planted individuals per plot were as follows: 125 for Slow Complementary, 130 for Moderate Complementary, and 120 for the two Redundant treatments. We identified four separate areas (blocks) with appropriate conditions while using surveying equipment to lay out five plots in each block (Figure 1). Assignment of treatments to plots was random, with 20 plots measuring 20 m by 20 m and a 5 m perimeter buffer. We aimed for a 10 m distance between the buffers for each plot, but actual distances depended on terrain and avoidance of gullies and treefall gaps.

To evenly distribute the plants across each plot we set up a grid across each planting area with the number of quadrats depending on the number of large tree species designated for that treatment. These large tree species served as foci, with other species planted around them in a stratified random design (see Figure 1 for spatial configuration in each treatment). Plant spacing was based on adult plant size, such that large plants were placed 2 m away from their nearest neighbor, and medium and small plants were placed 1.5 m and 1 m away, respectively. Planting was done in stages from April 2013 to January 2014 because different species were ready for transfer at different times. All outplants were grown on Hawaiʻi Island from locally available propagules. When a preexisting native tree was located where an outplant was supposed to be planted we relocated the outplants, making sure that no plant was placed <1 m from any other plant. Plots were weeded before planting because several months had passed after clearing, and new nonnative seedlings had popped up after the disturbance. After planting, plots were weeded at 4- to 6-month intervals; native species plantings and recruits were left intact and invasive species were removed.

Data Collection

Experimental measurements commenced in January 2014 after all individuals had been planted and tagged for long-term monitoring. Carbon values in this article focus on summed aboveground biomass data collected in April and May 2016, which integrate the growth of outplanted individuals and recruits (seedlings of existing or outplant species) during 2 yr of experimental conditions. Data originate from individual on-site woody species but exclude biomass removed from study plots, belowground biomass, and herbaceous species biomass. Data collected for carbon analysis were plant height and diameter at breast height (DBH) at 1.3 m for all stems ≥1.0 cm diameter. Species were grouped in one of three categories: existing, outplants, and recruits. Existing species were trees left in situ after commencing experimental treatments (also inclusive of initial trees present in reference plots). Outplants refer to those species meant to define experimental treatment mixtures (i.e., all native and nonnative plants installed in cleared experimental plots). Recruits are defined as all new growth originating during the experiment from either existing seed pools or reproducing outplants.

We also wanted to determine if abiotic variables (light, soil nutrients, soil pH) might contribute to outplant and recruit C storage, regardless of treatment. Before the experiment (2012) and again during outplanting (2014), we took hemispherical photos to estimate percentage canopy cover. The photos were taken with a Canon EOS 5D camera and Canon EF 15 mm fisheye lens before analysis using WinsCanopy software (Regent Instruments, Inc., Quebec City, Canada). In July 2012 soils were sampled no deeper than 10 cm using trowels ($n = 4$ per plot, with one sample in each subplot). Volumetric soil core data are not expressed on an area basis due to difficulties associated with the extremely rocky terrain. Roots and debris were handpicked out of soil samples to maintain soil aggregates, dried at 60°C, and ground. Soils were analyzed for carbon (C) and nitrogen (N) in a Costech 4010 Elemental Analyzer (Costech Analytical Technologies, Valencia, California), and for

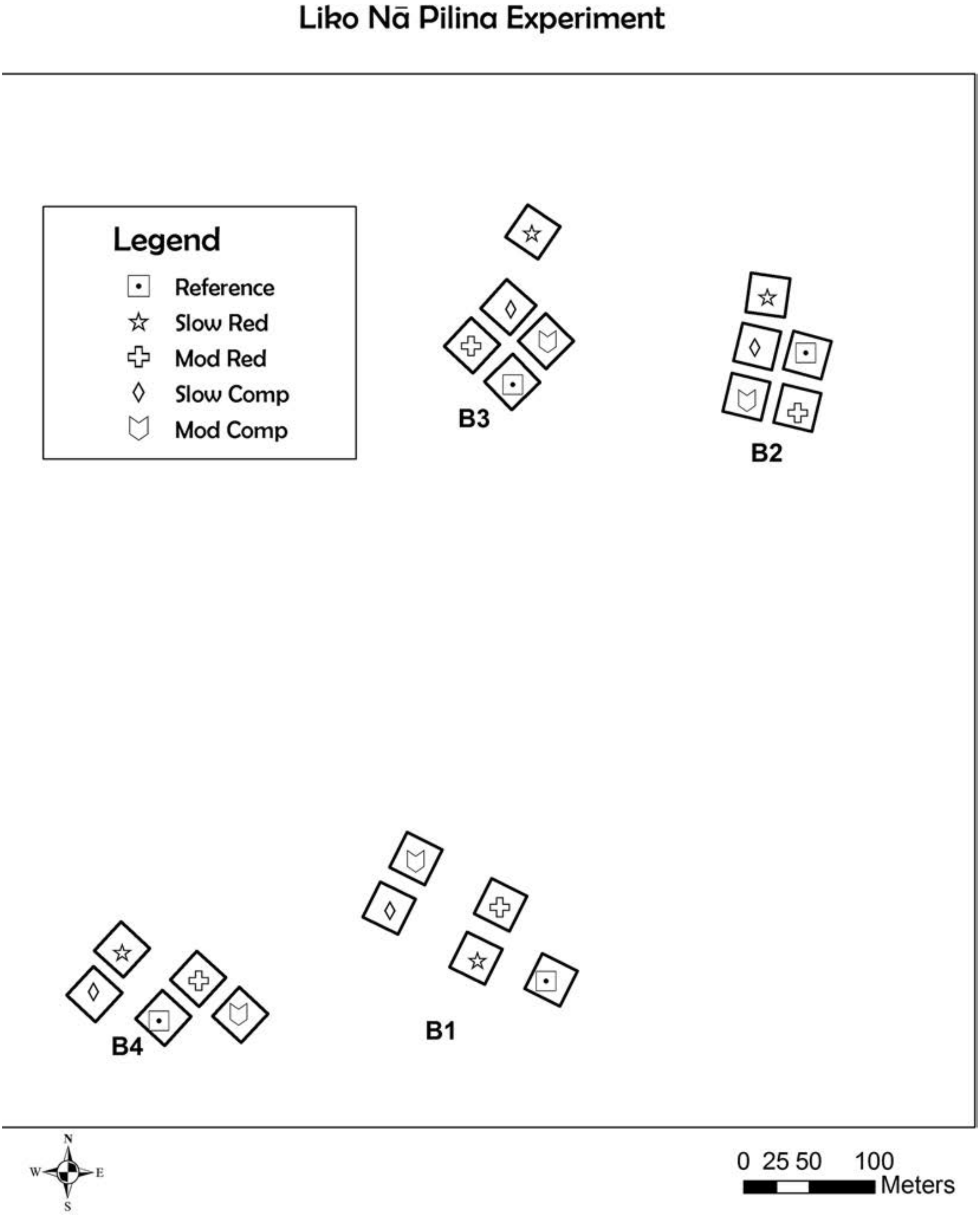

Figure 1. Map of the study site and Liko Nā Pilina experimental locations. Reference treatments include plots 1, 7, 12, and 19. Slow Redundant treatments include plots 2, 6, 15, and 16. Moderate Redundant treatments include plots 3, 9, 11, and 18. Slow Complementary treatments include plots 4, 8, 13, and 17. Moderate Complementary treatments include plots 5, 10, 14, and 20.

phosphorus (P) on a Technicon AutoAnalyzer AAI with parts from Pulse Instrumentation (Mequon, Wisconsin) after a modified Truog extraction. Cations (Mg, Ca, K, Na) were analyzed after ammonium acetate extraction on a Varian Vista MPX ICP-OES (Varian Analytical Instruments, Walnut Creek, California). All laboratory analyses were done at the Analytical Laboratory at University of Hawai‘i at Hilo.

Calculations

Carbon in aboveground biomass was calculated for outplanted and recruit trees and compared among all treatments. Calculations were completed using allometric equations for individual species or those generally applicable for species in wet tropical forests as described in past studies and the literature (Asner et al. 2011) (Supplemental Table S1). These equations use DBH, wood density, and height as independent variables. For most species, aboveground biomass was determined by diameter-to-biomass equations, supplemented with additional diameter-to-height equations as needed. For all individuals with a measureable DBH, the General Wet Forest equation (Chave et al. 2014), Hawai‘i-derived equations (Asner et al. 2011), or more species-appropriate equations (Donato et al. 2012, Hung et al. 2012, Goodman et al. 2013) were utilized. Tree heights were determined as needed via Asner et al. (2011) or field data when available. Where required, wood density estimates originated from Asner et al. (2011), Chave et al. (2009), the Global Wood Density database (Little and Wadesworth 1964, Anon. 1974, Benthall 1984, Chundoff 1984, Oey 1990, Flynn and Holder 2001, Tree Talk 2005), or previous field measures (R. Ostertag and field assistants, unpubl. data). Calculations include all stems ≥1 cm DBH, but exclude secondary growth such as branches below breast height. Biomass to C-equivalent conversions followed wood production industry standards (Alabama Forestry Commission 2016; D. D. Rayome, R. Ostertag, and S. Cordell, unpubl. data).

Authors' Note: Supplemental materials available online at BioOne (http://www.bioone.org/toc/pasc/current) and Project MUSE (http://muse.jhu.edu/journal/166).

Statistical Analysis

Statistics were examined using R 3.1.2 (R Core Team 2014) and JMP 11.2.0 (SAS 2013). To examine the effects of experimental planting, we compared the C amount in the outplants plus recruits as the response variable because this biomass represents growth in response to the experimental conditions. We focused on the plot level rather than the individual level because C in the plots integrate survival and growth. C values were *ln* transformed to achieve normality and equal variances. To examine the effects of the hybrid community treatments, we ran a complete randomized block analysis of variance (ANOVA), based on procedures by Logan (2010), followed by Tukey's tests to compare among the treatments. To examine differences in C across species, we examined the outplants and recruits separately, because it was a fairer comparison across species. Only a few species had recruits, and these were generally small individuals with small amounts of C. We ran one-way ANOVA tests for the outplants and the recruits; we did not test for a treatment effect here because we previously had verified by two-sample *t* tests that all the species found in multiple treatments (see Table 1) were not significantly different in C amounts.

We suspected that environmental variables also influenced C gain and chose several additional analyses to assess this potential connection. First, we utilized one-way ANOVA for pretreatment soil and light variables to test possible treatment differences before experimental manipulation. Among treatments, there was no significant difference in canopy openness, soil pH, or nutrients (C, N, P, Mg, Ca, Na, K). To test whether these abiotic variables influence C storage in outplants (independent of assigned treatment), we ran Pearson correlation tests between outplant C and seven environmental variables: soil pH, C, N, P, Mg, K, and canopy openness in 2014 at the start of the experiment. We omitted some variables from the analysis that were highly correlated (r > 0.8) to other soil variables and would have been redundant (i.e., Ca was omitted because it was correlated with Mg, and Na was omitted because it was correlated with C).

RESULTS

After 2 yr of experimental treatment conditions, our results indicate support for "Moderate" C cycling species mixtures but lack of support for "Complementary" mixtures. Existing native C totals in treatment plots ranged from 0.10 kg to over 6,200 kg, and reference plots that included invasives ranged from 0.14 kg to 5,652.01 kg. The hybrid community treatment type significantly influenced C storage in outplants ($F = 19.8$; df = 3, 9; $P < .0003$), but the block effect was not significant ($F = 0.813$; df = 3, 9; $P = .81$). The Moderate Redundant treatment had significantly more C than the other three treatments (Figure 2).

C measures at the treatment level were driven by a handful of species. Outplants ($F = 63.03$; df = 15, 715; $P < .0001$) and recruits ($F = 6.09$; df = 3, 204; $P = .0005$) species varied significantly in their C. Total experimental C value ranged greatly (Table 2, Figure 3). For most cases, the differences in treatments can be explained by responses of individual species therein. For outplants, *Artocarpus altilis*, *Cibotium glaucum*, *Terminalia catappa*, *Rhus sandwicensis*, and *Persea americana* all had high C contributions (Table 2, Figure 3). Of these, the overwhelming majority of new outplant C originated from the 622 kg contribution of *A. altilis*. Further, *Aleurites moluccana*, *Morinda citrifolia*, *Samanea saman*, *Syzygium malaccense*, and *Mangifera indica* all had notable contributions in at least one treatment type. In contrast, recruit biomass was most heavily influenced by contributions from *R. sandwicensis*, *Pipturus albidus*, and *C. glaucum* (Table 2, Figure 3). Of these, *R. sandwicensis* contributed the majority of new recruit C, over 30.39 kg. Further, environmental conditions had little influence on the aboveground C values. Before experimental conditions, there were no significant differences in canopy openness, soil pH, or nutrients (C, N, P, Mg, Ca, Na, K). The only significant effect of environmental conditions was that plots with lower soil P had significantly more outplant C (r = –0.5239, $P = .0373$), but none of the other environmental variables had any significant differences. In addition, none of the environmental variables was related to the existing tree density of basal area before the start of the experiment (data not shown).

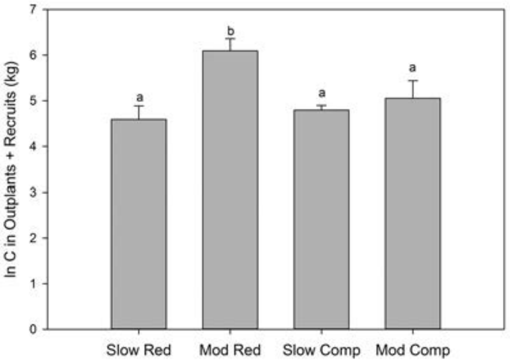

FIGURE 2. Mean (and standard error, $n = 4$) C found in the biomass across the four Liko Nā Pilina hybrid community treatment types. Only the Moderate Redundant treatment type differed significantly in C measures. Nontransformed values for treatments are 0.82 (standard error 0.89) for Slow Redundant, 3.62 (standard error 3.76) for Moderate Redundant, 0.90 (standard error 0.88) for Slow Complementary, and 1.22 (standard error 2.84) for Moderate Complementary. Statistically different treatments are denoted a and b.

DISCUSSION

We predicted that the treatment composed of species with moderate C cycling traits and more complementary functional trait values would have increased C storage when compared with treatments of species having slower C cycling traits or more redundant functional traits. However, as shown by our results after 2 yr of Liko Nā Pilina experimental conditions, the Moderate Redundant treatment had higher C storage than the other three treatments (Figure 2). Contrary to our expectations, core species in the two Moderate treatments, although chosen in part to have trait values related to increased

TABLE 2

Aboveground Carbon Mass for the Four Hybrid Treatments and Reference in the Liko Nā Pilina Experiment

Species Code	Hybrid Treatments/ Reference	Existing	Survived	kg/plant	Outplant	Survived	kg/ plant	Recruit	Survived	kg/ plant
ALEMOL	Slow Comp	0	0	0	94.43	20	4.72	0	0	0
	Mod Comp	0	0	0	83.32	20	4.17	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	0	0	0	0	0	0
	Ref	0	0	0				0	0	0
ANTPLA	Slow Comp	0	0	0	0	0	0	0	0	0
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	1.35	7	0.19	0	0	0
	Mod Red	0	0	0	0	0	0	0	0	0
	Ref	0	0	0				0	0	0
ARTALT	Slow Comp	0	0	0	0	0	0	0	0	0
	Mod Comp	0	0	0	488.35	21	23.25	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	622.08	20	31.10	0	0	0
	Ref	0	0	0				0	0	0
CALINO	Slow Comp	0	0	0	10.85	19	0.57	0	0	0
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	12.97	20	0.65	0	0	0
	Mod Red	0	0	0	0	0	0	0	0	0
	Ref	0	0	0				0	0	0
CIBGLA	Slow Comp	317.06	18	17.61	0	0	0	0	0	0
	Mod Comp	151.88	9	16.88	0	0	0	0	0	0
	Slow Red	0	0	0	269.06	72	3.74	0	0	0
	Mod Red	27.78	2	13.89	300.74	70	4.30	0	0	0
	Ref	86.49	4	21.62				0	0	0
CIBMEN	Slow Comp	43.32	4	10.83	0	0	0	0	0	0
	Mod Comp	100.25	10	10.03	0	0	0	0	0	0
	Slow Red	9.09	2	4.54	0.94	1	0.94	0	0	0
	Mod Red	19.67	3	6.56	3.33	1	3.33	0	0	0
	Ref	623.05	16	38.94				0	0	0
DIOSAN	Slow Comp	6306.52	22	286.66	0	0	0	0	0	0
	Mod Comp	5087.85	17	299.29	0	0	0	0	0	0
	Slow Red	786.48	14	56.18	0	0	0	0	0	0
	Mod Red	834.37	8	104.29645	0	0	0	0	0	0
	Ref	2383.90	18	132.44				0	0	0
MANIND	Slow Comp	0	0	0	21.65	15	1.44	0	0	0
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	33.87	16	2.12	0	0	0
	Mod Red	0	0	0	49.97	19	2.63	0	0	0
	Ref	0	0	0				0.78	1	0.78
METPOL	Slow Comp	28252.29	21	1345.35	0	0	0	0	0	0
	Mod Comp	43376.90	23	1885.95	0	0	0	0	0	0
	Slow Red	47778.93	38	1257.34	0	0	0	0	0	0
	Mod Red	46349.04	26	1782.66	0	0	0	0	0	0
	Ref	40395.35	27	1496.1242				0	0	0
MORCIT	Slow Comp	0	0	0	66.98	40	1.67	0	0	0
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	0	0	0	0	0	0
	Ref	0	0	0				0	0	0
MYRLES	Slow Comp	0	0	0	0	0	0	1.11	4	0.28
	Mod Comp	164.72	1	164.72	0	0	0	0	0	0
	Slow Red	573.06	2	286.53	0	0	0	0.55	1	0.55
	Mod Red	2.92	2	1.46	0	0	0	1.73	3	0.58
	Ref	615.57	5	123.11				0.29	2	0.15

TABLE 2 (continued)

Species Code	Hybrid Treatments/ Reference	Existing	Survived	kg/plant	Outplant	Survived	kg/ plant	Recruit	Survived	kg/ plant
PANTEC	Slow Comp	44.70	1	44.70	0	0	0	0	0	0
	Mod Comp	270.12	10	27.01	0	0	0	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	0	0	0	0	0	0
	Ref	0	0	0				0	0	0
PERAME	Slow Comp	0	0	0	57.33	22	2.61	0	0	0
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	121.13	22	5.51	0	0	0
	Ref	0	0	0				0	0	0
PIPALB	Slow Comp	0	0	0	2.35	5	0.47	22.34	30	0.74
	Mod Comp	0	0	0	3.48	9	0.39	21.74	40	0.54
	Slow Red	0	0	0	0	0	0	9.81	15	0.65
	Mod Red	0	0	0	0	0	0.00	14.77	25	0.59
	Ref	0	0	0				0	0	0
PSYHAW	Slow Comp	1429.24	53	26.97	0	0	0	3.35	17	0.20
	Mod Comp	1680.47	63	26.67	0	0	0	5.18	13	0.40
	Slow Red	1670.13	93	17.96	0	0	0	2.49	8	0.31
	Mod Red	1173.10	88	13.33	0	0	0	4.59	8	0.57
	Ref	1284.75	56	22.94				2.78	4	0.70
PSYODO	Slow Comp	0	0	0	0	0	0	0	0	0
	Mod Comp	0	0	0	1.38	6	0.23	0	0	0
	Slow Red	0	0	0	1.01	6	0.17	0	0	0
	Mod Red	0	0	0	3.88	10	0.39	0	0	0
	Ref	0	0	0				0	0	0
RHUSAN	Slow Comp	0	0	0	192.88	74	2.61	5.93	16	0.37
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	280.32	79	3.55	30.39	28	1.09
	Ref	0	0	0				0	0	0
SAMSAM	Slow Comp	0	0	0	0	0	0	0	0	0
	Mod Comp	0	0	0	53.15	20	2.66	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	55.19	19	2.90	0	0	0
	Ref	0	0	0				0	0	0
SYZMAL	Slow Comp	0	0	0	0	0	0	0	0	0
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	54.01	32	1.69	0	0	0
	Mod Red	0	0	0	0	0	0	0	0	0
	Ref	0	0	0				0	0	0
TERCAT	Slow Comp	0	0	0	0	0	0	0	0	0
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	287.02	40	7.18	0	0	0
	Ref	0	0	0				0	0	0
TETHAW	Slow Comp	0	0	0	0	0	0	0	0	0
	Mod Comp	0	0	0	0	0	0	0	0	0
	Slow Red	0	0	0	20.33	12	1.69	0	0	0
	Mod Red	0	0	0	17.49	14	1.25	0	0	0
	Ref	0	0	0				0	0	0
THEPOP	Slow Comp	0	0	0	5.70	5	1.14	0	0	0
	Mod Comp	0	0	0	4.94	6	0.82	0	0	0
	Slow Red	0	0	0	0	0	0	0	0	0
	Mod Red	0	0	0	0	0	0	0	0	0
	Ref	0	0	0				0	0	0

Note: Rows indicate total carbon mass in kilograms, number of surviving plants, and average plant mass for existing, outplant, and recruited individuals. See Table 1 for species codes. *Cocos nucifera* and *Prichardia beccariana* were excluded from analysis.

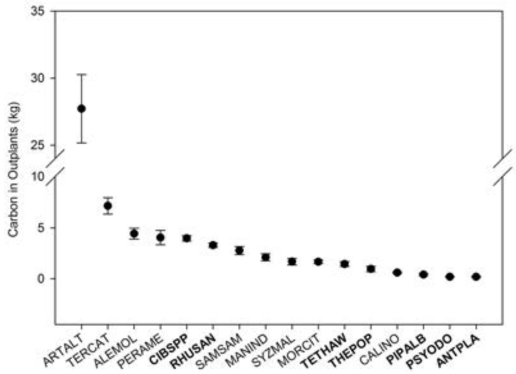

Figure 3. Mean (and standard error, $n = 16$) C found in the biomass across Liko Nā Pilina hybrid community treatment outplanted species. Species codes in **bold** type indicate native species (see Table 1 for species codes). Of contributing species, *Artocarpus altilis* had the most influence on C measures. Species values in individual treatments are displayed in Table 2. Species included here are outplants only; there was no significant difference between treatments with respect to carbon accumulation.

rates of C cycling, were in some cases surpassed in growth in the field by "noncore" species. Further, Redundant species mixtures composed of fast-growing and high carbon-accumulating species might provide a benefit to a restoration project earlier, whereas Complementary mixes might support long-term carbon accumulation. In our system, the level of weeding required was high; therefore the Moderate Redundant treatment has the advantage of being more likely to obtain quick canopy closure and aid in preventing additional maintenance. Our experimental mixes were selected based on functional trait expression of adult specimens, and the results after 2 yr may not represent mature trees. It is therefore important in restoration planning to recognize the importance of emphasizing growth trajectories within the greater scope of species life history when prescribing restoration designs. Discarding the value of Moderate Complementary mixtures would be unwise without contextualizing results at the species level. Outplant and recruit species including *A. altilis*, *C. glaucum*, *T. catappa*, *R. sandwicensis*, and *P. americana* are indeed influencing C, but they are growing at the same rate regardless of treatment (Figure 3). For example, *A. altilis* is successfully naturalized or cultivated in almost all suitable terrestrial ecosystems due in part to its ease of management, vigorous growth habit, and versatility in use (Janick and Paull 2008, Breadfruit Institute 2016). Although the functional trait approach used in this experiment may not be best for all species types or successional stages, it is important to report and understand early results for comparison with later successional stages that may favor complementarity for sustainable productivity and invasion resistance.

We found that measuring C storage in outplanted individuals and recruits was an appropriate metric for evaluating effects on aboveground C in restoration approaches. It has been shown in these forests that once invaded, C cycling and storage is altered and no longer benefits C storage in the long term due to decreased longevity of invasives (Hughes and Denslow 2005, Mascaro et al. 2012, Asner et al. 2016). Indeed, shifting C in a deliberate way toward native and noninvasive exotic species has implications for structural and subsequent ecosystem process changes. Current reference plots as well as that from both pre-experimental conditions and nearby lowland sites indicates that increased invasive C detracts from native species recovery (Cordell et al. 2016). These new C cycling regimes may affect overall integrity and long-term resilience, especially when dwindling forests face continued pressure from impacts of continued global change.

Our experimental work emphasizes the potential of Hawaiian forests as a simple and unique perspective for examining C, with species invasions, human impacts, and management interventions all occurring simultaneously (Friday et al. 2015, Ostertag et al. 2015, Asner et al. 2016). Carbon content varies among tropical tree species (Martin and Thomas 2011, Orihuela-Belmonte et al. 2013), yet the relatively few species in historic Hawaiian lowland wet forests store C comparably to that of more biodiverse forests in other regions. Similarly invaded mature Hawaiian wet lowland forests store 72.8 Mg C ha^{-1} (Asner et al. 2016), and the managed density of our experiment allows up to

291 Mg C ha^{-1}. This total includes reference conditions as well as existing trees, 4.02 Mg C ha^{-1} in outplanted individuals, and 0.19 Mg C ha^{-1} in recruits. Comparable tropical wet forests in Bolivia store approximately 67.5 Mg C ha^{-1}, and those in Brazil store 90 Mg C ha^{-1} (Jespen 2006).

CONCLUSIONS

Overall, we consider our experiment an important contribution to the growing literature on including C aspects in restoration as well as the importance of increasing stored C in forests globally (FAO 2010, Raunikar et al. 2010, Hurmekoski and Hetemäki 2013, Payn et al. 2015). Our experiment supports the finding that mixed species plantings benefit C balances with peripheral benefits for other ecosystem services (Lindenmayer et al. 2012, Hulvey et al. 2013). We have previously shown the approach to be both appropriate and cost-effective for the Hawaiian lowland wet forest context [Cordell et al. 2016; D. D. Rayome, R. Ostertag, and S. Cordell (unpubl. data)]. It is important to note that our experimental forest is still developing: canopy closure has not yet occurred, nor have several other factors commonly associated with a mature wet tropical forest. Changing experimental and environmental conditions continue to influence overall forest ecology, and we expect treatments to continue positive C cycling as plots mature and more-complex forest dynamics begin to unfold. We expect C and other services to vary after maturity as well, providing a basis for treatment comparison well into the coming decades. Longer-lived species will likely affect C through their growth, and more prolific species or those with traits more useful for survival will affect C dynamics in ways that support competition-driven C balances (Lusk et al. 2008, Suding et al. 2008). Finally, we understand that a more comprehensive understanding of C would benefit from inclusion of belowground C and not measured aboveground biomass (herbaceous and immature plant matter, snags, and other coarse woody debris; on-site carbon cycling through leaf detritus and connected trophic webs). Focus on more comprehensive C effects allows for more informed restoration planning and increased likelihood of successful interventions (Pokorny et al. 2005, Cordell et al. 2016). The vital snapshot of early C values in this study will be useful for contrasting with later results when the trade-offs between rate of C accumulation and functional redundancy are realized.

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SUPPLEMENTAL TABLE S1

Equations Used for Diameter-to-Height and Diameter-to-Aboveground Biomass for Liko Nā Pilina Experimental Species (after Asner et al. 2011)

Scientific Name	Diameter-to-Height Model	DBH Min	DBH Max	Diameter-to-AGB Model	DBH Min	DBH Max
Aleurites moluccana	H=exp(0.148+0.9772(ln(D)–0.1276*(ln(D)^2)))	2.1	43.5	B=0.0673*(0.38*D^2*H)^0.976	N/A	N/A
Antidesma platyphyllum	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.67*D^2*H)^0.976	N/A	N/A
Artocarpus altilis	Not required for AGB	N/A	N/A	B=0.1245*(D)^(2.4163)	N/A	N/A
Calophyllum inophyllum	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.57*D^2*H)^0.976	N/A	N/A
Cibotium glaucum	H=exp(–0.6277+1.691*ln(D))*1.1386/100	2	58	B=Π*(D/2)^2*H*100*0.22/1000	N/A	N/A
Cibotium menziesii	H=exp(–0.6549+1.8683*ln(D))*1.1705/100	2.8	65.2	B=Π*(D/2)^2*H*100*0.21/1000	N/A	N/A
Diospyros sandwicensis	H=–2.1177+15.9999*(1–exp(–0.1178*D))	2	53.9	B=0.0673*(0.74*D^2*H)^0.976	N/A	N/A
Mangifera indica	H=exp(0.5272+0.8675*(ln(D))–0.069*(ln(D))^2)	1.1	161.8	B=0.0673*(0.53*D^2*H)^0.976	N/A	N/A
Metrosideros polymorpha	Not required for AGB	N/A	N/A	B=exp(–2.1311+2.5011*ln(D))*1.0671	1.8	30
Morinda citrifolia	(D ≤ 1.6) H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	1.6	B=0.0673*(0.63*D^2*H)^0.976	N/A	N/A
Morinda citrifolia	(D > 1.6) H=exp((–0.2695)+1.4513(ln(D))–0.2712(ln(D))^2)	>1.6	15.2	B=0.0673*(0.63*D^2*H)^0.976	N/A	N/A
Myrsine lessertiana	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.53*D^2*H)^0.976	N/A	N/A
Pandanus tectorius	Not required for AGB	N/A	N/A	B=exp(–5.66+3.23*ln(D))	N/A	N/A
Persea americana	H=exp(0.3028+0.8605*(ln(D))–0.0369*(ln(D))^2)	1.5	38	B=0.0673*(0.55*D^2*H)^0.976	N/A	N/A
Pipturus albidus	H=exp(0.6561+0.2104(ln(D))+0.1676(ln(D))^2)	1.2	7.4	B=0.0673*(0.3*D^2*H)^0.976	N/A	N/A
Polyscias hawaiensis	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.5*D^2*H)^0.976	N/A	N/A
Pritchardia beccariana	Not required for AGB	N/A	N/A	B=–3.3488+2.7483(ln(D))	N/A	N/A
Psychotria hawaiiensis	H=9.2527*(1–exp(–0.1863*D))	0.8	19.9	B=0.0673*(0.54*D^2*H)^0.976	N/A	N/A
Psydrax odorata	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.5*D^2*H)^0.976	N/A	N/A
Rhus sandwicensis	H=exp(0.763+0.2639*(ln(D))+0.222*(ln(D))^2)	1.4	7.4	B=0.0673*(0.54*D^2*H)^0.976	N/A	N/A
Samanea saman	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.45*D^2*H)^0.976	N/A	N/A
Syzygium cumini	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.67*D^2*H)^0.976	N/A	N/A
Syzygium malaccense	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.642*D^2*H)^0.976	N/A	N/A
Terminalia catappa	H=exp(0.5120+0.7583*ln(D)–0.0322*ln(D)^2)*1.0409	N/A	N/A	B=0.0673*(0.6625*D^2*H)^0.976	N/A	N/A
Thespesia populneoides	H=exp(0.5397+0.3191*(ln(D))+0.0404(ln(D))^2)	1.8	104	B=0.0673*(0.63*D^2*H)^0.976	N/A	N/A

Note: All aboveground biomass equations required diameter at breast height (DBH) in cm (height of 1.3 m). Equations also requiring height were met with either DBH-based height estimation equations or individual field data. Species that did not meet minimum DBH requirements (*Cocos nucifera*, *Pritchardia beccariana*) were excluded from analysis. For some species, diameter-to-height models were not required for calculating aboveground biomass (AGB). N/A indicates species without DBH size limitations.