

# Restoring Ecosystem Services Tool (REST): a Computer Program for Selecting Species for Restoration Projects Using a Functional-Trait Approach

Donald Rayome, Nicole DiManno, Rebecca Ostertag, Susan Cordell, Bryson Fung, Anthony Vizzone, Pauleen Pante, and Reuben Tate



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#### **Abstract**

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This report describes the Restoring Ecosystem Services Tool (REST) computer program, which was developed to assist users in selecting plant species for more effective landscape management. Many habitats have been altered to the extent that it is no longer possible to restore their plant communities to their preexisting conditions. In these cases, a functional trait-based restoration approach to restoring some degree of ecosystem services, functionality, and structure may be helpful. To conduct functional trait-based restoration, information about the functional characteristics of species is required, and decisions are made by choosing a combination of species that have trait profiles that meet desired restoration goals. However, the value and applicability of functional trait-based restoration has been limited in its accessibility to land managers and stakeholders. The REST program is specifically designed to help users select a suite of plant species whose life history traits relate to addressing a specific management objective. Trait data from global databases have been incorporated into the program, providing some data from many species. Users define management objectives from a menu of available restoration goals (drought tolerance, fire tolerance, successional facilitation, or carbon storage) to filter for connected functional traits. Once the user has chosen appropriate functional traits for analysis, a potential species pool, chosen by the user, is required for analysis. Alternatively, users may upload their own trait and species data as a .csv file. REST then applies the statistical technique of principal components analysis to visualize species position in "trait space." The program provides written and visual analysis that compares the influence of each of the functional traits. The user can run REST with various species combinations, then apply this information to decisions about which species will best meet restoration objectives. New data and program versions can be found at https://hilo.hawaii.edu/faculty/ostertag/. Please contact Dr. Rebecca Ostertag at ostertag@hawaii.edu for program questions or concerns.

Keywords: Functional traits, ecosystem services, land management, drought tolerance, fire tolerance, successional facilitation, carbon storage.

# **Summary**

This report documents Version 1 of the Restoring Ecosystem Services Tool (REST), including its development, software, and use in restoration and landscape management. REST is a computer program that allows comparison of plant species through the use of principal components analysis (PCA). The program compares associated functional traits of potential species mixes that can be used to meet land management goals, and has applicability in all terrestrial ecosystem types. It is simple and flexible as a management tool, providing an informed basis for decisionmaking that can complement other protocols prior to restoration or other forms of intervention.

Section 1 provides an introduction for the underlying premises leading to REST's development. These include background concepts in ecosystem restoration and management, the importance of species selection, the value of applying plant functional traits in interventions, and considerations when selecting functional traits for analysis in REST.

Section 2 describes how intervention attempts in the Hawaiian lowland forest environment led to REST's structural development. Specifically, this case study focuses on the realities of intervening in heavily modified landscapes as exemplified by the *Liko Nā Pilina* hybrid restoration experiment. Here we present five steps leading from initial conceptualization, identification of management goals, and preliminary data collection to the PCA inherent to REST that informs final species choices. In **Step Five**, we use the *Liko Nā Pilina* case study to provide detailed instructions on how to use the REST tool when one maintains one's own trait database.

Section 3 details the REST user interface, including restoration goals, species selection, functional traits selection, and value editing. This chapter also further details the four restoration goals and 270 functional trait options within REST, noting functional trait connections to goals as well as brief descriptions, formatting within the program, and suggested references for additional information.

Section 4 presents a technical overview of constructing REST as a compact Windows<sup>TM</sup>-based software program as well as program caveats and future directions.<sup>1</sup>

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# 1.0 Background

Restoration, in its broadest sense, involves improving conditions at a site to meet desired objectives. Traditionally, improving site conditions has meant an effort to return to a former, less-disturbed state, and much has been learned by examining recovery rates across ecosystem types (e.g., Rey Benayas et al. 2009). Yet in an increasing number of ecosystems, it is not feasible to return to a previous state for reasons that include the lack of reference sites or historical baseline conditions, irreversible climate change, and colonization by highly invasive nonnative species that cannot practically be removed (Hobbs et al. 2014, Zedler et al. 2012). Further, active forms of restoration via planting or encouraging specific species (Holl and Aide 2011) often proceed while information is lacking about species ecology, genetics, physiology, and evolutionary biology (Jones 2013). Choosing plant species for restoration can be a difficult task because it is not always clear which species are the most appropriate to achieve a particular restoration goal. A multivariate approach that allows users to identify a range of species likely to help them meet restoration objectives is one potential solution. Appropriate species chosen based on their life history characteristics can then be combined in a simulated community to see how these species are related to each other in their characteristics.

## 1.1 Importance of Species Selection in Restoration

One major stumbling block in designing restoration plans is deciding which species to use. The motivation for this approach to species choice comes from the desire to merge practical and ecological restoration techniques, as well as the recognition that species choice for restoration can be a difficult and value-laden process. There are practical concerns such as cost, availability of seeds, and ability to propagate that can partially dictate decisions. Yet in many cases, little is known about each species' life history and how each will interact with other species when planted together, particularly if the planting might represent new combinations that are not seen in the field. Situations in which species that do not share an evolutionary history are thrust together provide relevant examples. These new combinations could arise because of invasion by nonnative species, range shifts of species resulting from climate change, or new species distributions resulting from land use activities. Although "novel ecosystems" (Hobbs et al. 2006) are becoming widespread, there is a very limited understanding in the ecological literature about the long-term implications of new species interactions and their effects on ecosystem functioning.

## 1.2 The Value of a Functional Trait-Based Approach

Functional trait-based restoration is based on the principle that ecosystem function depends in part on the expression of various morphological, structural, physiological, or chemical traits of organisms as well as environmental filters and the interaction between traits and environments. Functional traits reflect fundamental life-history and resource-use tradeoffs (Reich 2014). Because these traits vary predictably across environments, it is assumed that they are the products of natural selection. For plants, global datasets show how traits vary continuously along abiotic resource availability gradients and across biomes (Chave et al. 2009, Donovan et al. 2011, Reich 2014, Wright et al. 2005). Evolutionary tradeoffs faced by organisms in resource acquisition (e.g., light, water, and nutrient uptake) and resource processing (e.g., net primary productivity) result in different ways to make a living, termed the "worldwide 'fast-slow' plant economics spectrum" (Reich 2014). Plant species on the slow end of the spectrum have low rates of resource acquisition and processing, which requires leaf, stem, and root traits that are more conservative and efficient in resource use than plant species on the fast end of the spectrum. Being a slow species is advantageous under low-resource conditions because resource conservation traits enhance survival, but being a slow species can be a drawback under higher resource conditions. In a given biome, there is selection for trait convergence, but within a more localized community, it is likely that interspecific competition ensures that species differ along the slow-fast continuum (Reich 2014). Thus, at the community and ecosystem levels, consideration of functional trait values can help explain the distribution of species, the assembly of communities, and the rate of ecosystem processes (Reich 2014; Reich et al. 1999, 2003).

At the community level, the functional trait profiles of species can be represented by functional diversity. Simply put, functional diversity is a way to define diversity of species traits within a community or ecosystem, encompassing metrics that focus on the magnitude, variation, and dissimilarity in species' functional traits (Schleuter et al. 2010). Considering functional diversity rather than species diversity may be a more promising approach for addressing questions of how species influence the structure and function of ecosystems (Laureto et al. 2015) or community assembly (Bhaskar et al. 2014). Therefore, selecting species for restoration projects that have a specific set of trait values should influence competitive interactions, resource availability, and ecosystem structure and functioning. Ideally, these functional traits should be easily defined and measured, so that the approach is transportable and flexible, and the predicted successional outcome of restoration can be tested (Ostertag et al. 2015). For example, selecting species with a broad range of functional traits (i.e., low niche overlap or inversely high functional divergence) may preclude exotic species from invading if their functional trait values are already represented in the community (Funk et al. 2008).

Because functional traits differ among species and environments in predictable ways, they can be linked to ecosystem properties and used in restoration to achieve specific objectives in ecosystem functioning (Funk et al. 2008). For example, the growth and recruitment of species with certain functional traits could be selected for by choosing species that facilitate plant and animal recruitment. If the objective is to build a community that will be less likely to burn, one could choose species with traits such as high leaf water content and low levels of volatile compounds.

Although most studies attempting to link traits to ecosystem properties have been carried out in relatively simple systems, the field can be expanded to incorporate increasingly complex systems with higher species and life form diversity. The Restoring Ecosystem Services Tool (REST) program allows the user to design new simulated communities to make some assessments about which combinations of species may be best for specific restoration goals. REST has some data incorporated into it, yet allows users to enter their own species list and trait data. This strategy for species selection is generalizable and flexible, allowing users to choose the species and desired functional outcomes, while acknowledging limiting factors such as economics (e.g., cost of seed/plants, labor, time); logistics (e.g., availability of species, project or budget timelines); and predictability of climate or disturbance regimes, as well as the goals and expectations of stakeholders. The choice of species for restoration objectives is not limited to the scores from their traits alone, but could also incorporate other aspects, such as maintaining a diverse and resilient community that fosters the desired environmental outcomes. REST can be used iteratively; e.g., it can be reset and run again after removing species to continually refine choices.

## 1.3 Importance of Functional Traits: What to Consider

Another difficult decision is the choice of traits. In part, restoration goals determine the traits that should be of interest to consider for a particular restoration project. For example, if the aim is to build an ecosystem that is tolerant of fires, traits such as bark thickness and leaf water content may be of interest. In general, there are six traits that the literature suggests are helpful in the attempt to understand life histories of various species (box 1).

These traits appear often in global analyses (Adler et al. 2014, Kunstler et al. 2016, van Bodegom et al. 2014). If you have no prior plant functional trait knowledge, examining these six traits will provide a good foundation. When you chose a restoration goal in the REST program, it will populate with a list of suggested functional traits that might be linked to your restoration needs.

#### Box 1

#### Key Traits Reflect Resource Use and Life History

- Foliar Nitrogen (resource acquisition)
- Seed mass (reproductive investment and dispersal)
- Specific leaf area (resource allocation)
- Wood density (resource allocation)
- Leaf lifespan (resource allocation)
- Maximum plant height (dispersal)

# 2.0 Hawaiian Lowland Forest Context Leading to REST Development

The Hawaiian archipelago has many extremes of biological invasion, one of which is the remnant Hawaiian lowland wet forest (Zimmerman et al. 2008) that led to the development of REST. Approximately half the flora in Hawaii is not native (Wagner et al. 1999), and a number of invaders have been shown to have strong ecosystemlevel effects on carbon and nitrogen cycling and native biological diversity (e.g., Hughes and Denslow 2005, Litton et al. 2006, Vitousek and Walker 1989). A combination of events has led to systematic alteration of low-elevation lands, including (1) small-scale clearing and burning for agriculture and housing by Hawaiians prior to European contact (Kirch 2002); (2) large-scale clearing for sugarcane agriculture (Cuddihy and Stone 1990); (3) planting and aerial seeding of nonnative trees by territorial foresters, stemming from their lack of understanding about native forest function (Woodcock 2003); and (4) intentional and accidental introduction of many alien plants and animals that benefited from a mild climate, limited interspecific competition, and enemy release (Denslow 2003). The result is a series of communities dominated by mixtures of species that share no evolutionary history, and which contain high proportions of nonnative species classified as invasive.

REST is a culmination of more than a decade of research conducted in a heavily invaded Hawaiian lowland wet tropical forest. Numerous restoration attempts led to the development of the restoration project "*Liko Nā Pilina*: Developing Novel Ecosystems that Enhance Carbon Storage, Native Biodiversity, and Human Mobility in Lowland Hawaiian Forests," funded by the Strategic Environmental Research and Development Program (SERDP).

# 2.1 Focus on Functionality as a Realistic Restoration Compromise

In these highly altered habitats, we have no clear historical guide to what species should be planted to achieve traditional restoration goals, and it has become clear that maintaining these forests as all-native species assemblages is unsustainable in terms of labor, logistics, and cost (Cordell et al. 2009, Ostertag et al. 2009). Functional trait-based restoration can involve the use of species not originally found in a given site—including exotic species (Ewel and Putz 2004, Schlaepfer et al. 2011)—guiding the biodiversity toward more favorable species assemblages. The application of functional trait theory in restoration and management is an exciting new approach that can be used to understand the persistence of species and ecosystems as well as build model communities with desired ecosystem functions.

## 2.2 Liko Nā Pilina as a PCA-Based Functional Traits Example

The Liko Nā Pilina project evaluates four different combinations of species to determine the effectiveness of native and nonnative species mixes, or "hybrid ecosystems," for their ability to maintain valuable forest structure and ecosystem services (see Ostertag et al. 2015 for more details). The Hawaiian name reflects the growing relationships that are developing in these new mixtures. The experimental species mixtures were designed using ecological theory related to community assembly rules and functional traits. In each community mixture, four core species were chosen based on functional traits that relate to carbon sequestration (note management goal 1 below), while the six additional species were chosen based on their traits being either redundant or complementary to the core species. Selecting species based on redundancy or complementarity is testing community assembly theory, in relation to invasion resistance, as it has been hypothesized that species with characteristics that complement one another will occupy different niche spaces and lead to a community that resists invasions while allowing native recruitment (note management goals 2 and 3). The particular management goals of this experiment are to develop hybrid ecosystems with the following traits:

- Capable of sequestering substantial amounts of carbon
- Resistant to invasion so that the hybrid ecosystems can maintain themselves with relatively little labor input
- Sustain a broad range of native biological diversity
- Remain open enough at ground level to allow unrestricted human movement

The *Liko Nā Pilina* site is a lowland (30 m above sea level) wet forest at the Keaukaha Military Reservation (KMR, 19°42'15"N, -155°2'40"W) in Hilo, Hawaii. A defining site feature is the substrate—an 'a'ā lava flow dated as being 750 to 1,500 years old. This substrate, challenging for farming or mobility, is why this landscape remains uncleared. Rainfall averages 3347 mm/yr (Giambelluca et al. 2013), and mean annual temperature is 22.7 °C (Giambelluca et al. 2014). Native trees in the canopy and midstory define the forest, but these species are not regenerating under current conditions (Cordell et al. 2009). Rather, nonnative trees and shrubs comprise approximately 45 percent of the basal area (Ostertag et al. 2009). As methods for selecting and comparing aspects of potential *Liko Nā Pilina* candidate species informed the development of REST, the trait-based method we used employs five steps:

#### Step 1: Articulate objectives and constraints—

Because restoring this area to an all-native ecosystem is no longer economically feasible, we elected to create hybrid ecosystems with objectives to increase carbon storage, provide invasion resistance, and enhance native seedling regeneration.

#### **Step 2: Select appropriate functional traits**—

We selected a set of traits related to successional facilitation and carbon storage (table 1). Two variables are categorical (stature and canopy architecture) and were given ordinal numbers as a code.

#### Step 3: Determine pool of species for trait sampling and restoration potential—

Users must define their species pool based on contextually unique knowledge and objectives. To choose species for the experiment, we compiled a list of candidate species capable of surviving in lowland wet forest (LWF) environments in east Hawaii Island. For our purposes, LWF was defined as <700 m elevation and >2500 mm annual rainfall (Price et al. 2007). These climatic conditions are compatible with the study site where the hybrid ecosystem experiment was conducted. In

Table 1—List of functional traits measured in the candidate species for the *Liko Nā Pilina* experiment (after Ostertag et al. 2015)

Functional trait	Biological significance	Trait range	Source of data
Leaf-to-petiole ratio	Light acquisition, self-shading	2.81-200.00	Measured
Leaf thickness (mm)	Resource acquisition, longevity, resource use	0.17 - 1.40	Measured
Leaf mass per area (g/m <sup>2</sup> )	Photosynthesis, resource availability, longevity	8.24-469.22	Measured
Leaf N percentage (%)	Concentration of RuBisCO, photosynthesis, fast to slow strategies	0.55–2.25	Measured
Leaf C percentage (%)	Leaf construction, resource use	32.62-49.63	Measured
Leaf C:N	Leaf longevity, fast-to-slow strategies	14.82-79.78	Measured
Leaf P (%)	Leaf quality	trace-0.30	Measured
Wood density/specific gravity (g/cm <sup>3</sup> )	Diameter growth rate, mortality rate, hydraulic capacity, carbon storage	0.16–1.51	Measured
Instantaneous water use efficiency	Water use efficiency, resource use and acquisition	42.26–154.16	Calculated
Plant height at maturity (m)	Competitive vigor, plant fecundity, light acquisition	5-30	Bibliographic
Seed mass (g)	Dispersal, longevity, survival	<0.01-2.50	Bibliographic
Leaf area (cm <sup>2</sup> )	Photosynthetic capacity, resource allocation	2.8->1000	Measured
Leaf water content (%)	Resource use and allocation, fast-slow strategies	2.59-85.9	Measured
Stature <sup>a</sup>	Dispersal, longevity, carbon storage	1–3	Observation
Canopy architecture <sup>b</sup>	Light interception, stability	1–3	Observation

C = carbon; N = nitrogen; P = phosphorus; RuBisCO = ribulose-1,5-bisphosphate carboxylase/oxygenase.

<sup>&</sup>lt;sup>a</sup> Vertical position in the forest (1 = understory; 2 = mid-story; 3 = overstory).

<sup>&</sup>lt;sup>b</sup> Clustering of branches relative to the canopy (1 = bottom; 2 = middle; 3 = top).

addition, these species were chosen because they were not considered invasive, determined by using Hawaii Weed Risk Assessment scores (Daehler 2009). We examined 29 species for the overall species pool and aimed to use REST to condense to a smaller list that would allow us to simplify the logistics surrounding our experiment (i.e., fewer species to purchase, propagate, and plant).

#### Step 4: Collection and preparation of trait data—

We sampled plant traits across the full range of conditions in which Hawaiian LWF is found to account for both site and environmental heterogeneity. In total, we sampled traits at 25 sites throughout east Hawaii Island in addition to using existing data from the literature. The most time- and effort-consuming steps in making species choices via trait use involve creating the potential species pool and collecting trait data. However, some shortcuts can be taken for those who do not have the resources to collect original data. REST contains some global trait databases, while other data can be sought out through the literature. There is also a variety of resources that provide background on data collection methods. The *Prometheus-Wiki* (http://prometheuswiki.publish.csiro.au/tiki-custom\_home.php) provides protocols in ecological and environmental plant physiology and is updated by the research community. Another useful reference is Cornelissen et al. (2003) (http://cef-cfr.ca/uploads/Membres/CornelissenProtocol.pdf), which provides standards for functional trait measurements.

#### Step 5: Using REST data analysis for final species choice—

*Installation*—To install REST, double-click the newest version of *RESTInstaller* and follow the instructions found in the installation wizard (please note that, as this is an executable file, administrative or other permissions will be required to allow installation). The program will then install itself as well as create shortcuts for easy access.

**Program on startup and personal database upload**—On startup, after loading, the program will appear as in the screenshot shown in figure 1. As a part of the REST loading process, an Internet connection is required to update the database with any species additions or trait changes. However, REST can also start from the most recent archived version. During Step 4, the *Liko Nā Pilina* project created its own functional trait database, which included 29 species and 15 traits. REST provides users with the option to import a personal database of species and traits in the form of a .csv file (fig. 2) in order to skip the manual process of selecting traits and species. In the event that the user has not created their own database, REST also provides the option to use the species and trait data currently stored within; this manual process is outlined in section 3.0, "REST User Interface." After selecting

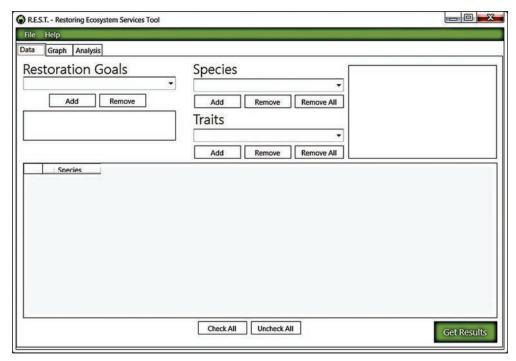


Figure 1—Initial REST interface once program has loaded.

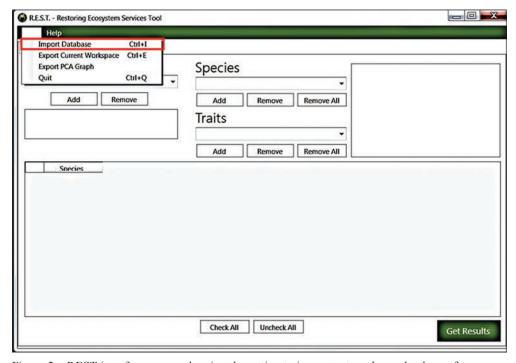


Figure 2—REST interface screen showing the option to import external .csv databases for manipulation in the program.

the "import database" option, the screen-captured notification will appear as shown in figure 3. This window's purpose is to warn the user that only .csv files will be accepted: select OK. After acknowledging the previous warning, a new window will appear that allows you to browse for the .csv files you wish to use (fig. 4). All .csv files can be imported, but if they are not formatted correctly, the program will notify you that an error has occurred and it will read your .csv file only partially.

The format should be species in the first column followed by traits (fig. 5). The units of each trait should be added to the trait name. Species and traits will appear in the program exactly as typed. Note that if a species or trait is already in the database but spelled differently, it will appear as a new trait or species. If you would like to follow along with the example in the rest of this section, import the file called LikoNaPilina.csv.

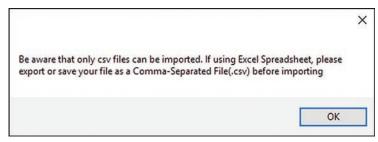


Figure 3—Warning screen indicating that external databases must be in the .csv (comma-separated) file type prior to import and use.

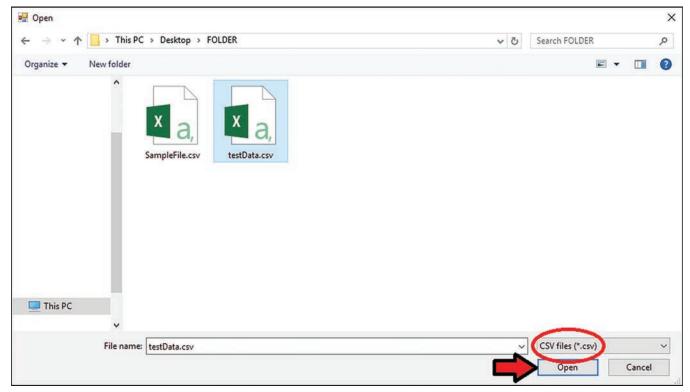


Figure 4— File browse interface allowing user database import into REST.

4	Α	В	С	D	E
1	Species	Trait1 (mm)	Trait2 (g)	Trait3 (m)	Trait4 (%)
2	species1	40	2	10	
3	species2	200	9	20	
4	species3	10	3	50	
5					
6					
-					

Figure 5—Example of .csv file formatting for use in REST.

REST PCA graph, analysis and interpretation—Once the personal database has been imported successfully, the largest section of the Data tab will show the project data: species, traits, and values (fig. 6). Also, in this tab, the upper right corner will list the traits included in the desired analysis. (Note: the "Restoration Goals," "Species," and "Traits" dropdown menus are not used in this example but will be explained in full in section 3.0, "REST User Interface.") The Liko Nā Pilina project's first desired analysis step was to compare all 29 species across the 15 different traits using PCA. To complete this analysis, Check All was selected, followed by the Get Results, both options being provided at the bottom of the Data tab. Figures 7 and 8 show the Principal Components Analysis (PCA) results in the Graph and Analysis tabs in REST with the completed PCA. Each species is a point in "trait space." Points closer together are more similar. Points are evaluated for their closeness in two directions:

- Horizontally along the x axis (Principal Component Axis 1; PCA 1)
- Vertically along the y axis (Principal Component Axis 2; PCA 2).

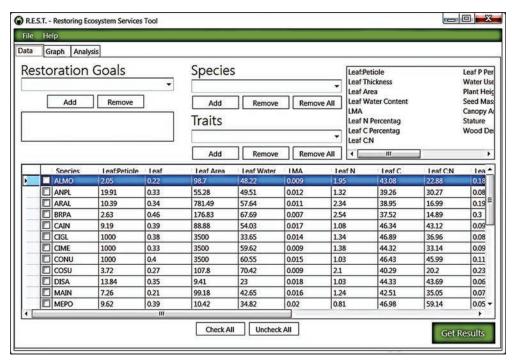


Figure 6—Data tab of REST user interface after uploading the *Liko Nā Pilina* projects .csv file.

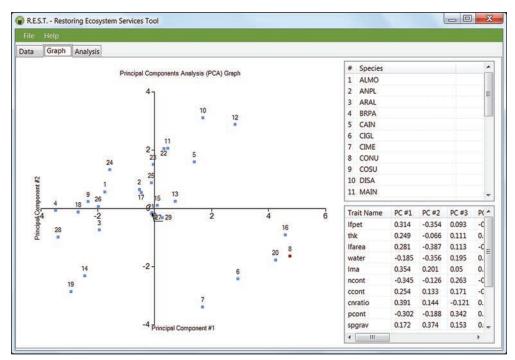


Figure 7—Graph tab of REST user interface after completing a principal components analysis for all of *Liko Nā Pilina*'s 29 species and 15 traits.

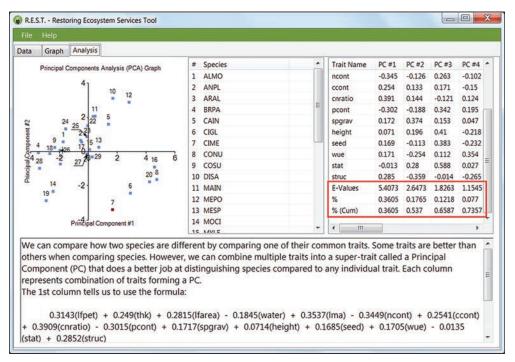


Figure 8—Analysis tab of REST user interface after completing a principal components analysis for all of *Liko Nā Pilina*'s 29 species and 15 traits.

In figures 7 and 8, species 7 and 10 are very similar to each other along PCA 1 but not along PCA 2. In the subsequent output, you can determine that PCA 1 is the most correlated with the traits Leaf C:N (0.391) and LMA (0.354). Thus species 7 and species 10 are very similar in those traits. A finding such as this example should be evaluated by the user, who will make decisions based on community theory and whether redundancy or complementarity is desired across the chosen species (i.e., how similar the species should be in trait profiles). Positive values indicate that a trait increases its value as that axis increases value, while negative values indicate an inverse relationship. For example, as you move to the right along PCA 1, Leaf Nitrogen (N) Percentage values decrease (-0.345), so that species 7 and 10 would have lower leaf N concentrations than all the species positioned to the left of them along PCA 1 (ranging from species 13 to species 4). When examining along PCA 2, it is noted that PCA 2 is positively correlated with specific gravity (0.374) yet negatively with leaf area (-0.387). Thus, species 7 and species 10 are quite different in those two traits, a factor of their growth habits—species 7 is a tree fern, and species 10 is a slow-growing canopy tree.

Another important output to consider is the eigenvalues and variation explained by examining the data along these two dimensions. An eigenvalue reflects the amount of variance in the data in a given axis direction (Quinn and Keogh 2002). For using REST, understanding the percentage of variation explained is sufficient. The highlighted box in figure 8 shows that PCA 1 explains about 36 percent of the variation in the data. Adding PCA 2 explains another 17 percent, for a total of about 53 percent of the variation explained. Principal components analysis will never explain all of the variation in two axes, particularly if there are many traits. In addition, many of the traits examined may be correlated with each other. Low eigenvalues may not be ideal, but the more important consideration is the graph to determine relative distances among species.

Based on the PCA, we made decisions to eliminate some species, thus simplifying the logistics involved in our experiment:

- Species 6 and species 7 are both tree ferns, yet species 6 was more available from growers. We decided to include only species 6, as the two species are close together on the PCA, and thus occupy similar trait space.
- Species 4 is similar to species 28. However, species 4 presents propagation challenges, guiding selection toward species 28.
- We used a similar logic with species 14 and species 19—we eliminated species 19 because it does not regenerate on its own.
- Species 15 was similar to species 13. On site, species 13 would be placed at the lowest elevation of its range, potentially affecting survivorship potential. Thus, we eliminated species 13 in favor of species 15.

- Species 26 and species 29 were also similar. We eliminated species 29 as it is less common in the LWF environment than species 26.
- Species 9 was deemed unnecessary because it was in a cluster with a large number of species.
- We also decided to eliminate the canopy trees already existing on site (species 10, 12, and 22).

The analysis can be easily run again by deselecting the nine above-mentioned species within the **Data** tab. Note the ways in which the output, graph, and PC values of the first analysis (fig. 8) differ from the new analysis (fig. 9).

After this initial PCA was conducted, resulting in a simplified species list, further PCAs were run to select species mixes based on the *Liko Nā Pilina* research questions and objectives. To elaborate, a PCA was run using a reduced trait list that included only those traits related to carbon storage/fast-to-slow strategies, in order to select core species that would facilitate slow and moderate carbon turnover. Once the carbon core species were identified, additional species selections per community mix were made based on Euclidean distances (i.e., close = redundant, far = complementary) visualized in trait space. (For a more detailed explanation, see Ostertag et al. 2015).

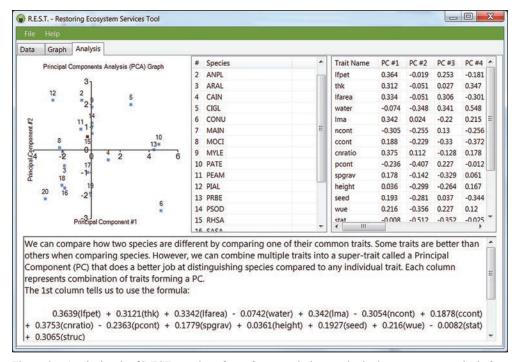


Figure 9—Analysis tab of REST user interface after completing a principal components analysis for the reduced *Liko Nā Pilina*'s dataset of 20 species across 15 traits.

Export workspace and export PCA graph—Users must take care to document past results outside of REST—once parameters have been reset for a new PCA output, previous parameters and results are not kept in program memory. Export Workspace provides users with the option to export a personal database of species and traits to access their results in the future (fig. 10). Similar to importing data, exported data takes the form of a .csv file. This same exported file can be used outside of REST as well as imported again for future use, increasing the versatility of result data. Furthermore, project PCA graphs can be exported as .jpeg files using the Export PCA Graph function (fig. 10).

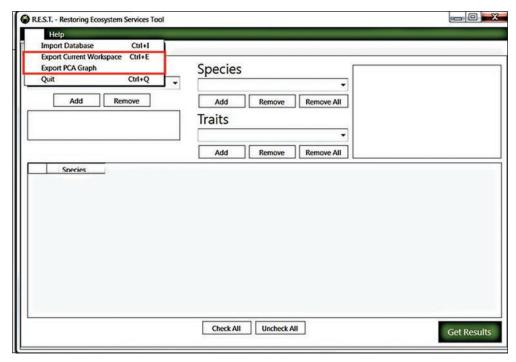


Figure 10—REST interface screen showing the option to Export Current Workspace results as a .csv file for use outside of the program, along with the option to Export PCA Graph.

#### 3.0 REST User Interface

#### 3.1 Restoration Goals

If desired, users can choose a restoration goal from the displayed dropdown menu in figure 11 by selecting the goal and clicking "Add." Selecting a restoration goal will shorten the list of traits available in the "Trait" dropdown menu: displaying only those traits that pertain to that particular goal (fig. 12).

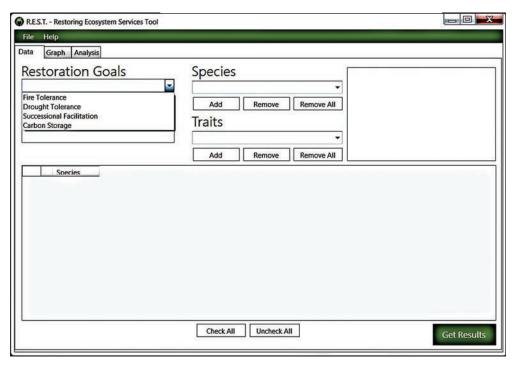


Figure 11—Options for restoration goals in the REST program.

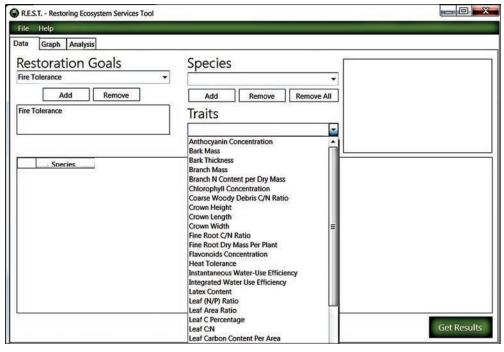


Figure 12—REST filters functional traits as they pertain to meeting a chosen restoration goal.

#### Species selection—

To choose a species, select a name from the menu or type the name. Click "Add" to include it in the analysis. After adding the species, the species will be added to the selected species window as shown in figure 13.

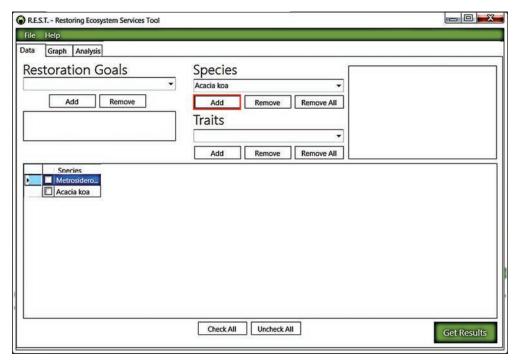


Figure 13—REST interface showing the "Add" option for species inclusion.

#### Trait selection—

To choose a trait, select from the dropdown menu or type in the trait name (fig. 14). If a species has data for a trait, the value will be visible in the trait column to the right of the species name. If there is more than one value for a species' trait in the databases compiled in the program, REST will take an average. Note that if a species has no value listed, then there are no current data in the program for that species. Values are required, as REST will not complete a PCA unless all species have values for all selected traits (users are encouraged to share their values with the authors as appropriate to augment future program and database updates). At this juncture, if a value is missing from the desired analysis, users should decide whether they would like to remove the species or trait from the analysis. To remove the species, simply uncheck the box to the left of that species. To remove the trait,

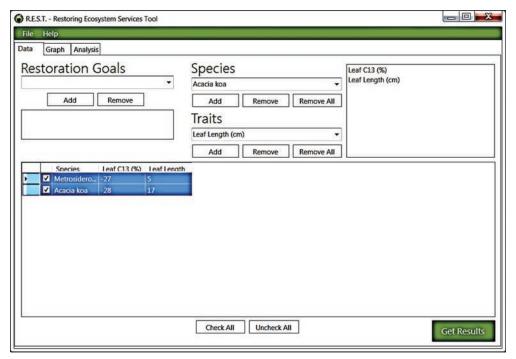


Figure 14—Trait selection in the REST user interface.

select the trait where it is listed in the trait box (top right corner) and select **Remove**. The REST program may be enhanced in the future with updated data in the database or program enhancements. We welcome any suggestions for future features you would like to see. Please send suggestions to ostertag@hawaii.edu. The REST database is still being actively built, and the program will become more user friendly as more of the data gaps are filled.

#### Edit values—

To edit a trait value, the user can simply double-click on the value and enter the change. Please note that units should be consistent for that trait in the trait list (some units and formatting differ in REST than their real-world counterparts because of programming constraints). Note that the changed value will not be stored in the REST database, but used only for the PCA conducted by the user.

#### View graph—

When you are finished selecting your combination of traits and species, click the **Get Results** button. You will get an error message if you have not selected at least two species and two traits. Note that the graph and analysis output involved at this step were detailed in the previous section.

#### 3.2 Restoration Goals and Functional Traits

REST currently has four restoration goals built into the program:

- Fire tolerance
- Drought tolerance
- Successional facilitation
- Carbon storage

The following are restoration goals for optional use in REST. By definition, included restoration goals filter potential functional trait inputs into those specific to the goal and appropriate for more targeted analysis. Because REST is user-defined, these four goals serve as a basis for popular intervention outcomes, but inputs can be increased, decreased, or otherwise altered as needed.

#### 3.2.1 Fire tolerance (FT)—

Fire is a threat to many ecosystems, especially in light of species invasions, greater human development, and climate alteration. Alternatively, the presence of fire events may be a natural part of other ecosystems. Traits related to flammability are included here.

#### 3.2.2 Drought tolerance (DT)—

Similar to fire tolerance, the potentials for drought and water use by plants are important concerns for intervention strategies. Traits relating to water storage and use are included here.

#### 3.2.3 Successional facilitation (SF)—

One goal of restoration may be to assist ecosystem recovery to another state with increased animal use or plant species more closely aligned with historical observation. Traits that can help with modifying conditions such as growth, reproduction, and dispersal are included here. For more information, see Pugnaire and Valladares (1999).

#### 3.2.4 Carbon storage (CS)—

One management goal may be to maximize carbon storage across the landscape. Traits that are associated with plant growth and nutrient cycling are included here.

#### 3.2.5 Functional traits in REST—

Below is a list of all functional traits as defined in the most recent version of REST. Entries include brief definitions, measurement units, useful information for measurement, and references for additional information where appropriate. Connections to restoration goals are denoted using two-letter abbreviations (FT, DT, SF, and CS, respectively). Each trait was assigned to one or multiple restoration goals. This assignment was subjective based on the collective field experiences of the authors.

Users of REST have the flexibility to add or subtract traits using the checkboxes next to each trait. Many of these traits are listed here because they are part of global databases. Note that, for some traits, there are very few species with data. For more information about specific functional traits, we recommend a variety of references, including Cornelissen et al. (2003), CSIRO (2013), Fitter and Hay (2002), Pugnaire and Valladares (1999), Reich (2014), and the Prometheus Wiki (http://prometheus-wiki.org). Traits are as follows:

Alkaloids—Chemically basic compounds generally related to plant protection from external environmental insults. Quinine, morphine, and caffeine are examples of natural alkaloids. In REST, alkaloids are measured as a percentage (%) of the noted alkaloid(s). (SF)

Altitude (min and max)—Range of elevations in which a given species occurs, with low and high, respectively, defining minimum and maximum limits. Altitude is measured in meters (m). (DT)

Annual growth rate (biomass, diameter, and height increments)—Increases, in mass in kilograms and diameter or height in centimeters, of a given plant on an annual basis (kg/yr and cm/yr). Annual growth rates indicate a growth investment and should be considered on a whole-plant basis. (CS, DT, FT)

**Annual leaf production**—Leaves produced by a given species over a single year, measured as the total number of leaves per year (#/yr). (CS)

**Annual seed production**—Seeds produced by a given species over a single year, measured as the total number of seeds (#/yr). **(SF)** 

Anthocyanin concentration—Amount of anthocyanins (chemical plant pigments) in a given plant, expressed as a percentage (%). (DT, FT, SF)

**Bark litter ash per mass**—Ash content (g/kg) measured in the bark litter of a given plant. **(CS, DT, FT, SF)** 

**Bark litter C per mass**—Carbon content (g/kg) measured in the bark litter of a given plant. **(CS, DT, FT, SF)** 

**Bark litter C/N ratio**—Amount of carbon compared to the amount of nitrogen found in the bark litter of a given plant. In REST, this is expressed as kilograms of carbon divided by kilograms of nitrogen (formatted as kg C/kg N). **(CS, DT, FT, SF)** 

**Bark litter decomposition rate**—The breakdown of plant bark into less complex organic matter, expressed as a k constant. **(CS, FT, SF)** 

**Bark litter lignin per mass**—Lignin content (g/kg) measured in the bark litter of a given plant. (CS, DT, FT, SF)

**Bark dry mass**—Measured in grams (g). (FT, DT, CS)

**Bark thickness**—Measured in millimeters (mm). (FT, DT, CS)

**Branch mass**—Total mass of all branches on a given plant, measured in kilograms per plant (kg/plant). (FT, DT, CS, SF)

**Branch N per dry mass**—Nitrogen content of dried branches, expressed as grams of nitrogen per grams of dry branch mass (g N/g DW). (FT, DT, CS, SF)

*Canopy N retention time*—Number of years (yr) that nitrogen is being stored within a species canopy. **(CS, SF)** 

Canopy P retention time—Number of years (yr) that phosphorus is being stored within a species canopy. (CS, SF)

*Chlorophyll concentration*—Percentage (%) of a given plant that is chlorophyll. This trait is related to carbon uptake and utilization of light. (FT, DT, CS, SF)

*Carbon-13 (C*<sub>13</sub>) *content*—Proportion of plant tissues that consist of carbon-13 isotopes, an indicator of photosynthetic pathway and integrated water-use efficiency. Carbon-13 ( $C_{13}$ ) is measured in parts per million (‰). (**FT, DT, CS, SF**)

*Coarse woody debris C/N ratio*—Amount of carbon compared to the amount of nitrogen in the debris of a given plant. In REST, this is expressed as kilograms of carbon divided by kilograms of nitrogen (formatted as kg C/kg N). **(FT, DT, CS, SF)** 

*Crown area*—Measured in square meters (m<sup>2</sup>). (FT, DT, CS, SF)

*Crown height*—Shortest distance between ground level and the upper limit of living material for a measured plant (crowns in trees). This trait is expressed in meters (m). **(FT, DT, CS, SF)** 

*Crown length*—Measured in meters (m). (FT, DT, CS, SF)

*Crown width*—Measured in meters (m). (FT, DT, CS, SF)

**DBH** at maturity—Diameter of a plant in centimeters (cm) at breast height (typically 1.3 m) when a plant is fully mature. (DT, CS)

**Dispersal period length**—Number of days (d) that a plant is dispersing seeds. (SF)

**Dispersal unit length**—Measured in millimeters (mm). (CS, SF)

Dispersal unit thickness—Measured in millimeters (mm). (CS, SF)

*Dispersal unit width*—Measured in millimeters (mm). (CS, SF)

*Fern spore length*—The main units of fern reproduction, expressed in micrometers (µm). **(SF)** 

Fern spore mass—Expressed in milligrams (mg). (SF)

*Fern spore volume*—Expressed in micrometers (µm<sup>3</sup>). (SF)

*Fern spore width*—Expressed in micrometers (µm). (SF)

*Fine root C/N ratio*—Amount of carbon compared to the amount of nitrogen in the fine roots of a given plant. In REST, this is expressed as kilograms of carbon divided by kilograms of nitrogen (formatted as kg C/kg N). (FT, DT, CS, SF)

*Fine root dry mass per plant*—Mass of roots in kilograms (kg/plant). **(FT, DT, CS, SF)** 

*Flavonoids*—Chemical compounds associated with nitrogen fixation, pollinator attraction, and photosynthesis. Flavonoids are measured as a percentage (%). (FT, DT, CS, SF)

Flowering period length—Number of days (d) that a plant produced flowers. (SF)

*Freeze exposure*—A plant's ability to withstand freezing conditions, defined as temperatures consistently below 0 °C (32 °F) prior to plant death. In REST, freeze exposure is measured in hours (h). **(CS, SF)** 

*Fruit C percentage*—Carbon content (%) measured in the fruit of a given plant. **(CS, SF)** 

*Fruit C/N ratio*—Amount of carbon compared to the amount of nitrogen found in the fruit of a given plant. In REST, this is expressed as kilograms of carbon divided by kilograms of nitrogen (formatted as kg C/kg N). **(CS, SF)** 

Fruit diameter—Measured in centimeters (cm). (CS, DT, SF)

*Fruit fleshiness*—Calculated as ((fresh mass – dry mass)/fresh mass) and represented as a percentage (%). **(CS, SF)** 

Fruit length—Length in centimeters (cm) of a fruit. (CS, DT, SF)

*Fruit mass*—Amount of an individual fruit of a given plant species, measured in grams (g). **(SF)** 

Fruit N percentage—Proportion (%) of a fruit that is nitrogen. (CS, SF)

*Fruit P percentage*—Proportion (%) of a fruit that is phosphorus. (CS, SF)

Fruit width—Width in centimeters (cm) of a fruit. (CS, DT, SF)

*Germination time (minimum and maximum)*—Number of days (d) that a plant reproductive unit (such as a seed or spore) takes to sprout. **(SF)** 

*Hawaii weed risk assessment score*—The likelihood of invasion or "taking over" of a given plant species as outlined by the *Hawaii Weed Risk Assessment Guide* and other observational guides regarding plant-ecosystem interactions. For more information, see Daehler (2009). **(DT, SF)** 

*Heat tolerance*—A plant's ability to withstand temperature conditions above its generally accepted upper limit. Heat tolerance is measured in hours (h). **(FT, DT, CS, SF)** 

*Instantaneous water use efficiency*—One measure of water use efficiency, instantaneous, regards the ability of a plant to utilize water while capturing carbon via photosynthesis. Instantaneous water use efficiency is measured in millimoles of carbon gained as a proportion of moles of water lost (μmol CO<sub>2</sub>/mol H<sub>2</sub>O). (FT, DT, CS, SF)

Integrated water use efficiency—The ratio of water used in plant metabolism to water lost by productivity. This is measured by the  $\delta^{13}$ C (parts per thousand;  $^{0}/_{00}$ ) signature found in leaf tissue. (FT, DT, CS, SF)

*Inflorescence N percentage*—Proportion (%) of an inflorescence that is nitrogen. **(CS, SF)** 

*Inflorescence P percentage*—Proportion (%) of an inflorescence that is phosphorus. **(CS, SF)** 

*Latex content*—Percentage (%) of latex production in a given plant. (FT, DT, SF)

**Latitude** (N & S)—Global range of latitude within which a plant can survive, with minimum and maximum defining respective limits for a given plant. This is measured in degrees (deg). (DT)

*Leaf and fine root turnover*—Timing of shorter lived tissue replacement in plants. Turnover is measured per year (yr). **(FT, DT, CS, SF)** 

**Leaf**  $A_{max}$ —An abbreviation for maximal assimilation, leaf  $A_{max}$  is the maximum rate of photosynthesis of a leaf. The unit for  $A_{max}$  is micromoles per square meter

per second (formatted as  $\mu$ mol/m²/s).  $A_{max}$  influences carbon cycling and resource use efficiency. (CS, DT)

Leaf  $A_{sat}CO_2$  (per area and per mass)—An abbreviation for leaf maximum photosynthetic rate at saturating  $CO_2$ , leaf  $A_{sat}CO_2$  is measured in micromoles per square meter per second ( $\mu$ mol/m²/s) and micromoles per gram per second ( $\mu$ mol/g/s). (CS)

Leaf abaxial and adaxial cuticle thickness—Thickness in micrometers (µm) of the cuticle, a protective film covering the epidermal cells, on the lower and upper side of the leaf, respectively. The cuticles function is to help reduce water loss to the atmosphere. (FT, DT, CS, SF)

*Leaf abaxial and adaxial epidermis thickness*—Thickness in micrometers (μm) of the epidermal cells on the lower and upper side of the leaf, respectively. The main functions of epidermal cells are to help reduce water loss and regulate gas exchange. (FT, DT, CS, SF)

**Leaf abaxial and adaxial guard cell length**—Leaf abaxial and adaxial guard cells are cells that are used to control gas exchange via the stomata located on the lower and upper sides of a leaf, respectively. The abaxial and adaxial guard cell length is expressed in micrometers ( $\mu$ m). (DT)

**Leaf abaxial and adaxial guard cell width**—Leaf abaxial and adaxial guard cells are cells that are used to control gas exchange via the stomata located on the lower and upper sides of a leaf, respectively. The abaxial and adaxial guard cell width is expressed in micrometers (μm). **(DT)** 

*Leaf abaxial and adaxial stomatal pore length*—Length of stomata, expressed in micrometers ( $\mu$ m), on the lower and upper side of the leaf, respectively. The main functions of the stomata are to regulate gas exchange and help reduce water loss. (**DT**)

*Leaf Al per mass*—The aluminum content of overall dry leaf mass in grams (g Al/kg). **(FT, DT, CS, SF)** 

**Leaf anthocyanin (per area and per mass)**—Leaf anthocyanins are pigments that protect against excess sunlight and assist in recovering remaining nutrients prior to leaf senescence. Leaf anthocyanins are expressed on a per-area (μg/cm²) and permass (g/kg) basis. (DT, CS, SF)

Leaf area—Measured in square centimeters (cm<sup>2</sup>). (DT, CS, SF)

**Leaf area index**—Defined as the one-sided green leaf area per unit of ground surface area  $(m^2/m^2)$  of a broadleaf canopy type. **(CS, FT, SF)** 

**Leaf area ratio** (LAR)—The photosynthetic surface area of a plant as a proportion of total dry mass. LAR is measured in square centimeters per gram (cm<sup>2</sup> g<sup>-1</sup>). (FT, DT, CS, SF)

*Leaf area/sapwood area ratio*—Leaf area/sapwood area ratio (cm<sup>2</sup>/mm<sup>2</sup>) is calculated by dividing the leaf area of a species by its respective stem sapwood area. **(CS, DT)** 

*Leaf B per mass*—Boron content of overall dry leaf mass in grams (g B/kg). (FT, DT, CS, SF)

*Leaf C content per area*—Carbon content of a leaf in kilograms spread over a square meter (kg  $C/m^2$ ). (CS, FT, SF)

**Leaf C (percentage and per area)**—Carbon content of a leaf, expressed on a percentage (%) and per-area (g C/m²) basis. (FT, CS, SF)

*Leaf C/N ratio*—Ratio of carbon to nitrogen content within a leaf, expressed as kilograms carbon to kilograms nitrogen (kg C/kg N). (FT, CS)

*Leaf C/P ratio*—Ratio of carbon to phosphorus content within a leaf, expressed as kilograms carbon to kilograms phosphorus (kg C/kg P). (FT, CS)

**Leaf**  $\delta^{13}C$ —Carbon-13 isotope content within a leaf, expressed in parts per million (‰). (FT, CS)

**Leaf Ca (percentage, per area, and per mass)**—Leaf Ca percentage (%) = proportion of a leaf that is calcium. Leaf Ca per area = total amount of calcium contained within a given leaf area in grams per square meter (g Ca/m²). Leaf Ca per mass = calcium content of overall dry leaf mass in kilograms (g Ca/kg). (CS, SF)

*Leaf Ca/Sr ratio*—Ratio of calcium to strontium content within a leaf, expressed as kilograms calcium to kilograms strontium (kg Ca/kg Sr). (CS, FT)

**Leaf carotenoid (per area and per mass)**—Leaf carotenoids are pigments that serve two functions: absorbing light energy to transfer to chlorophyll for use in photosynthesis, and protecting chlorophyll from photodamage. Leaf carotenoids are expressed on a per-area ( $\mu$ g/cm<sup>2</sup>) and per-mass (g/kg) basis. (**FT, SF**)

*Leaf carotenoid/chlorophyll ratio*—Ratio of carotenoid pigments to chlorophyll content within a leaf, expressed as kilograms carotenoid to kilograms chlorophyll (kg carotenoid/kg Chl). **(FT, SF)** 

*Leaf cellulose percentage*—Proportion (%) of a leaf that is cellulose. (FT, DT, CS, SF)

Leaf chlorophyll a and chlorophyll b (per area)—Total amount of chlorophyll (a and b, respectively) contained within a given leaf area in micrograms per square centimeter (μg Chl a/cm² and μg Chl b/cm²). (CS, DT, SF)

**Leaf chlorophyll (per area and per mass)**—Leaf chlorophyll per area is the chlorophyll content in grams over a square meter of leaf (g Chl/m²). Leaf chlorophyll per mass is the chlorophyll content in grams to kilograms of leaf (formatted as g Chl/kg). **(CS, DT, SF)** 

**Leaf chlorophyll a/chlorophyll b ratio**—Ratio of chlorophyll a to chlorophyll b within a leaf, expressed as kilograms chlorophyll a to kilograms chlorophyll b (kg Chl a/kg Chl b). **(FT, DT, CS, SF)** 

*Leaf chlorophyll/N ratio*—Ratio of chlorophyll to nitrogen content within a leaf, expressed as kilograms chlorophyll to kilograms nitrogen (kg Chl/kg N). (FT, DT, CS, SF)

**Leaf construction cost (per area and per mass)**—Cost per area (cm<sup>2</sup>) and cost per mass (g) = glucose invested by plants to synthesize carbon skeletons and nitrogenous compounds (Baruch and Goldstein 1999). **(CS, DT)** 

*Leaf Cu per mass*—Copper content in grams to kilograms of leaf mass (g Cu/kg). **(CS, SF)** 

Leaf dark respiration (per area and per mass)—The measure of plant respiration that occurs during the absence of light per area ( $\mu$ mol/m<sup>2</sup>/s) and per mass ( $\mu$ mol/g/s). (CS, DT)

*Leaf density*—Leaf mass in milligrams within a cubic millimeter (mg/mm<sup>3</sup>). **(FT, CS, SF)** 

*Leaf diameter*—Measured in centimeters (cm). (CS, DT, SF)

Leaf dry mass—Mass of a dried leaf in grams (g). (FT, DT, CS, SF)

**Leaf dry matter content (LDMC)**—Total mass of dry matter in a leaf, expressed as grams of dry matter over grams of total leaf matter (g/g). (FT, DT, CS, SF)

*Leaf epidermis cell area*—Area of leaf epidermis in square micrometers ( $\mu$ m<sup>2</sup>). (DT, CS, SF)

*Leaf epidermis cell length*—Length of leaf epidermis in square micrometers  $(\mu m^2)$ . (DT, CS, SF)

*Leaf epidermis volume/leaf volume*—Proportion of leaf volume occupied by the leaf epidermis in cubic millimeters (mm<sup>3</sup>/mm<sup>3</sup>). (DT, CS, SF)

**Leaf Fe (percentage and per mass)**—Leaf Fe percentage (%) = proportion of a leaf that is iron. Leaf Fe per mass = iron content of overall dry leaf mass in kilograms (g Fe/kg). **(CS, SF)** 

*Leaf hypodermis thickness*—Thickness of the layer of cells directly beneath the epidermis, expressed in micrometers (µm). (CS, DT, SF)

*Leaf hypodermis volume/leaf volume*—Proportion of leaf volume occupied by the leaf hypodermis in cubic millimeters (mm<sup>3</sup>/mm<sup>3</sup>). (DT, CS, SF)

Leaf instantaneous photosynthetic nitrogen-use efficiency (PNUE)—Ratio of photosynthesis to leaf nitrogen content, expressed as micromoles of CO<sub>2</sub> to moles of N (μmol CO<sub>2</sub>/mol N). (CS, DT, SF)

Leaf instantaneous photosynthetic phosphorus-use efficiency (PPUE)—Ratio of photosynthesis to leaf phosphorus content, expressed as micromoles of CO<sub>2</sub> to moles of P (μmol CO<sub>2</sub>/mol P). (CS, DT, SF)

Leaf integrated photosynthetic nitrogen-use efficiency (PNUE)—Ratio of photosynthesis to leaf nitrogen content, expressed as micromoles of CO<sub>2</sub> to moles of N (μmol CO<sub>2</sub>/mol N). (CS, DT, SF)

Leaf integrated photosynthetic phosphorus-use efficiency (PPUE)—Ratio of photosynthesis to leaf phosphorus content, expressed as micromoles of CO<sub>2</sub> to moles of P (μmol CO<sub>2</sub>/mol P). (CS, DT, SF)

*Leaf intercellular/leaf volume*—Proportion of leaf volume occupied by the leaf intercellular space in cubic centimeters (cm<sup>3</sup>/cm<sup>3</sup>). (DT, CS, SF)

Leaf intercellular CO<sub>2</sub> concentration—Amount of carbon dioxide in a leaf measured in parts per million (ppm) and micromoles per mol (μmol/mol). (DT, CS, SF)

**Leaf internode length**—Measured in centimeters (cm). (DT)

Leaf  $J_{max}$  maximum rate of electron transport—Leaf  $J_{max}$ , an abbreviation for leaf maximum rate of electron transport, is measured in micromoles per square meter per second ( $\mu$ mol/m<sup>2</sup>/s) and micromoles per gram per second ( $\mu$ mol/g/s). (CS)

Leaf K (percentage, per area, and per mass)—Leaf K percentage (%) = proportion of a leaf that is potassium. Leaf K per area = total amount of potassium contained within a given leaf area in grams per square meter (g  $K/m^2$ ). Leaf K per mass = potassium content of overall dry leaf mass in kilograms (g K/kg). (FT, DT, CS, SF)

Leaf lamina length—Measured in centimeters (cm). (DT, CS, SF)

Leaf lamina thickness—Measured in micrometers (µm). (FT, DT, CS, SF)

*Leaf latex production*—Measured in milligrams (mg). (FT, DT)

Leaf length—Measured in centimeters (cm). (DT, CS, SF)

*Leaf lifespan*—Measured in days (d). (DT, CS, SF)

Leaf light absorption—Measured in moles per mole (mol/mol). (DT, CS, SF)

Leaf light compensation point—Leaf light compensation point ( $\mu$ mol/m<sup>2</sup>/s) = amount of light intensity on the light curve where the rate of photosynthesis exactly matches the rate of respiration. (CS, SF)

Leaf lignin percentage—Proportion (%) of a leaf that is lignin. (FT, DT, CS, SF)

*Leaf lignin/N ratio*—Ratio of lignin to nitrogen content within a leaf, expressed as kilograms lignin to kilograms nitrogen (kg lignin/kg N). **(FT, DT, CS, SF)** 

*Leaf mesophyll cell area*—Area of leaf mesophyll in square micrometers (μm²). (DT, CS, SF)

Leaf mesophyll thickness—Measured in micrometers (µm). (DT, CS, SF)

**Leaf Mg (percentage, per area, and per mass)**—Leaf Mg percentage (%) = proportion of a leaf that is magnesium. Leaf Mg per area = total amount of magnesium contained within a given leaf area in grams per square meter (g Mg/m²). Leaf Mg per mass = magnesium content of overall dry leaf mass in kilograms (g Mg/kg). (DT, CS, SF)

*Leaf mid-day water potential*—This indicator of mid-day water stress is measured in megapascals (MPa). **(DT)** 

**Leaf Mn (percentage, per area, and per mass)**—Leaf Mn percentage (%) = proportion of a leaf that is manganese. Leaf Mn per area = total amount of manganese contained within a given leaf area in grams per square meter (g Mn/m<sup>2</sup>). Leaf Mn per mass = manganese content of overall dry leaf mass in kilograms (g Mn/kg). (CS, SF)

Leaf N (percentage, per area, and per mass)—Leaf N percentage (%) = proportion of a leaf that is nitrogen. Leaf N per area = total amount of nitrogen contained within a given leaf area in grams per square meter (g  $N/m^2$ ). Leaf N per mass = nitrogen content of overall dry leaf mass in kilograms (g N/kg). (FT, DT, CS, SF)

**Leaf N resorption**—Percentage (%) of nitrogen regained by the plant prior to leaf senescence, a nutrient conservation strategy. **(CS, SF)** 

**Leaf N retranslocation (percentage, per area, and per mass)**—The removal of nitrogen from the leaves into the perennial part of the plant prior to senescence, expressed as a percentage (%), on an area basis (g/m²), and on a mass basis (g/kg), respectively. **(CS, SF)** 

*Leaf N/C ratio*—Proportion of nitrogen to carbon within plant leaves in kilograms (kg N/kg C). (FT, DT, CS, SF)

*Leaf N/Ca ratio*—Proportion of nitrogen to calcium within plant leaves in kilograms (kg N/kg Ca). **(FT, DT, CS, SF)** 

*Leaf N/P ratio*—Proportion of nitrogen to phosphorus within plant leaves in kilograms (kg N/kg P). (FT, DT, CS, SF)

**Leaf**  $N^{15}$ —Nitrogen-15 isotope content in a leaf, expressed in parts per million (‰). **(CS, SF)** 

**Leaf**  $NH_4^+$ —Ammonium content in a leaf, expressed in grams per kilogram (g/kg). **(CS, SF)** 

*Leaf NO*<sub>3</sub>—Nitrate content in a leaf, expressed in grams per kilogram (g/kg). **(CS, SF)** 

**Leaf**  $O^{18}$ —Oxygen-18 isotope content in a leaf, expressed in parts per million (‰). (CS, SF)

*Leaf osmolarity*—This measure of osmotic potential within leaves is expressed in millimoles per kilogram (mmol/kg). **(DT, FT)** 

**Leaf P (percentage, per area, and per mass)**—Leaf P percentage (%) = proportion of a leaf that is phosphorus. Leaf P per area = total amount of phosphorus contained within a given leaf area in grams per square meter (g  $P/m^2$ ). Leaf P per mass = phosphorus content of overall dry leaf mass in kilograms (g P/kg). **(CS)** 

*Leaf P resorption*—Percentage (%) of phosphorus regained by the plant prior to leaf senescence, a nutrient conservation strategy. **(CS, SF)** 

**Leaf P retranslocation (percentage, per area, and per mass)**—Removal of phosphorus from the leaves into the perennial part of the plant prior to senescence, expressed as a percentage (%), on an area basis (g/m²), and on a mass basis (g/kg). **(CS, SF)** 

*Leaf P/Ca ratio*—Proportion of phosphorus to calcium within plant leaves in kilograms (kg P/kg Ca). **(FT, DT, CS, SF)** 

*Leaf palisade thickness*—Thickness in micrometers (μm) of palisade cells, which contain many chloroplasts and function to absorb maximum light for photosynthesis, located in the mesophyll layer of a leaf. (FT, DT, CS, SF)

**Leaf perimeter**—Distance in millimeters (mm) measured around the outer edge of a leaf. (DT, CS, SF)

**Leaf pH**—Acidity of a leaf, expressed as a pH value in REST. (FT, DT, CS, SF)

**Leaf phenol percentage**—Percentage (%) of plant compounds containing a phenol group. These range from simple compounds synthesized in response to environmental insults to those more volatile. Capsaicin and serotonin are common examples, while certain phenols show associations with litterfall decomposition, resistance to fungal or other pests, and increased fire duration and intensity. **(FT)** 

*Leaf photon flux density*—Measured in moles per square meter of leaf area per second (mol/m<sup>2</sup>/s). **(FT, DT, CS, SF)** 

*Leaf photosynthetic electron transport*—Measured in micromoles per square meter of leaf area per second (μmol/m²/s). (FT, DT, CS, SF)

Leaf photosynthesis rate (per leaf area and per leaf mass and per unit N)—Leaf photosynthesis rate/leaf area = conversion of carbon dioxide to simple sugar over a given leaf area ( $\mu$ mol/m<sup>2</sup>/s). Leaf photosynthesis rate is also expressed on a per-leaf mass basis ( $\mu$ mol/g/s) and leaf-per-unit N basis ( $\mu$ mol CO<sub>2</sub> (mol N/s). (FT, DT, CS, SF)

*Leaf pre-dawn water potential*—This indicator of pre-dawn water stress is measured in megapascals (MPa). **(DT)** 

Leaf protein percentage—Proportion (%) of a leaf that is protein. (CS, FT)

**Leaf pubescence per area**—Density of hairs relative to the surface area of the leaf and is expressed as grams per square meter (g/m²). (CS, DT, SF)

Leaf respiration rate (per area and per mass)—Measured on an area basis as micromoles of  $CO_2$  per square meter per second (µmol  $CO_2/m^2/s$ ) and on a mass basis as nanomoles of  $CO_2$  per gram per second (nmol  $CO_2/g/s$ ). (CS, DT)

*Leaf S per mass*—Sulfur content of overall dry leaf mass in kilograms (g S/kg DW). **(CS, SF)** 

*Leaf Sr*<sup>87</sup>/*Sr*<sup>86</sup> *ratio*—Proportion of the strontium-87 isotope to the strontium-86 isotope within plant leaves in grams (kg Sr87/kg Sr86). (FT, DT, CS, SF)

*Leaf surface area*—Measured in square meters (m<sup>2</sup>). (FT, DT, CS, SF)

**Leaf tannin percentage**—Percentage (%) of protein-binding compounds produced by plants as a response to predation, fire intensity, or other environmental insults. **(FT, SF)** 

Leaf thickness—Measured in millimeters (mm). (FT, DT, CS)

Leaf timing—Number of days (d) prior to leaf emergence. (DT, CS, SF)

*Leaf transpiration*—Amount of evaporation from leaf surfaces measured in kilograms (kg). **(DT)** 

**Leaf transpiration rate**—Rate at which evaporation from leaf surfaces occurs, measured in millimoles or moles per square meter of leaf area per second (mmol  $H_2O/m/s$  and mol  $H_2O/m/s$ , respectively). **(DT)** 

*Leaf*  $V_{cmax}$  (per area and per mass)—An abbreviation for leaf maximum carboxylation rate, leaf  $V_{cmax}$  is measured in micromoles per square meter per second ( $\mu$ mol/m/s) as well as micromoles per gram per second ( $\mu$ mol/g/s). (CS)

*Leaf vascular bundle thickness*—Thickness in micrometers (μm) of the vascular tissue within a leaf that assists in the transport of sugars, water, and minerals. **(DT)** 

*Leaf water content*—Proportion (%) of water within a leaf. (DT, CS, SF)

**Leaf weight ratio**—Ratio of leaf mass to plant mass, expressed as grams over grams (g/g). (FT, DT, CS, SF)

*Leaf width*—Measured in centimeters (cm). (DT, CS, SF)

**Leaf Zn (percentage, per area, and per mass)**—Leaf Zn percentage = proportion (%) of a leaf that is zinc. Leaf Zn per area = total amount of zinc contained within a given leaf area in grams per square meter (g Zn/m²). Leaf Zn per mass = zinc content of overall dry leaf mass in kilograms (g Zn/kg). (SF, SF)

*Leaf/sapwood area ratio*—Proportion of leaves to sapwood in square millimeters (expressed as mm<sup>2</sup>/mm<sup>2</sup>). (FT, DT, CS)

**Leaf litter acetylene reduction rate**—The amount of nitrogenase activity (related to  $N_2$  fixation) found in a species leaf litter by using the acetylene reduction assay method, measured as nanomoles per gram per hour (nmol/g/hr) or grams per day (g/d). (CS, SF)

*Leaf litter ash per mass*—Ash (i.e., minerals) content of overall dry leaf mass in kilograms (g ash/kg). (CS, DT, FT)

**Leaf litter C (percentage and per mass)**—Leaf litter C percentage (%) = proportion of leaf litter that is carbon. Leaf C per mass = carbon content of overall dry leaf litter mass in kilograms (g C/kg). **(CS, FT, SF)** 

*Leaf litter C/N ratio*—Ratio of carbon to nitrogen content within leaf litter, expressed as kilograms carbon to kilograms nitrogen (kg C/kg N). (CS, FT)

*Leaf litter C/P ratio*—Ratio of carbon to phosphorus content within leaf litter, expressed as kilograms carbon to kilograms phosphorus (kg C/kg P). **(CS, FT)** 

**Leaf litter Ca (percentage and per mass)**—Leaf litter Ca percentage (%) = proportion of leaf litter that is calcium. Leaf Ca per mass = calcium content of overall dry leaf litter mass in kilograms (g Ca/kg). **(CS, SF)** 

**Leaf litter cellulose (percentage and per mass)**—Leaf litter cellulose percentage (%) = proportion of leaf litter that is cellulose. Leaf cellulose per mass = cellulose content of overall dry leaf litter mass in kilograms (g cellulose/kg). **(CS, SF)** 

Leaf litter decomposition (rate and mass loss)—Breakdown of dead leaves into less complex organic matter, expressed as a rate (k) and percentage (%) of mass lost. (CS, FT, SF)

**Leaf litter K (percentage and per mass)**—Leaf litter K percentage (%) = proportion of leaf litter that is potassium. Leaf litter K per mass = potassium content of overall dry leaf litter mass in kilograms (g K/kg). **(CS, SF)** 

**Leaf litter lignin (percentage and per mass)**—Leaf litter lignin percentage (%) = proportion of a leaf that is lignin. Leaf litter lignin per mass = lignin content of overall dry leaf litter mass in kilograms (g lignin/kg). (FT, DT, CS, SF)

*Leaf litter lignin/N ratio*—Ratio of lignin to nitrogen content within leaf litter expressed as kilograms lignin to kilograms nitrogen (kg lignin/kg N). (FT, DT, CS, SF)

*Leaf litter lignin/P ratio*—Ratio of lignin to phosphorus content within leaf litter expressed as kilograms lignin to kilograms phosphorus (kg lignin/kg P). (FT, DT, CS, SF)

**Leaf litter Mg (percentage and per mass)**—Leaf litter Mg percentage (%) = proportion of leaf litter that is magnesium. Leaf Mg per mass = magnesium content of overall dry leaf litter mass in kilograms (g Mg/kg). **(CS, SF)** 

*Leaf litter moisture percentage*—Water content (%) present in leaf litter prior to drying. **(DT, FT)** 

**Leaf litter Mo (percentage and per mass)**—Leaf litter Mo percentage (%) = proportion of leaf litter that is molydenum. Leaf Mo per mass = molydenum content of overall dry leaf litter mass in kilograms (g Mo/kg). **(CS, SF)** 

Leaf litter N (percentage and per mass)—Leaf litter N percentage (%) = proportion of leaf litter that is nitrogen. Leaf N per mass = nitrogen content of overall dry leaf litter mass in kilograms (g N/kg). (CS, SF)

*Leaf litter N/Ca ratio*—Ratio of nitrogen to calcium content within leaf litter expressed as kilograms nitrogen to kilograms calcium (kg N/kg Ca). (CS, FT)

*Leaf litter N/P ratio*—Ratio of nitrogen to phosphorus content within leaf litter expressed as kilograms nitrogen to kilograms phosphorus (kg N/kg P). **(CS, FT)** 

Leaf litter Na (percentage and per mass)—Leaf litter Na percentage (%) = proportion of leaf litter that is sodium. Leaf Na per mass = sodium content of overall dry leaf litter mass in kilograms (g Na/kg). (CS, SF)

*Leaf litter nonpolar extractives percentage*—Proportion (%) of leaf litter that is in the form of nonpolar extractives (i.e., fats, oils, and waxes). **(CS, SF)** 

**Leaf litter P (percentage and per mass)**—Leaf litter P percentage (%) = proportion (%) of leaf litter that is phosphorus. Leaf P per mass = phosphorus content of overall dry leaf litter mass in kilograms (g P/kg). **(CS, SF)** 

*Leaf litter P/Ca ratio*—Ratio of phosphorus to calcium content within leaf litter expressed as kilograms phosphorus to kilograms calcium (kg P/kg Ca). (CS, FT)

Leaf litter phenols (percentage and per mass)—Percentage (%) of plant compounds containing a phenol group. These range from simple compounds synthesized in response to environmental insults to those more volatile. Capsaicin and serotonin are common examples, while certain phenols show associations with litterfall decomposition, resistance to fungal or other pests, and increased fire

duration and intensity. Phenols in leaf litter have been expressed on a percentage (%) and per-mass (g/kg) basis. (FT)

**Leaf litter tannins (percentage and per mass)**—Percentage (%) of protein-binding compounds produced by plants as a response to predation, fire intensity, or other environmental insults. Leaf litter tannins are expressed on a percentage (%) and per-mass (g/kg) basis. (FT, SF)

**Leaf litter water solubles (percentage and per mass)**—Leaf litter water solubles percentage (%) = proportion of leaf litter that is water soluble (i.e., amino acids and simple sugars). Leaf litter solubles are also expressed on a per-mass basis (g/kg). **(CS, SF)** 

*Modulus of elasticity*—The "push back," or resistance to deforming but not breaking when force is applied, expressed in megapascals (MPa). (FT, DT, CS)

*N fixation*—Effect of nitrogen-fixing organisms in direct association with a given plant species, expressed as a percentage (%). **(FT, DT, CS, SF)** 

*Nitrogen-15 content*—Proportion of plant tissues that utilize the  $N_{15}$  isotope, an indicator of how plants utilize atmospheric nitrogen.  $N_{15}$  content is measured in percent (%). **(FT, DT, CS, SF)** 

**Petiole length**—Measured in millimeters (mm). **(DT)** 

**Plant annual growth rate**—Vertical increase in growth per year, measured in centimeters per year (cm/yr). (FT, DT, CS, SF)

**Plant height at maturity**—Height in meters (m) that a plant attains when no longer considered to be in juvenile growth forms. **(FT, DT)** 

**Plant lifespan (average longevity)**—Time in years (yr) that a plant is expected to survive from germination to death. This can range from days for a plant with a relatively simple life history to thousands of years for slow-growing species or those with clonal growth habits. **(CS, SF)** 

**Postfire seed emergence**—Percentage (%) of seeds that germinate after fire events. **(FT, CS, SF)** 

**Postfire seed survival**—Percentage (%) of seeds that remain viable following fire events. (FT, CS, SF)

**Quantum efficiency** ( $Q_E$ )—Effectiveness of capturing energy available in solar radiation measured in micromoles per square meter per second (umol/m/s). (**DT**, **CS**)

**Quantum yield**—Micromoles of  $CO_2$  fixed per micromoles of photons absorbed (µmol  $CO_2$ /µmol photons) in photosynthesis. **(DT, CS)** 

**Relative growth rate, or RGR (biomass increment, height increment, and percentage)**—Increases in both mass in grams and stature in centimeters of a given plant per day (g/d; cm/d). RGR has also been represented by percentage (%). RGR indicates a growth investment and should be considered on a whole-plant basis. **(CS, DT, FT)** 

**Resprouting ability clipping**—Percentage (%) of damaged growth areas (leaves, branches, and related) that rejuvenate following pruning, forager browsing, or other direct removal. **(CS, SF)** 

**Resprouting ability fire**—Percentage (%) of damaged growth areas (leaves, branches, and related) that rejuvenate following combustion, extreme heat, desiccation, or other conditions associated with fire. (FT, CS, SF)

**Resin**—Percentage (%) of certain phenolic compounds secreted by plants in response to environmental insults. These generally refer to compounds associated with pines and aromatics such as copal, frankincense, and myrrh, but not sap, latex, or other gum-like substances. **(FT, SF)** 

**Root C percentage**—Carbon content of a leaf, expressed as a percentage (%). (CS, FT)

**Root C/N ratio**—Ratio of carbon to nitrogen content within a root expressed as kilograms carbon to kilograms nitrogen (kg C/kg N). **(CS, FT)** 

Root dry mass—Mass of a dried root in grams (g). (CS, DT, FT, SF)

**Root lignin percentage**—Proportion (%) of a root that is lignin. (CS, DT, FT, SF)

*Root lignin/N ratio*—Ratio of lignin to nitrogen content within a root, expressed as kilograms lignin to kilograms nitrogen (kg lignin/kg N). **(CS, DT, FT, SF)** 

**Root lignin/P ratio**—Ratio of lignin to phosphorus content within a root, expressed as kilograms lignin to kilograms phosphorus (kg lignin/kg P). (CS, DT, FT, SF)

**Root** N (percentage and per mass)—Proportion (%) of a root that is nitrogen. Root N per mass = nitrogen content of overall dry root mass in kilograms (g N/kg). (CS, SF)

**Root P (percentage and per mass)**—Proportion (%) of a root that is phosphorus. Root P per mass = phosphorus content of overall dry root mass in kilograms (g P/kg). **(CS, SF)** 

*Root/shoot ratio*—Proportion of belowground to aboveground growth in plants (kg root/kg shoot). **(FT, DT, CS, SF)** 

**Rooting depth**—Extent in meters (m) a given plant extends below ground level. (FT, DT, CS, SF)

**Saponins**—Percentage (%) of chemical compounds known for their ability to create foamy or frothy conditions when subjected to water. Saponins can serve as pest deterrents as they are often bitter and decrease palatability. **(FT, SF)** 

Sap flux (per unit sapwood area and per unit leaf area)—Sap flux, a measurement used to estimate tree-level transpiration, is expressed on a per-unit-sapwood area basis (mmol/cm/s) and a per-unit-leaf-area basis (kg/mol/m²). (CS, DT, FT)

**Sapwood area**—Area of the living wood that engages in transport of water measured in square centimeters (cm<sup>2</sup>). **(CS, DT, FT)** 

**Seed bank density**—Number of seeds present per square meter of seed bank (#/m²). **(SF)** 

Seed diameter—Width in centimeters (cm) of a seed. (CS, DT, SF)

**Seed dispersal distance**—Distance in meters (m) that seeds can disperse from a mature plant. This trait is related to successional facilitation. **(SF)** 

Seed length—Length in millimeters (mm) of a seed. (DT, CS, SF)

**Seed longevity**—Time in years (yr) that a seed remains viable. (FT, DT, SF)

**Seed mass**—Measured in milligrams (mg). (SF)

**Seed number**—Expected number of seeds produced per plant. (SF)

**Seed number per inflorescence**—Number of seeds produced per flowering event, expressed as 1/inflorescence. **(SF)** 

**Seed** N percentage—Proportion (%) of a seed that is nitrogen. (CS, SF)

**Seed P percentage**—Proportion (%) of a seed that is phosphorus. (CS, SF)

**Seed terminal velocity**—Maximum speed a seed attains while airborne after detaching from a plant, expressed in meters per second (m/s). **(SF)** 

Seed thickness—Measured in centimeters (cm). (FT, DT, CS, SF)

Seed volume—Measured in cubic centimeters (cm<sup>3</sup>). (CS, DT, SF)

**Seed width**—Width in millimeters (mm) of a seed. (CS, DT, SF)

Seeds per fruit—Number of seeds produced per individual fruit. (SF)

**Shoot** N percentage—Proportion (%) of a shoot that is nitrogen. (CS, SF)

**Shoot P percentage**—Proportion (%) of a shoot that is phosphorus. (CS, SF)

**Shoot water potential**—An indicator of water availability and thus potential water stress. Shoot water potential is measured in megapascals (MPa). **(DT)** 

*Specific leaf area*—Mass in grams of a given square centimeter of leaf area  $(cm^2/g)$ . This trait is the inverse of leaf mass per area (LMA), another trait commonly used in the literature. LMA was used for the *Liko Nā Pilina* example in section 2.2. (DT, CS, SF)

*Stem conduit diameter*—Size in micrometers ( $\mu$ m) of fluid-conducting stem portions. **(DT)** 

*Stem cross-sectional area*—Area in square micrometers ( $\mu$ m<sup>2</sup>) of fluid-conducting stem portions. **(DT)** 

Stem diameter—Measured in millimeters (mm). (FT, DT, CS, SF)

Stem dry mass—Measured in grams (g). (FT, DT, CS, SF)

Stem length—Measured in millimeters (mm). (FT, DT, CS, SF)

**Stem N (percentage and per mass)**—Stem N percentage = proportion of a stem that is nitrogen (%); stem N per mass = nitrogen content of overall dry stem mass in kilograms (g N/kg). **(CS, SF)** 

**Stem P (percentage and per mass)**—Stem P percentage = proportion of a stem that is phosphorus (%); stem P per mass = phosphorus content of overall dry stem mass in grams (g P/kg). **(CS, SF)** 

Stem respiration rate (stem volume)—The exchange of plant gases via stem tissues over a given volume ( $\mu$ mol/m/s). (DT, CS)

*Stem respiration rate (surface area)*—Exchange of plant gases via stem tissues over a given area ( $\mu$ mol/m/s). **(DT, CS)** 

Stem volume—Measured in cubic millimeters (mm<sup>3</sup>). (FT, DT, CS)

Stem litter ash per mass—Ash (i.e., mineral) content of overall dry stem mass in kilograms (g ash/kg). (FT, DT, CS)

**Stem litter C (percentage and per mass)**—Stem litter C percentage (%) = proportion of stem litter that is carbon; stem C per mass = carbon content of overall dry stem litter mass in kilograms (g C/kg). **(CS, FT)** 

*Stem litter C/N ratio*—Ratio of carbon to nitrogen content within stem litter, expressed as kilograms carbon to kilograms nitrogen (kg C/kg N). (CS, FT)

**Stem litter Ca (percentage and per mass)**—Stem litter Ca percentage (%) = proportion of stem litter that is calcium; stem Ca per mass = calcium content of overall dry stem litter mass in kilograms (g Ca/kg). **(CS, SF)** 

Stem litter decomposition (rate and mass lost)—The breakdown of dead stems into less complex organic matter, expressed as a rate (k) or percentage of mass lost (%). (CS, FT, SF)

Stem litter K (percentage and per mass)—Stem litter K percentage (%) = proportion of stem litter that is potassium; stem K per mass = potassium content of overall dry stem litter mass in kilograms (g K/kg). (CS, SF)

Stem litter lignin (percentage and per mass)—Stem litter lignin percentage (%) = proportion of a leaf that is lignin. Stem litter lignin per mass = lignin content of overall dry stem litter mass in kilograms (g lignin/kg). (FT, DT, CS, SF)

Stem litter Mg (percentage and per mass)—Stem litter Mg percentage (%) = proportion of stem litter that is magnesium. Stem litter Mg per mass = magnesium content of overall dry stem litter mass in kilograms (g Mg/kg). (CS, SF)

**Stem litter N (percentage and per mass)**—Stem litter N percentage (%) = proportion of stem litter that is nitrogen. Stem litter N per mass = nitrogen content of overall dry stem litter mass in kilograms (g N/kg). **(CS, SF)** 

**Stem litter nonpolar extractives percentage**—Proportion (%) of stem litter that is in the form of nonpolar extractives (i.e., fats, oils, and waxes). **(CS, SF)** 

Stem litter P per mass—Stem litter P per centage (%) = proportion of stem litter that is phosphorus. Stem litter P per mass = phosphorus content of overall dry stem litter mass in kilograms (g P/kg). (CS, SF)

Stem litter phenol percentage—Percentage (%) of plant compounds containing a phenol group. These range from simple compounds synthesized in response to environmental insults to those more volatile. Capsaicin and serotonin are common examples, while certain phenols show associations with litterfall decomposition, resistance to fungal or other pests, and increased fire duration and intensity. (FT)

**Stem litter tannin percentage**—Percentage (%) of protein-binding compounds produced by plants as a response to predation, fire intensity, or other environmental insults. **(FT, SF)** 

**Stem litter water soluble percentage**—Proportion (%) of stem litter that is water soluble (i.e., amino acids and simple sugars). **(CS, SF)** 

Stomata conductance (per area and per mass)—Stomata conductance per leaf area = amount of carbon dioxide conducted per square meter of leaf area per second ( $\mu$ mol CO<sub>2</sub>/m/s). Stomata conductance is also expressed on a mass basis ( $\mu$ mol CO<sub>2</sub>/g/s). (DT, CS, SF)

Stomata density—Number of stoma per square millimeter (stom/mm<sup>2</sup>). (DT, CS, SF)

*Tensile strength of wood*—Amount of force in megapascals (MPa) that can be applied to wood prior to breaking. **(CS)** 

**Terpenes**—Percentage (%) of compounds serving a variety of protective, regulatory, and other functions in most organisms. Terpenes are often associated with resins and can be found in plants such as conifers, citrus, and members of the carrot family. (FT)

*Time to maturity*—Time in months (mo) required for a germinated seed to no longer be considered juvenile. **(SF)** 

*Time to reproduction*—Time in months (mo) for a germinated seed to be capable of producing viable reproductive structures including flowers, seeds, and related. **(SF)** 

*Transpiration rate*—Transpiration, the rate of water movement through a plant and its evaporation from aerial parts, is measured in kilograms per day (kg/d) and is calculated by multiplying sap flow velocity by sapwood area. (CS, DT, FT)

*Wood density/specific gravity*—Amount of wood present within a cubic meter, measured in grams per cubic meter (g/m³). **(CS)** 

#### 4.0 Technical Overview

REST was constructed using the Microsoft Visual Studio 2015 Windows Forms<sup>™</sup> platform. The main program is composed of three parts: graphical user interface (GUI), database, and analysis. The GUI was created exclusively with tools found in the Windows Forms resources. The database itself is hosted on a secure lab computer implemented using PHPmyAdmin and is updated periodically as new data become available. The analysis portion includes all algorithms and functions hidden from the user. Principal component analysis output graphs are generated using the

Accord.Net open source framework. REST is optimized for Windows-based operating systems only (other platforms may be available in the future).

Initially, development of REST did not take into consideration the computation time needed for searching through large databases of plant species and associated functional traits. Computation time thus became an issue for prototypes, one solved through the use of search algorithm refactorization. All algorithms involved in database searches were rewritten to use a revised hashing function, changing time complexity to O(1) over the previous linear searches and nested loop structures with time complexity of  $O(n^2)$ . However, even with optimizing search algorithms through refactorization, a notable delay remained upon program start. Depending on the device's Internet connection, a 1- to 2-minute lag occurred, requiring a local database on the user's computer. Implementing the local database reduced startup time to approximately 20 seconds while also allowing offline program use via an archived past version (database updates occur once reconnected).

Further program development benefitted from different techniques such as Agile methods and more traditional methods. Agile methods were a suitable software development process that accelerated productivity, while more precisely meeting programming requirements. Regular developer-scientist meetings informed prototyping and supported a more holistic product as requirements evolved during software development. Specifically, the Agile method of pair programming produced a notable acceleration in feedback and error correction. As a result, use of this technique increased design quality and developer satisfaction while decreasing time and coding effort, an important benefit as REST's program size continued to expand. The larger the program became, the more effort was required to insert additional lines of code. All written code is nonlinear and exists in the context of the larger program. Thus, care was taken to develop a proper foundation of code, one verified through pair programming to increase optimization and efficiency for acceptable computation times and larger databases. Through these initial efforts, future iterations of REST can be expanded while maintaining program and database integrity.

# 4.1 Caveats for Using REST

REST is best used as an iterative tool to compare different combinations of species. However, limiting factors exist outside of REST that practitioners should consider. These include economics (e.g., cost of seed/plants, labor, or time), logistics (e.g., availability of species, project, or budget timelines), resilience to climatic change or disturbance regimes, and goals, objectives, or other expectations of stakeholders. The process used by REST allows the data to provide an unbiased and objective

first step, followed by practical concerns of limiting factors prior to final species choices. In this regard, REST can serve as a complement to other landscape-management decision tools at the local, regional, or ecosystem level.

Risks of using REST as a management assistance program are few. As the program is both user-defined and creates simulated outcomes, the majority of risk tends toward the end user. Vetting of sites, trait and final species selection, and enacting conditions necessary for trait expression are all at the discretion of users. Suboptimal site conditions, seed germination, transplant survival, and related variables are inherent risks in any intervention attempt. Using REST during planning stages may help to decrease the severity of such circumstances if different species combinations are compared objectively. Yet, the REST user must bring to the table a site-specific understanding of (1) restoration goals, (2) target species, (3) community assembly rules, and (4) desired community densities, as the REST program does not address these areas.

In REST, we have accessed publicly available global databases that contain trait data for a variety of the world's species and compiled them into the program. However, there are many species with limited trait data and many species not in the program. For this reason, REST allows the user to import data on species and traits as a .csv file. Another caveat for using REST is choosing to input categorical variables; as REST uses principal components analysis (PCA), a statistical technique in which it is proper to statistically analyze only continuous variables. Yet, categorical variables could be added by the user by coding each category with a number. For example, if you wanted to include dispersal type, a file could be inputted with the dispersal type coded so that wind = 1, water = 2, animal = 3, and gravity = 4. In that case, the user would need to import data as a .csv file. Although it may not be viable to include categorical variables from a strictly statistical sense, the output from including these variables might still be useful in conveying restoration methods to the user, as the intent of the program is to offer useful visuals; we do not suggest using the statistical output beyond making species decisions for restoration planning. Any use of the PCA output for scientific publications should be reviewed by a statistician. Some important categorical variables include carbon pathway, growth habit, reproductive life history, shade tolerance, nitrogen-fixation capacity, and vegetative spread.

From a hardware perspective, REST is relatively compact, an artifact of design with the decreased processing speeds and storage capacities of field computers in mind. When installed, REST requires less than 1 GB of RAM and 512 MB of disk space, allowing for smooth program operation and visual renderings. Because of its size, REST can be run from flash drives or SD cards. REST requires momentary

Internet connectivity at startup for program and database update purposes, but can function offline after initial installation, as the master traits database will be copied to the user's local drive. Users can freely edit their local database copy as they please. However, users will not be able to directly edit the master trait database, nor will their local database changes be relayed to the host computer, preserving trait data integrity. Rather, users are encouraged to update their local databases periodically, noting that any local changes will need to be exported and reentered during the update process.

#### 4.2 Future Directions for REST

REST is an evolving program with many directions for future development. The program database contains several thousand entries ranging from rare endemics to more cosmopolitan species. More species, functional traits, and restoration goals are currently being drawn from regionally exclusive species traits lists, a comprehensive literature review, new data generated by *Liko Nā Pilina* and other projects, and information provided by managers familiar with REST. Efforts to expand REST data are ongoing and updated regularly. New versions can be found at https://hilo.hawaii.edu/faculty/ostertag/.

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## U.S. Equivalents

When you know:	Multiply by:	To find:
Micrometers (μm)	0.000394	Inches
Millimeters (mm)	0.0394	Inches
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Meters	1.094	Yards
Square meters (m <sup>2</sup> )	10.76	Square feet
Cubic millimeters (mm <sup>3</sup> )	0.00006102	Cubic inches
Milligrams (mg)	0.00003527	Ounces
Grams (g)	0.0352	Ounces
Grams	0.0022	Pounds
Kilograms (kg)	2.205	Pounds
Kilograms	0.0011	Tons
Megapascal (MPa)	145.038	Pounds per square inch
Degrees Celsius (°C)	$1.8(^{\circ}C) + 32$	Degrees Fahrenheit

#### References

Adler, P.; Salguero-Gómez, R.; Compagnoni, A.; Hsu, J.S.; Ray-Mukherjee, J.; Mbeau-Ache, C.; Franco, M. 2014. Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences of the United States of America. 111(2): 740–745.

**Allaby, M. 2012.** A dictionary of plant sciences. 3<sup>rd</sup> ed. Oxford, United Kingdom: Oxford University Press. 544 p.

**Bhaskar, R.; Dawson, T.E.; Balvanera, P. 2014.** Community assembly and functional diversity along succession post-management. Functional Ecology. 28(5): 1256–1265.

- Chave, J.; Coomes, D.A.; Jansen, S.; Lewis, S.L.; Swenson, N.G.; Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. Ecology Letters. 12(4): 351–366. doi:dx.doi.org/10.1111/j.1461-0248.2009.01285.x.
- **Cochrane, M., ed. 2009.** Tropical fire ecology: climate change, land use, and ecosystem dynamics. Chichester, United Kingdom: Springer-Praxis. 682 p.
- Cordell, S.; Ostertag, R.; Rowe, B.; Sweinhart, L.; Vasquez-Radonic, L.; Michaud, J.; Cole, T.C.; Schulten, J.R. 2009. Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. Biological Conservation. 142: 2997–3004.
- Cornelissen, J.H.C.; Lavorel, S.; Garnier, E.; Diaz, S.; Buchanan, N.; Gurvich, D.E.; Reich, P.B.; ter Steege, H.; Morgan, H.D.; van der Heijden, M.G.A.; Pausas, J.G.; Poorter, H. 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. Australian Journal of Botany. 51: 335–380.
- Commonwealth Scientific and Industrial Research Organisation [CSIRO]. 2013. Prometheus Wiki: protocols in ecological & environmental plant physiology. http://prometheuswiki.publish.csiro.au/tiki-custom\_home.php. (12 November 2015).
- **Cuddihy, L.W.; Stone, C.P. 1990.** Alteration of native Hawaiian vegetation—effects on humans, their activities and introductions. Honolulu, HI: University of Hawai'i Press. 128 p.
- **Daehler, C. 2009.** Weed risk assessments for Hawaii and Pacific Islands. http://www.botany.hawaii.edu/faculty/daehler/wra/default2.htm. (25 February 2016).
- **Denslow, J.S. 2003.** Weeds in paradise: thoughts on the invasibility of tropical islands. Annals of the Missouri Botanical Garden. 90(1): 119–127.
- **Devlin, R.M. 1975.** Plant physiology. 3<sup>rd</sup> ed. New York: Van Nostrand Company. 577 p.
- **Donovan, L.A.; Maherali, H.; Caruso, C.M.; Huber, H.; de Kroon, H. 2011.**The evolution of the worldwide leaf economics spectrum. Trends in Ecology and Evolution. 26(2): 88–95.
- Douma, J.C.; Aerts, R.; Witte, J.P.M.; Bekker, R.M.; Kunzmann, D.; Metelaar, K.; van Bodegom, P.M. 2012. A combination of functionally different plant traits provides a means to quantitatively predict a broad range of species assemblages in NW Europe. Ecography. 35(4): 364–373.

- **Drenovsky, R.E.; James, J.J. 2010.** Designing invasion-resistant plant communities: the role of plant functional traits. Rangelands. 32(1): 32–37.
- **Ewel, J.J.; Putz, F.E. 2004.** A place for alien species in ecosystem management. Frontiers in Ecology and the Environment. 2(7): 354–360.
- Fahn, A. 1982. Plant anatomy. 3<sup>rd</sup> ed. Elmsford, NY: Pergamon Press. 600 p.
- **Fitter, A.H.; Hay, R.K.M. 2002.** Environmental physiology of plants. 3<sup>rd</sup> ed. San Diego, CA: Academic Press. 367 p.
- Fry, E.L.; Power, S.A.; Manning, P. 2013. Trait-based classification and manipulation of plant functional groups for biodiversity—ecosystem function experiments. Journal of Vegetation Science. 25: 248–261.
- **Funk, J.L.; Cleland, E.E.; Suding, K.N.; Zavaleta, E.S. 2008.** Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution. 12: 695–703.
- Giambelluca, T.; Chen, Q.; Frazier, A. [et al.]. 2011. Rainfall atlas of Hawai'i. http://rainfall.geography.hawaii.edu. (2 June 2016).
- Giambelluca, T.W.; Shuai, X.; Barnes, M.L. [et al.]. 2014. Evapotranspiration of Hawai'i. Final report submitted to the U.S. Army Corps of Engineers—Honolulu District and the Commission on Water Resource Management, State of Hawai'i. http://evapotranspiration.geography.hawaii.edu/. (28 November 2018).
- Hobbs, R.J.; Arico, S.; Aronson, J.; Baron, J.S.; Bridgewater, P.; Cramer,
  V.A.; Epstein, P.R.; Ewel, J.J.; Klink, C.A.; Lugo, A.E.; Norton, D.; Ojima,
  D.; Richardson, D.M.; Sanderson, E.W.; Valladares, F.; Vilà, M.; Zamora,
  R.; Zobel, M. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography. 15: 1–7.
- **Hobbs, R.J.; Higgs, E.; Hall, C.M. [et al.]. 2014.** Managing the whole landscape: historical, hybrid, and novel ecosystems. Frontiers in Ecology and the Environment. 12(10): 557–564.
- **Holl, K.D.; Aide, T.M. 2011.** When and where to actively restore ecosystems? Forest Ecology and Management. 261: 1588–1563.
- **Hughes, R.F.; Denslow, J.S. 2005.** Invasion by a N<sub>2</sub>-fixing tree alters function and structure in wet lowland forests of Hawaii. Ecological Applications. 15(5): 1615–1628
- **Jepson Flora Project. 2006.** Ecological flora of California. http://ucjeps.berkeley.edu/efc/dbase.html. (11 July 2016).

- **Jones, T.A. 2013.** Ecologically appropriate plant materials for restoration applications. BioScience. 63: 211–219.
- **Kattge, J.; Díaz, S.; Lavorel, S. [et al.]. 2011.** TRY—a global database of plant traits. Global Change Biology. 17: 2905–2935.
- **Kendall, C. 2004.** Resources on isotopes: periodic table—nitrogen. Menlo Park, CA: U.S. Department of the Interior, Geological Survey, Isotopes Tracers Project. http://www.rcamnl.wr.usgs.gov/isoig/period/n\_iig.html. (21 March 2016).
- **Kirch, P.V. 2002.** On the road of the winds: an archaeological history of the Pacific Islands before European contact. Berkeley, CA: University of California Press. 446 p.
- **Kunstler, G.; Falster, D.; Coomes, D.A. [et al.]. 2016.** Plant functional traits have globally consistent effects on competition. Nature. 529: 204–207.
- **Laureto, L.M.O.; Cianciaruso, M.V.; Samia, D.S.M. 2015.** Functional diversity: an overview of its history and applicability. Natureza & Conservação: Brazilian Journal of Nature Conservation. 13: 112–116.
- **Litton, C.M.; Sandquist, D.R.; Cordell, S. 2006.** Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. Forest Ecology and Management. 231: 105–113.
- Ostertag, R.; Cordell, S.; Michaud, J.; Cole, T.C.; Schulten, J.R.; Publico, K.M.; Enoka, J.H. 2009. Ecosystem and restoration consequences of invasive woody species removal in Hawaiian lowland wet forest. Ecosystems. 12: 503–515.
- Ostertag, R.; Warman, L.; Cordell, S.; Vitousek, P.M. 2015. Using plant functional traits to restore Hawaiian rainforest. Journal of Applied Ecology. 52: 805–809.
- **Paula, S.; Pausas, J.G. 2013.** BROT: a plant trait database for Mediterranean Basin species. Version 2013.06. http://www.uv.es/jgpausas/brot.htm. (11 July 2016).
- Price, J.; Gon, S.M., III; Jacobi, J.D.; Matsuwaki, D.; Mehrhoff, L.; Wagner, W.; Lucas, M.; Rowe, B. 2012. Mapping plant species ranges in the Hawaiian Islands: developing a methodology and associated GIS layers. Open-File Report 2012-1192. Reston, VA: U.S. Department of the Interior, Geological Survey. 34 p. + appendix.
- **Pugnaire, F.I.; Valladares, F., eds. 1999.** Handbook of functional plant ecology. New York: Marcel Dekker. 920 p.

- **Quinn, G.P.; Keough, M.J. 2002.** Experimental design and data analysis for biologists. Cambridge, United Kingdom: Cambridge University Press. 537 p.
- **Reich, P.B. 2014.** The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. Journal of Ecology. 102(2): 275–301.
- Reich, P.B.; Ellsworth, D.S.; Walters, M.B.; Vose, J.M.; Gresham, C.; Volin, J.C.; Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology. 80(6): 1955–1969.
- Reich, P.B.; Wright, I.; Cavender-Bares, J.; Craine, M.; Oleksyn, J.; Westoby,
  M.; Walters, M.B. 2003. The evolution of plant functional variation: traits,
  spectra, and strategies. International Journal of Plant Sciences. 164(S3): 143–164.
- **Rey Benayas, J.M.; Newton, A.C.; Diaz, A.; Bullock, A.M. 2009.** Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science. 325(5944): 1121–1124.
- Schlaepfer, M.A.; Sax, D.F.; Olden, J.D. 2011. The potential conservation value of non-native species. Conservation Biology. 25(3): 428–437.
- Schleuter, D.; Daufresne, M.; Massol, F.; Argillier, C. 2010. A user's guide to functional diversity indices. Ecological Monographs. 80(3): 469–484.
- **Sonnier, G.; Navas, M.-L.; Fayolle, A.; Shipley, B. 2012.** Quantifying trait selection driving community assembly: a test in herbaceous plant communities under contrasted land use regimes. Oikos. 121(7): 1103–1111.
- **Thomson, F.J.; Moles, A.T.; Auld, T.D.; Kingsford, R.T. 2011.** Seed dispersal distance is more strongly correlated with plant height than with seed mass. Journal of Ecology. 99(6): 1299–1307.
- **U.S. Department of Agriculture, Natural Resources Conservation Service** [USDA NRCS]. 2016. The PLANTS database. Greensboro, NC: National Plant Data Team. http://plants.usda.gov. (11 July 2016).
- van Bodegom, P.M.; Douma, J.C.; Verheijen, L.M. 2014. A fully traits-based approach to modeling global vegetation distribution. Proceedings of the National Academy of Sciences of the United States of America. 111(38): 13733–13738.
- **Vitousek, P.M.; Walker, L.R. 1989.** Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs. 59(3): 247–265.

- Wagner, W.L.; Herbst, D.R.; Sohmer, S.H. 1999. Manual of the flowering plants of Hawaii. Honolulu, HI: University of Hawaii Press and Bishop Museum Press. 1952 p.
- Way, D.A.; Katul, G.G.; Manzoni, S.; Vico G. 2014. Increasing water use efficiency along the C<sub>3</sub> to C<sub>4</sub> evolutionary pathway: a stomatal optimization perspective. Journal of Experimental Botany. 65(13): 3863–3693. doi:10.1093/jxb/eru205.
- **Woodcock, D. 2003.** To restore the watersheds: early 20<sup>th</sup> century tree planting in Hawaii. Annals of the Association of American Geographers. 93(3): 624–635.
- Wright, I.J.; Reich, P.B.; Cornelissen, J.H.C.; Falster, D.S.; Garnier,
  E.; Hikosaka, K.; Lamont, B.B.; Lee. W.; Oleksyn, J.; Osada, N.; Poorter;
  H.; Villar, R.; Warton, D.I.; Westoby, M. 2005. Assessing the generality of global leaf trait relationships. New Phytologist. 166(2): 485–496.
- Zedler, J.B.; Doherty, J.M.; Miller, N.A. 2012. Shifting restoration policy to address landscape change, novel ecosystems, and monitoring. Ecology and Society. 17(4): 36. http://www.ecologyandsociety.org/vol17/iss4/art36/.
- Zimmerman, N.; Hughes, R.F.; Cordell, S.; Hart, P.; Chang, H.K.; Perez, D.; Kaipoalohaakala Like, R.; Ostertag, R. 2008. Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai'i. Biotropica. 40(3): 277–284.

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