

‘Chardonnay’ paired with leaf economics traits and a side of soil compaction

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Abstract

Functional trait variation in plants of the same species or genotype are a critical determinant of ecosystem processes, especially in agroecosystems where single crop species or genotypes exist in very high abundances. Yet to date only a small number of studies have evaluated if, how, or why traits forming the Leaf Economics Spectrum (LES) vary within crops, despite such studies informing our understanding of: 1) the environmental factors that drive crop LES trait variation; and 2) how domestication has altered LES traits in crops vs. wild plants. We assess intragenotype variation in LES traits in wine grape variety ‘Chardonnay’ (*Vitis vinifera*)—among the world’s most commercially important crops, across a soil compaction gradient: one of the most prominent characteristics of agricultural soils that may drive crop trait variation. ‘Chardonnay’ traits covary along an intragenotype LES in patterns that were qualitatively similar to, though statistically distinguishable from, those observed among wild plants: resource acquiring vines expressed a combination of high mass-based photosynthesis (A_{mass}), mass-based dark respiration (R_{mass}), leaf nitrogen concentrations (N), coupled with low leaf mass per area (LMA); the opposite set of trait values defined the resource conserving end of the ‘Chardonnay’ LES. Traits related to resource acquisition (A_{mass} , R_{mass} , and leaf N) declined with greater bulk density, while traits related to investment in leaf construction costs (LMA) increased with greater bulk density. Compared to wild plants, ‘Chardonnay’ expressed lower R_{mass} for a given rate of A_{mass} , and an unexpected positive covariation between leaf carbon (C) concentrations and R_{mass} , A_{mass} , and leaf N . Our findings uncover a deeper understanding of both the domestication syndromes in grapevines, and expand our understanding of trait-based crop responses to environmental change and gradients.

Introduction

The Leaf Economics Spectrum (LES) is a framework for understanding the causes and consequences of differences in the comparative ecophysiology, morphology, and biochemistry of plants (I. J. Wright et al., 2004). On one end of the LES, are species expressing “resource acquiring” trait syndromes that include high maximum leaf-level photosynthesis (A) and dark respiration (R) rates, high leaf nitrogen (N) concentrations, and low leaf mass per unit area (LMA). The other end of the LES is defined by plants expressing the opposite suite of trait values, which represent “resource conserving” trait syndromes (I. J. Wright et al., 2004). Variability in traits along the LES underpin differences in how plant species respond to environmental conditions and change (e.g. I.J. Wright et al., 2005), and are central in driving relationships between plant species composition and ecosystem functioning (e.g. P.B. Reich, Rich, Lu, Wang, & Oleksyn, 2014). Correlations and trade-offs among LES traits detected across thousands of plant species, both within and across biomes (P.B. Reich et al., 1999; P. B. Reich, Walters, & Ellsworth, 1997; Thomas et al., 2020), have also informed our understanding of the evolutionary and environmental factors that constrain leaf form and

function (Donovan, Maherali, Caruso, Huber, & de Kroon, 2011; P.B. Reich et al., 2003; Shipley, Lechowicz, Wright, & Reich, 2006).

The original formulation and early research on the LES, focused trait differences across plant species or communities (P. B. Reich et al., 1997; I. J. Wright et al., 2004). However more recently, meta-analyses have argued and shown that variation within species constitutes a considerable proportion (e.g., ~29% of LMA and leaf N) of total LES trait variation within plant communities (Albert et al., 2010; Fajardo & Siefert, 2018; Siefert et al., 2015). Extending from this work, studies have now begun focusing on evaluating how plants of the same species differ in their LES traits, with conspecific plants commonly differing from one another along an intraspecific LES (Hayes et al., 2019; Martin et al., 2017; Niinemets, 2015). Moreover, in unmanaged systems, the within-species variation that exists in certain LES traits has also been found to be a significant correlate of ecosystem structure, function, and responses to environmental change (Laforest-Lapointe, Martínez-Vilalta, & Retana, 2014; Mitchell, Ames, & Wright, 2021; Siefert & Ritchie, 2016; see also Westerband, Funk, & Barton, 2021 and references therein).

Research on LES trait variation and relationships within species also informs an understanding of how and why the functional ecology of crops varies in managed agroecosystems. Specifically, studies have shown that individuals of the same crop species or genotype express wide variation in their LES traits, often along an intraspecific or intragenotypic Leaf Economics Spectrum. This includes studies detecting within species or genotype LESs that exists in several of the world’s most common crops including soy (Hayes et al., 2019), rice (Xiong & Flexas, 2018), coffee (Gagliardi, Martin, Virginio Filho, Rapidel, & Isaac, 2015; Martin et al., 2017), wheat (Roucou et al., 2018), and maize (Martin et al., 2018). Across these studies, intraspecific or intragenotypic LES trait variation in crops was a statistical correlate of agroecosystem functions including yield (Gagliardi et al., 2015; Hayes et al., 2019), photosynthetic N-use efficiency (Xiong & Flexas, 2018), tissue decomposition (Coleman, Martin, Thevathasan, Gordon, & Isaac, 2020), N₂-fixing structures (Martin et al., 2019), and soil microbial diversity (Fulthorpe, Martin, & Isaac, 2019).

Studies on crops have also helped elucidate the factors that cause plants to differentiate along a given intraspecific or intragenotypic LES, which to date includes temperature and precipitation regimes (Martin et al., 2018), soil nutrient availability (Buchanan, Isaac, Van den Meersche, & Martin, 2019), plant ontogenetic stages (Hayes et al., 2019) or size (Martin & Isaac, 2021), or light (Gagliardi et al., 2015). Results differ across crops and spatial scales, though generally studies have found plants of the same crop move towards the resource conserving end of a within-species- or -genotype LES (i.e., plants expressing low A , low leaf N, high LMA) under the following: 1) hot and dry environments (Martin et al., 2017); 2) shaded conditions, such as those in agroforestry systems (Gagliardi et al., 2015); and 3) following reproductive onset (Hayes et al., 2019; Martin & Isaac, 2021). While these studies are instructive, there remain important factors that may also lead to differences in crop traits along an intraspecific or intragenotypic LES that have yet to be explored.

Soil compaction is a major characteristic of land degradation worldwide, and a primary contributor to reductions in agricultural productivity and sustainability (Colombi & Keller, 2019; Hamza & Anderson, 2005; Nawaz, Bourrie, & Trolard, 2013). In some instances, increased soil compaction results in higher rates of A , growth, and yield (Morales, Pavlovič, Abadía, & Abadía, 2018). Though more often, growth and yield reductions in plants under compaction occur as the cumulative consequence of reductions in root growth, which in turn limit water and nutrient uptake; compaction also triggers complex plant signalling pathways, which ultimately reduce leaf-level A via stomatal and non-stomatal factors (Colombi & Keller, 2019; Kozłowski, 1999; Lipiec & Stepniewski, 1995; Morales et al., 2018; Sadras, O’Leary, & Roget, 2005). Existing literature therefore supports the untested hypothesis that soil compaction drives trait covariation and/ or trade-offs along an intraspecific or intragenotypic LES. Specifically, when soil compaction gradients exist within a site, plants in high compaction should express resource conserving LES traits (i.e., low A , leaf N, and R , along with high LMA), while those in low compaction areas should express the opposite suite of traits.

Existing work on crops has also focused only on a subset of the six traits included in the original LES

formulation. Specifically, studies on coffee (Gagliardi et al., 2015; Martin et al., 2019), soy (Hayes et al., 2019), and rice (Xiong & Flexas, 2018) have largely analyzed how three LES traits— A , LMA or SLA, and leaf N —covary or trade-off within crop species or genotypes. For instance, Martin et al. (2017) found lower A for a given leaf N in coffee vs. wild plants, and based on this finding hypothesized that either artificial selection for caffeine, or luxury consumption of N-based compounds from soil amendments, has altered LES trait relationships in that crop. Conversely, Xiong and Flexas (2018) found that rice expressed a higher A for a given leaf N vs. wild rice plants, supporting the hypothesis that artificial selection has resulted in higher photosynthetic nitrogen-use efficiency in that crop. Other studies have found that while crops such as soy, wheat, and maize occupy the extreme resource-acquiring end of the LES (Martin et al., 2018; Milla, Osborne, Turcotte, & Violle, 2015), domestication has not necessarily altered the slope or strength of bivariate trait relationships among A , LMA, or leaf N (Hayes et al., 2019).

While these and other findings have informed our understanding of how artificial selection influences plant trait syndromes, certain LES traits—namely leaf R —have largely been omitted from these and other analyses on crop trait syndromes. Leaf R is among the six core traits forming the LES, which exists among plant species globally, being significantly correlated ($r^2=0.34-0.60$) to all other LES traits (I. J. Wright et al., 2004). The relationship between R and other traits along the global LES, reflect evolved physiological, biochemical, and structural trade-offs in plants: the physiological cost of R , in terms of plant carbon (C) metabolism, increases with greater leaf N and A and declines with increasing LMA (P.B. Reich et al., 1998; I.J. Wright et al., 2006; I. J. Wright et al., 2004). The incorporation of R into any LES is therefore central, as it reflects a quantifiable physiological cost of resource acquisition.

In crops, reducing R while maintaining plant growth and yield is one of several goals of selection programs, with research on tomato (Nunes-Nesi et al., 2005), canola (Hauben et al., 2009), cucumber (Juszczuk et al., 2007), and rye grass (Wilson & Jones, 1982) showing that reductions in plant C losses via R , due to artificial selection were related to higher yields. Therefore, one might expect that artificial selection may have altered the shape (i.e., the intercept and slope) and strength of the relationship between leaf R and other LES traits in crops vs. wild plants. Moreover, changes in crop leaf R have been evaluated in responses to soil nutrient amendments, irrigation, and growing temperatures, though relationships between leaf R and soil compaction are less commonly assessed (Amthor, 2012). Since, 1) croplands now cover at least $\sim 12.2-17.1$ million km^2 of Earth’s ice-free land (Ramankutty, Evan, Monfreda, & Foley, 2008), and 2) compaction is a central feature on an estimated 68 million ha of soils on the world’s arable lands (Colombi & Keller, 2019; Hamza & Anderson, 2005), then 3) understanding how R , and its relationship to other LES traits in crops, is influenced by compaction is particularly important for refining Earth System models (Atkin et al., 2015).

Here, we explored how LES traits vary in ‘Chardonnay’ (*Vitis vinifera* var. ‘Chardonnay’), one of the world’s most commercially important, widespread, and rapidly expanding winegrape varieties (Aryal & Anderson, 2013). We evaluated LES and related traits on individual ‘Chardonnay’ vines that exist across a soil compaction gradient, to address the following questions: 1) Is intra-genotype variation in Chardonnay LES traits related to soil compaction? If so, then 2) does soil compaction lead to ‘Chardonnay’ leaves and vines differentiating from one another along an intragenotype LES? Finally, we assess 3) whether or not the shape of a potential intra-genotype LES in Chardonnay differs from the LES detected across plants globally?

Methods

Study site and design

Our study was situated at the Niagara College Teaching Vineyard, a 16.2-ha operational vineyard situated at the Daniel J. Patterson Campus in Niagara-on-the-Lake, Ontario, Canada (43.1522° N, 79.1652° W). The vineyard is situated in the Niagara-on-the-Lake Regional Appellation, which is in turn nested within the Niagara Peninsula Appellation. Soils at the site are classified as imperfectly drained silty clays (to 40-100 cm depth) over clay loam till mixed with poorly drained lacustrine heavy clay. The farm is under commonly employed vineyard management systems, which includes applications of calcium nitrate and/ or muriate of potash and/ or sulphate of potash magnesium (K-Mag; 22-10.8-22), applied uniformly across the farm in

mid-June. Liquid calcium (8-0-0-10) is also applied as a foliar spray early in each growing season. In mid-June of each year cover crops are planted in every second row with 65% annual rye, 20% crimson clover and 15% eco-till radish through deep ripping, discing and harrowing passes. At the site there is 7.26-cm diameter tile drainage installed in every other row, and the site is not irrigated.

Our study was conducted over a 1-week period between July 1st and 7th, 2021, when vines were in the fruit setting/ berry development phenological stage (Coombe, 1995). We selected a total of 15 individual ‘Chardonnay’ vines (“Dijon Clone 76”) for functional trait analyses, which were distributed evenly across five different planting rows spaced 15-20 m apart (corresponding to an even 10 interceding planting rows). These sampling rows run parallel to one another, and broadly follow a soil compaction gradient that runs along a northwest to southeast orientation in the vineyard. This gradient is related to the vineyard’s imperfectly drained soils and hydrology. Generally, northwest areas and planting rows are well drained by mid- to late- May. By comparison, areas and planting rows in the southeast remain poorly drained for roughly an additional month, drying by mid- to late-June. Since farm machinery is required for foliar applications and cover crop plantings across the entire vineyard in mid- June, southeast areas of the vineyard therefore experience enhanced mechanical compaction every year in early late Spring/ early summer. Soil bulk density was collected for each sampled vine (described below) to a 10 cm depth, using a 1 cm diameter core borer, and varied significantly across rows (Analysis of Variance (ANOVA) $F_{4, 10}=5.84$, $p < 0.001$), with rows 1 through 5 expressing bulk density values of 1.36 ± 0.12 (S.D.) g cm^{-3} , 1.58 ± 0.08 g cm^{-3} , 1.67 ± 0.09 g cm^{-3} , 1.64 ± 0.1 g cm^{-3} , and 1.72 ± 0.1 g cm^{-3} , respectively.

Within each sampling row, three individual vines situated 13-15 m away from one another were chosen for leaf trait measurements. Each of the 15 vines chosen for our study, was between 1.5-2 cm in resprout diameter and free of any pest, pathogen, or mechanical damage. On each plant, we selected three recently developed and fully expanded leaves that were free of any damage or disease, and situated on the upper-most cane in full-sun conditions. This nested study design therefore resulted in leaf traits being measured on 45 leaves from 15 individual vines that were of the same size, age, rootstock and pruning regimes, which were in turn situated within five distinct sample rows.

Functional trait measurements

We quantified 13 physiological, morphological, and chemical traits for each individual leaf. To do so, we executed 14-point photosynthetic light-response curves on each leaf using a LI-6800 Portable Photosynthesis System (Licor Bioscience, Lincoln, Nebraska, USA), to measure area-based photosynthetic rates ($A_{\text{area}}; \mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) across a range of photosynthetic photo flux density (I) levels (i.e., 2000, 1500, 1200, 1000, 800, 600, 400, 200, 100, 80, 60, 40, 20, and 0 $\mu \text{ mol}$ photosynthetically active radiation (PAR) $\text{m}^{-2} \text{ s}^{-1}$). All photosynthetic rates were allowed to stabilize at each level of I for at least 120 seconds prior to data acquisition (Berry & Goldsmith, 2020; Salter, Merchant, Richards, Trethowan, & Buckley, 2019), with each light response curve therefore taking a minimum of 30 minutes to complete. All A_{area} measurements were made between 8:00-12:00 am to avoid mid-day stomatal closure, with leaf chamber conditions maintained at CO_2 concentrations of 400 ppm, relative humidity at 53.1-73.5%, leaf vapour pressure deficits of 1.2-1.7 KPa, and leaf temperatures between 24.3-31.6 °C.

Physiological traits were calculated for each leaf by fitting non-rectangular hyperbola to each of the 45 light response curves as:

$$A_{\text{area}} = R_{\text{area}} + \frac{\phi I + A_{\text{max}} - \sqrt{(\phi I + A_{\text{max}})^2 - 4\theta \phi I A_{\text{max}}}}{2\theta} \text{ Equation 1}$$

where R_{area} represents area-based leaf R rates ($\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), Φ is the apparent quantum yield of photosynthesis ($\text{mol CO}_2 \text{ mol PPF}^{-1}$), A_{max} is the light-saturated maximum area-based photosynthetic rate, and θ represents a curvature parameter. From these models, we also derived leaf-level light compensation points (LLCP, $\mu \text{ mol PAR m}^{-2} \text{ s}^{-1}$), calculated as I , where $A_{\text{area}}=0$. Light response curves were fitted using the ‘nls’ function in R v.3.3.3 statistical software (R Foundations for Statistical Computing, Vienna, Austria).

After light response curves were completed in the field, each leaf was immediately collected and transported to the University of Toronto Scarborough for morphological and chemical trait determinations. First, leaf area (cm^2) was measured using a LI-3100C leaf area meter (Licor Bioscience, Lincoln, Nebraska, USA), and all leaves were then dried at 65°C to constant mass and weighed (g). We then calculated LMA (g m^{-2}) as leaf mass/leaf area, and used these LMA values to calculate maximum mass-based photosynthetic (A_{mass}) and mass-based dark respiration rates (R_{mass}), as A_{max} or $R_{\text{area}} / \text{LMA}$, respectively. Lastly, dried leaf tissue was ground into a fine powder using a MM400 Retsch ball mill (Retsch Ltd., Hann, Germany), and ~ 0.1 grams of tissue was weighed and analyzed for C and N concentrations (both on a % mass basis) on a LECO CN 628 elemental analyzer (LECO Instruments, Ontario, Canada).

Analysis of leaf trait variation

We first evaluated if traits were either normally or log-normally distributed using the ‘fitdist’ function in the ‘fitdistrplus’ R package (Delignette-Muller & Dutang, 2015), with the highest log-likelihood scores indicating the best-fit data distribution. For traits that were normally distributed, we calculated descriptive statistics as means and standard deviations (SD), while medians, median and SD values were calculated for log-normal traits. We also calculated and present trait ranges and coefficients of variation (CV) for each trait. In addition we tested for differences in mean trait values as a function of planting rows, using analysis of variance (ANOVA). These descriptive statistics and ANOVAs were complemented by variance partitioning analyses, which were used to identify the primary sources of trait variation in our dataset. These analyses entailed fitting linear mixed models (using the ‘lme’ function in the ‘nlme’ R package (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2017)) to each trait individually (where $n = 45$ in all cases), where an intercept was the only fixed effect, and plant identity within sample row identity were included as nested random effects. The proportion of trait variation explained by each nested random effect, as well as the proportion of variation unexplained by the factors considered here, was then estimated using the ‘varcomp’ function in the ‘ape’ R package (Paradis, Claude, & Strimmer, 2004).

We then assessed the influence of soil compaction on both individual traits and multivariate trait syndromes. First, we fit separate mixed models for each trait individually, where trait values were predicted as a function of soil bulk density (included as a fixed effect), while accounting for plant identity nested within sampling row (included as nested random effects). We then used a Principal Component Analysis (PCA) to test if multivariate leaf trait syndromes of ‘Chardonnay’ varied as a function of planting row/compaction or vine identity. Our PCA included four LES traits (i.e., A_{mass} , R_{mass} , leaf N, and LMA), two traits derived from light response curves (i.e., Φ and LLCP), and one trait related to light interception (i.e., leaf area). The relationship between individual traits and each PCA axis was evaluated using the ‘dimdesc’ function in the ‘FactoMineR’ R package (Le, Josse, & Husson, 2008). Then, we used a permutational multivariate analysis of variance (PerMANOVA) based on Euclidean distances and 10,000 permutations, to test if multivariate trait syndromes vary as a function of planting row (reflecting the soil bulk density gradient), plant identity, and a row-by-plant interaction term. Based on our PerMANOVA results, we also visualized our PCA biplot with 95% confidence ellipses surrounding the data points within each sample row. All multivariate analyses were implemented in the ‘vegan’ R package (Oksanen et al., 2017).

Finally, we evaluated bivariate trait relationships among ‘Chardonnay’ leaves using Pearson correlation tests. However, one of the main goals of our analysis was to test for the presence of an intragenotype LES in Chardonnay, and evaluate if these relationships differed from the global LES defined by Wright et al. (2004). For this, we used standardized major axis (SMA) regressions to evaluate the slope of the bivariate trait relationships that exist among four LES traits measured in our study vines, including A_{mass} , R_{mass} , LMA, and leaf N. All of these SMA regressions had a sample size of $n = 45$, and were implemented with the ‘sma’ function in the ‘smatr’ R package (Warton, Duursma, Falster, & Taskinen, 2012). Then, we evaluated if these SMA slopes of the intragenotype ‘Chardonnay’ LES differed from the trait relationships found across a functionally and phylogenetically diverse set of plants species globally. This analysis entailed merging our ‘Chardonnay’ data with the GLOPNET dataset (i.e., the dataset used in the original LES analysis of Wright et al. (2004)), and testing for statistical differences in the SMA slope of each trait-trait relationship between

the ‘Chardonnay’ vs. GLOPNET, using the ‘slope.test’ function of the ‘smatr’ R package (Warton et al., 2012).

Results

‘Chardonnay’ functional trait variation in relation to soil bulk density

All leaf traits measured here, with the exception of LLCP, varied significantly across planting rows (Table S1). Photosynthesis and Φ varied most widely across the ‘Chardonnay’ vines and leaves evaluated here (CV=25.6-43.2), and all of these traits related to C assimilation rates declined significantly with soil compaction. Specifically, sampling row identity explained 45.4% and 64.8% of the variation in A_{area} and A_{mass} , respectively (Table 1). In turn, both declined significantly with higher bulk density ($p < 0.01$ in the mixed model slope term), with soil compaction explaining 31.3% and 40.3% of the variation in A_{area} and A_{mass} , respectively (Figure 1A-B, Table S2). Similarly, 42.9% of the variation in leaf Φ was explained by sampling row identity (Table 1), and this trait was negatively correlated with soil bulk density (mixed model slope term $p = 0.01$, marginal $r^2 = 0.243$; Figure 1F, Table S2). Although 19.3% and 26.0% of the variability in R_{area} and R_{mass} was attributable to sampling row identity (Table 1), and these traits differed significantly across rows (Table S1), neither of these traits was statistically correlated with soil bulk density when individual plant identity was accounted for in our mixed models (Figure 1D-E, Table S2). Across our dataset, LLCP was also not correlated with soil bulk density (marginal $r^2 = 0.03$), and sampling row explained <1% of the variation in this trait (Figure 1C).

Soil bulk density had a strong and statistically significant influence on LMA and leaf area, with planting row identity explaining 62.9% and 30.3% of the variation in these traits, respectively (Table 1). Both traits were significantly correlated to bulk density (mixed model slope $p < 0.01$, Figure 1, Table S2). Generally, ‘Chardonnay’ leaves were smaller in terms of leaf area and expressed a higher LMA in areas of higher soil compaction: leaf area varied by a factor of three across our dataset (CV=25.3), ranging from 44.0-153.9 cm² and declining significantly as bulk density increased, while LMA varied nearly 2-fold (range 63.5-111.2 g m⁻², CV=12.2) and increased significantly with higher bulk density (Figure 1G-H, Tables 1 and 2). Leaf dry mass did vary from 0.28-1.26 g across our dataset (CV=28.1), though this variation was weakly explained by planting row (15.5% variation explained) and was not related to soil bulk density (Figure 1I, Table S2). Therefore, statistically significant increases in LMA across a bulk density gradient were attributable to declines in leaf area, and not increases in leaf mass.

Compared to other suites of traits, leaf chemical traits including C and N concentrations were less variable across ‘Chardonnay’ leaves (CV=1.8 and 10.4, respectively). However, consistent with declines in photosynthesis and leaf Φ that occurred in relation to bulk density, leaf N concentrations also declined significantly as bulk density increased (mixed model slope $p = 0.04$, marginal $r^2 = 0.241$; Figure 1K, Table S2). Across all leaves, N concentrations ranged from 1.9-2.9% with sampling row explaining over half of the variation in this trait (Table 1). Leaf C also declined significantly with greater bulk density (mixed model slope $p < 0.04$, marginal $r^2 = 0.41$, respectively; Figure 1J, Table S2). Sampling row explained 54 and 56% of the variability in leaf N and C, respectively (Table 1).

Multivariate trait syndromes in ‘Chardonnay’ in relation to soil bulk density

The seven traits incorporated into our multivariate analysis covaried along two primary PCA axes, which accounted for 46.4% and 21.5% of variation in ‘Chardonnay’ physiological (A_{mass} , R_{mass} , Φ , LLCP), morphological (leaf area, LMA), and chemical (leaf N) traits (Figure 2). The first PCA axis represented ‘Chardonnay’ leaf trait covariation and trade-offs consistent with an intragenotype LES. Specifically, PCA axis 1 was most strongly and positively related to A_{mass} , leaf N, leaf Φ , and R_{mass} ($r = 0.644$ - 0.888 and $p < 0.001$ in all cases), all of which traded-off with LMA ($r = -0.615$, $p < 0.001$; Figure 2, Table S3). Therefore, ‘Chardonnay’ leaves expressing a higher PCA axis 1 score were associated with “resource acquiring” LES trait syndromes, while “resource conserving” LES trait syndromes characterized ‘Chardonnay’ leaves with lower PCA axis 1 scores (Figure 2). The second PCA axis reflected the covariation of traits associated with resource investment in light interception, including leaf area ($r = 0.431$, $p < 0.001$) and LMA ($r = 0.69$, p

<0.001), and leaf-level light requirements (LLCP, $r = 0.767$, $p < 0.001$; Figure 2, Table S3).

Planting row identity explained 39.6% of the variation in multivariate leaf trait syndromes in ‘Chardonnay’ (PerMANOVA $p < 0.001$, Table S4), with the rows of lowest bulk density being concentrated and differentiated (in terms of their 95% confidence ellipses) at the resource-acquiring end of PCA 1 axis (Figure 2). Planting rows with the highest mean bulk density (i.e., Row 5) did tend to be concentrated at the resource-conserving end PCA axis 1 (Figure 2). However, differentiation of leaves sampled in planting rows 2-5, where bulk density did increase albeit not significantly, was weaker along PCA axis 1. Soil bulk density, as represented categorically by planting row identity, did not influence ‘Chardonnay’ leaf position along PCA axis 2 with rows showing overlapping 95% confidence ellipses along this axis (Figure 2). Neither individual plant identity, nor its interaction with planting row, influenced the position of ‘Chardonnay’ leaves in multivariate trait space (PerMANOVA $p = 0.788$ and 0.301 , respectively, Table S4).

An intragenotype LES in Chardonnay driven by soil compaction

The four leaf traits included in the original interspecific LES (I. J. Wright et al., 2004) including A_{mass} , R_{mass} , leaf N, and LMA, were correlated with one another in patterns that were consistent with an intragenotype LES in ‘Chardonnay’ (Figure 3, see also Table S5 for complete trait correlation matrix). Specifically, A_{mass} , R_{mass} , and leaf N all covaried positively across leaves (SMA r^2 range=0.332-0.354, $p < 0.001$ in all three relationships; Figure 3D-F), while LMA traded-off negatively against all three of these traits (SMA r^2 range=0.146-0.397, $p [?]0.01$ in all three relationships; Figure 3A-C). Largely consistent with relationships found between these four traits and bulk density (Figure 1), as well as our PCA (Figure 2), ‘Chardonnay’ leaves generally differentiated from one along the intragenotype LES in relation to soil bulk density.

Although this differentiation was imperfect and entailed some overlap, generally A) leaves from vines grown in the lowest bulk density (sampling row 1) defined the resource acquiring end of the Chardonnay LES; B) those in the highest bulk density rows (sampling row 5) defined the resource conserving end of the Chardonnay LES; and C) those in intermediary sampling rows were interspersed between these endpoints along the intragenotype LES bivariate trait space (Figure 3). In all cases, LES trait relationships across the intragenotype LES in ‘Chardonnay’ were statistically different from those observed among wild plants in the GLOPNET dataset (test for differences in SMA slopes in ‘Chardonnay’ vs. wild plants $p [?]0.03$ in all six bivariate relationships; Figure 3, Table 2).

Discussion

In finding that ‘Chardonnay’ leaf traits covary and trade-off along an intragenotype LES, we contribute a new understanding of how LES traits covary in one of the world’s most commercially important and widespread crop species. This finding adds to the few existing studies that have quantified within-species or -genotype Leaf Economics Spectra in crops (Gagliardi et al., 2015; Hayes et al., 2019; Martin & Isaac, 2021; Martin et al., 2017), and complements the extensive literature documenting the causes and consequences of ecophysiological variation in grapevines (Keller, 2020). Moreover, our work here contributes to an understanding of how soil compaction—a critical feature of agricultural systems globally—is a managed environmental factor, correlated with crop differentiation along multivariate functional trait spectra.

Intraspecific trait variation and soil compaction

Differences in ‘Chardonnay’ leaf traits along the intragenotype LES found here, which were correlated with soil compaction, were largely attributable to variability in A_{mass} . This trait expressed the highest CV (43.2%), was the most strongly and negatively correlated to soil bulk density (marginal $r^2 = 0.403$), and in turn, centrally defined multivariate trait differences (i.e., $r = 0.831$ along Axis 1 in our PCA) and bivariate LES trait relationships in ‘Chardonnay’. Soil compaction may reduce photosynthesis through both stomatal limitations and N limitations (e.g. Morales et al., 2018), both of which therefore likely play a role in structuring the compaction-induced intragenotype LES in ‘Chardonnay’ observed here.

First, in our dataset, at saturating irradiance (where PPF $D = 2000 \mu \text{mol m}^{-2} \text{s}^{-1}$), log-transformed stomatal conductance (g_s , $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$) predicts 83.6% of the variation in log- A_{max} (simple linear regression p

<0.001, $n = 45$), and declines significantly with bulk density (mixed model slope = -0.46 ± 0.12 (s.e.), $p < 0.001$, marginal $r^2 = 0.407$; data not shown). This would indicate that stomatal limitations are at least partially driving differences in ‘Chardonnay’ leaves and plants along our intragenotype LES. Research has shown that when water is limited, cavitation in the petioles of grape leaves prevents embolisms from propagating to other parts of the plant, which in turn acts as a signal for reduced g_s via stomatal closure (reviewed by Gambetta et al., 2020). So in our study reductions in A_{\max} and g_s in relation to increased bulk density, and in turn differentiation of leaves along our intragenotype LES, are likely partially related to reduced ability to access soil water.

Second, we also found 1) a statistically significant positive correlation between leaf N and A_{\max} (Table S5), and 2) a statistically significant decline in leaf N as a function of soil bulk density (Figure 1). This would indicate that differences in plant N availability and assimilation—i.e., conversion of inorganic nitrate (NO_3^-) and ammonium (NO_4^+) into amino acids and proteins—across our site also drives intragenotype LES trait variation. Across a soil compaction gradient, N uptake is often reduced as plant roots are less able to forage N via root elongation (Colombi & Keller, 2019). At our site, where fertilizers are applied uniformly, reduced ability of roots to penetrate into areas of high soil N likely contributes to differences in leaf N across planting rows (Table S1), and in relation to soil bulk density (Figure 1).

These processes though are unlikely to be independent, and ultimately our intragenotype LES in ‘Chardonnay’—particularly the strong relationships between A_{mass} and leaf N in bivariate and multivariate trait space—likely owes to complex covariation, feedbacks, and pathways among soil N availability, N and C assimilation, and translocation of photosynthates (i.e., sucrose and starch). In short, N uptake and assimilation is often reduced when grapevine C status declines, since both are energy-dependent processes that require a supply of C through the Krebs cycle (Keller, 2020). So stomatal limitations to photosynthesis may also contribute to reduced N assimilation and leaf N concentrations. Path analyses would help uncover the causal pathways structuring LES trait covariation in ‘Chardonnay’ (e.g., see Shipley et al., 2006). Yet ultimately, literature suggests the intragenotype LES in ‘Chardonnay’ found here has likely arisen as a function of plant-, leaf-, and/or root-scale responses to micro-site variation in water or inorganic soil N availability, both of which are in turn influenced by soil compaction. Notably though, previous studies on intraspecific or intragenotypic variation in crops have not uncovered strong relationships between LES traits and soil N or moisture content, likely due to limitations of static point sampling these environmental variables (Isaac et al., 2017; Martin et al., 2019).

Leaf Economics traits in relation to crop domestication syndromes

Studies reporting differences in the LES traits relationships in crops vs. wild plants have supported inferences and hypotheses surrounding the unintended consequences of artificial selection (e.g. Milla et al., 2015; Roucou et al., 2018). Perhaps most consistent with hypotheses related to artificial selection is our find that in comparison to wild plants, ‘Chardonnay’ expressed a steeper increase in A_{mass} and R_{mass} per unit increase in leaf N. Specifically, based on our SMA models fits (Table S2), across the range of leaf N values in ‘Chardonnay’ observed here (1.9-2.9%), predicted A_{mass} increased by $\sim 84.3\%$ (from $0.06\text{--}0.38 \mu\text{mol CO}_2\text{g}^{-1}\text{s}^{-1}$) and R_{mass} increases by $\sim 71.8\%$ (from 0.008 to $0.028 \mu\text{mol CO}_2\text{g}^{-1}\text{s}^{-1}$). Comparatively, in wild plants from the GLOPNET dataset this same increase in leaf N from 1.9 to 2.9% corresponds to only a 47.0% predicted increase in A_{mass} (from 0.138 to $0.264 \mu\text{mol CO}_2\text{g}^{-1}\text{s}^{-1}$) and 42.2% increase in R_{mass} (from 0.028 to $0.048 \mu\text{mol CO}_2\text{g}^{-1}\text{s}^{-1}$). Higher photosynthetic rates for a given value or increase in leaf N concentrations have been similarly detected in rice (Xiong & Flexas, 2018), and may reflect conscious or unconscious artificial selection for more rapid growth responses to N availability in crops vs. wild plants. However, this is not universal among crops. Certain crops, namely coffee, show significantly lower increases in A_{mass} with greater leaf N (Martin & Isaac, 2021; Martin et al., 2017), while others including soy express A_{mass} -leaf N relationships that are statistically indistinguishable from those in wild plants (Hayes et al., 2019). In sum, the growing literature to which we contribute with our study indicates that LES trait relationships are a unique and idiosyncratic feature of crop domestication syndromes.

In this regard, a novel contribution from our work here is the integration of R into studies evaluating

intraspecific or intragenotypic LES in crops. Specifically, previous studies evaluating crop trait (co-)variation in comparison to non-domesticated wild plants have not included R in their analyses (Hayes et al., 2019; Martin et al., 2017; Milla, Morente-López, Alonso-Rodrigo, Martín-Robles, & Stuart Chapin III, 2014; Roucou et al., 2018; Xiong & Flexas, 2018), despite this trait representing a key trade-off along the LES (P.B. Reich et al., 1998; I. J. Wright et al., 2004). The LES trait relationships in ‘Chardonnay’ that included R_{mass} were qualitatively unique, in that none of these bivariate datasets and SMA models intersected the global LES defined by wild plants (Figure 2C, D, and E). Instead, at a given value of A_{mass} , LMA, or leaf N, in nearly all of the leaves measured here (i.e., 43 or 45 leaves), ‘Chardonnay’ R_{mass} was consistently lower than average vs. R_{mass} in wild plants. This indicates that domestication has favoured vines that express leaves with a low rate of C loss at a given rate of structural or chemical investment in C assimilation.

These results have two possible explanations: 1) even the lowest bulk density/compaction values at our study site still restrict physiological functioning; and/or 2) lower R_{mass} for a given value of A_{mass} , leaf N, or LMA is a signature of domestication in *Vitis vinifera* varieties. Since the primary targets of grape domestication are related to yield, quality, growth form, and harvestability (Keller, 2020), our findings point to an unintended consequence of domestication related to plant C economy. Expanding our work across a wider range of ‘Chardonnay’ growing sites (particularly where bulk density is lower) and grape varieties is therefore central in testing either proposed explanation.

One unexpected finding in our analysis here, were patterns of leaf C variation. Although not a primary focus of our analysis, since it is not considered a primary trait forming the LES (I. J. Wright et al., 2004), we found that this trait covaried in an unexpected pattern along the intragenotype LES in ‘Chardonnay’. Specifically, we detected a statistically significant positive relationship between leaf C and A_{mass} , R_{mass} , and leaf N, and a significant negative relationship between leaf C and LMA (Table S5). Furthermore, when incorporated into an additional PCA, leaf C covaried across the first PCA axis positively with A_{mass} , leaf N, and negatively with LMA (Table S6). Therefore in our dataset, leaf C covaries along LES traits such that higher leaf C values reflect a resource acquisitive trait syndrome. This finding is counter to studies of certain other domesticated plants where leaf C is by in large positively related to leaf construction costs, leaf dry matter content, and LMA (Gagliardi et al., 2015; Martin et al., 2017). In ‘Chardonnay’, coordination of leaf C along an intragenotype LES likely owes to the selection for C loading in leaves and plants in the form of sugars and starches (Keller, 2020).

Conclusions

Grapevines are among the world’s most commercially important crops, currently covering over 7.1 million ha of land in 2017 (Aryal & Anderson, 2013). Understanding how grapevine physiology responds to global environmental change drivers is therefore a critical avenue of research with implications for agricultural sustainability, as well as understanding how domestication has influenced the functional traits and trait relationships of crops. Our results contribute to both of these areas of research, but considerable opportunities remain. First, we show greater compaction leads to grapes expressing more resource-conservative trait syndromes. Extending this work to evaluate if leaf trait values along an intra-genotype LES Chardonnay are correlated with grape growth, yield, and quality, can aid in refining predictions of grapevine and vineyard responses to environmental conditions, at local- through to global scales (Morales-Castilla et al., 2020). Second, there remain surprisingly few analyses evaluating how multiple grape varieties differ in their LES traits (Greer, 2017). Expanding our study to multiple grape varieties presents an opportunity to test hypotheses on whether or not LES trait relationships in multiple grape varieties are constrained along a single intra-specific LES, or if different varieties express unique LES trait relationships. These lines of research, as informed by our findings here, present novel opportunities to explore how domestication histories influence crop ecophysiological strategies and responses to environmental change.

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Adam Martin: Conceptualization (equal); formal analysis (lead); funding acquisition (equal); investigation (equal); methodology (lead); project administration (equal); resources (equal); visualization (equal); writing – original draft preparation (lead); writing – review and editing (equal).

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Data Availability Statement

Data are not yet provided, but will be archived in the TRY Functional Trait Database upon publication of the manuscript.

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Figures and Tables

Table 1. Descriptive statistics for 11 leaf functional traits from 45 ‘Chardonnay’ leaves, measured in 2020 on 15 individual vines growing at a single site, across a soil compaction gradient. For the Descriptive Statistics columns, means and standard deviations (SD) are presented for normally distributed traits, while median and SD are presented for log-normally distributed traits; these determinations were based on the highest log-likelihood scores (highlighted in bold) in the Distribution Fitting columns. Variance Partitioning columns corresponded to the proportion of variability in each trait explained by planting row and individual plant identity, as well as the variability not explained by these factors. Trait acronyms are as follows: A_{area} : light saturated maximum photosynthetic rate on a per unit leaf area basis; A_{mass} : light saturated maximum photosynthetic rate on a per unit leaf mass basis; R_{area} : leaf respiration rate on a per unit leaf area basis; R_{mass} : leaf respiration rate on a per unit leaf mass basis; LLCP: leaf-level light compensation point; Φ : apparent quantum efficiency; LMA: leaf mass per unit area.

Trait Information	Trait	Distribution Fitting	Distribution Fitting	Descriptive Statistics	Descriptive Statistics	Descriptive Statistics	Variance Partitioning	Variance Partitioning	Variance Partitioning
Trait Group	Trait	Normal	Log-norm.	Mean/ Median ± SD	Range	CV	Row	Plant	Unexplained
Physiological	A_{max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	-133.4	-129.8	12.6±4.7	6.0-26.1	35.4	0.454	0.235	0.315
	A_{mass} ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$)	54.8	60.9	0.154±0.072	0.078-0.367	43.2	0.648	0.166	0.166
	R_{area} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.002	-3.1	0.74±0.24	0.21-1.26	33.0	0.193	0.288	0.515
	R_{mass} ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$)	192.7	193.0	0.009±0.003	0.003-0.017	37.1	0.260	0.150	0.515
	LLCP ($\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$)	-125.6	-128.6	14.2±4.0	5.3-22.2	27.0	<0.001	0.474	0.515
	Φ (mol CO ₂ mol PPF ⁻¹)	131.6	138.1	0.05±0.013	0.03-0.1	25.6	0.429	0.022	0.515
	Morphological	Area (cm ²)	-205.3	-205.2	89.6±23.5	44.0-153.9	25.3	0.303	<0.001
LMA (g m ⁻²)		-167.3	-166.5	82.0±10.1	63.4-111.2	12.2	0.629	<0.001	0.315

Trait Information	Trait Information	Distribution Fitting	Distribution Fitting	Descriptives	Descriptives	Descriptives	Variance Partitioning	Variance Partitioning	Variance Partitioning
Chemical	Dry mass (g)	5.8	4.2	0.77±0.24	0.28-1.26	28.1	0.154	0.024	0.8
	Carbon (%) mass)	-53.9	-52.9	43.4±0.8	41.5-45.7	1.8	0.555	0.161	0.2
	Nitrogen (%) mass)	1.8	3.6	2.24±0.24	1.9-2.92	10.4	0.543	0.335	0.1

Table 2. Leaf Economics Spectrum (LES) trait relationships in ‘Chardonnay’ and wild plant species. Presented here are the intercepts and slopes of standardized major axis regression models (SMA) fit to the ‘Chardonnay’ dataset ($n = 45$ in all models), and wild plants derived from the GLOPNET dataset (Wright et al. (2004); sample sizes noted in table). Only traits included in the original LES (I. J. Wright et al., 2004) are evaluated here. Also presented are results from a slope test evaluating differences in the SMA slopes of ‘Chardonnay’ vs. wild plants, where $p [?] 0.05$ indicates that the slope of a given bivariate LES trait relationship differed significantly across datasets. Trait acronyms are presented in Table 1.

Traits	Traits	Chardonnay	Chardonnay	Chardonnay	Chardonnay	GLOPNET	GLOPNET	GLOPNET
Independ.	Depend.	Intercept	Slope	Model r^2	Model p	Intercept	Slope	Model r^2
A_{mass}	LMA	105.91	-139.06	0.392	<0.001	235.87	-868.13	0.392
Leaf N	A_{mass}	-0.53	0.31	0.35	<0.001	-0.09	0.12	0.35
LMA	Leaf N	4.18	-0.03	0.397	<0.001	3.01	-0.01	0.397
A_{mass}	R_{mass}	0.01	0.05	0.355	<0.001	0.01	0.11	0.355
LMA	R_{mass}	0.04	-0.01	0.146	0.01	0.03	-0.01	0.146
Leaf N	R_{mass}	-0.03	0.02	0.333	<0.001	-0.01	0.02	0.333

Figure Legends

Figure 1. Relationships between 11 ‘Chardonnay’ leaf traits and soil bulk density. Trend lines correspond to statistically significant relationships (where $p [?] 0.05$ for the slope parameter) between traits and bulk density, based on linear mixed effects models predicting traits as a function of soil bulk density (as a fixed factor) while accounting for plant identity (as a random factor; see Table S2 for full model diagnostics and fits). Also presented are marginal r^2 values (“Marg. r^2 ”) for each relationship, which represents the proportion of variation in a given trait explained by fixed factors alone (i.e., bulk density and model intercept), and condition r^2 values (“Cond. r^2 ”), which represent the proportion of trait variation explained by fixed and random factors. Sample sizes for all models were 45 leaves, measured across 15 individual vines. Log-transformed trait values were used in models according to results presented in Table 1, and trait acronyms are presented in Table 1.

Figure 2. Principal Component Analysis (PCA) for seven ‘Chardonnay’ wine grape leaf traits measured in 2020 across a soil compaction gradient. Data point colours correspond to vine sampling rows, which are situated along a gradient of bulk density values, and dotted black lines represent 95% confidence ellipses for leaves across different rows. Planting row explained 39.6% of the multivariate trait variation evaluated here ($p [?] 0.001$, and see Table S4 for full Permutational Multivariate Analysis of Variance results). Trait acronyms are presented in Table 1.

Figure 3. Relationships across four Leaf Economics Spectrum traits in ‘Chardonnay’ wine grapes. Colours correspond to sampling rows reflecting a soil compaction gradient, black solid trend lines correspond to the standardized major axis (SMA) regression model of a given bivariate trait relationship in ‘Chardonnay’, and dashed black trend lines represent convex hull models that encapsulate the two-dimensional trait space occupied by ‘Chardonnay’ leaves. Also shown are the data and SMA models for the same LES trait relationships observed among wild plants in the GLOPNET dataset (grey dashed trend lines and points). Details on all SMA models shown here are presented in full in Table 2. Trait acronyms are presented in Table 1.

Figure 1

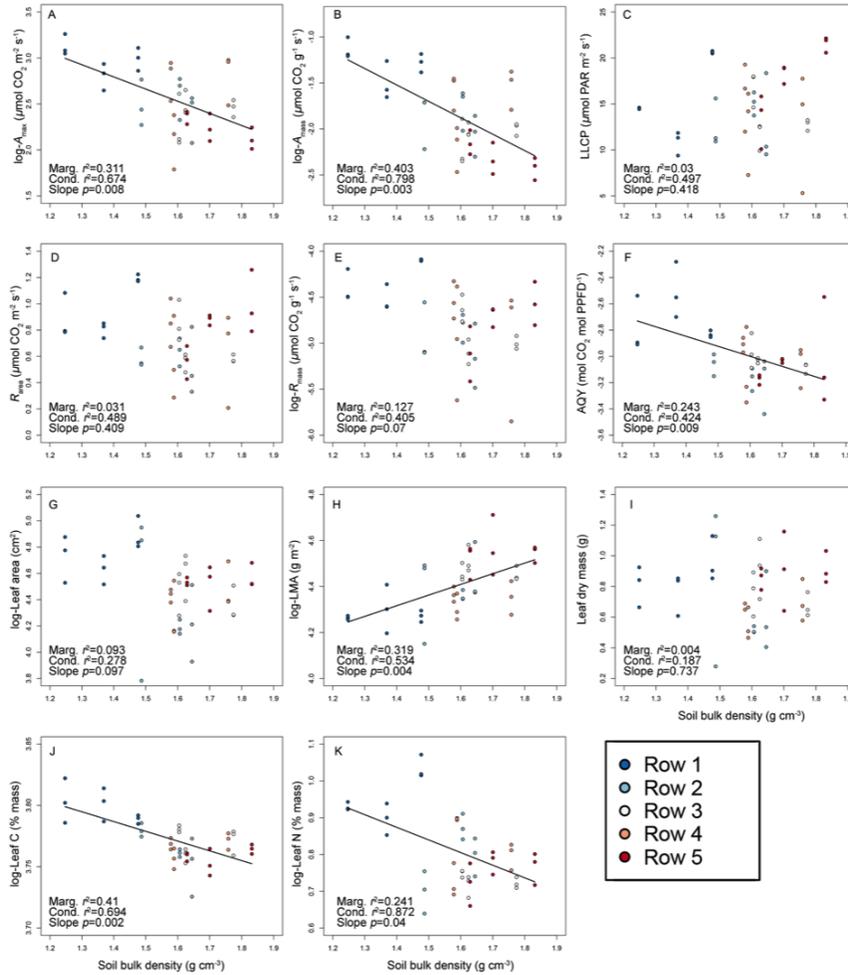


Figure 2

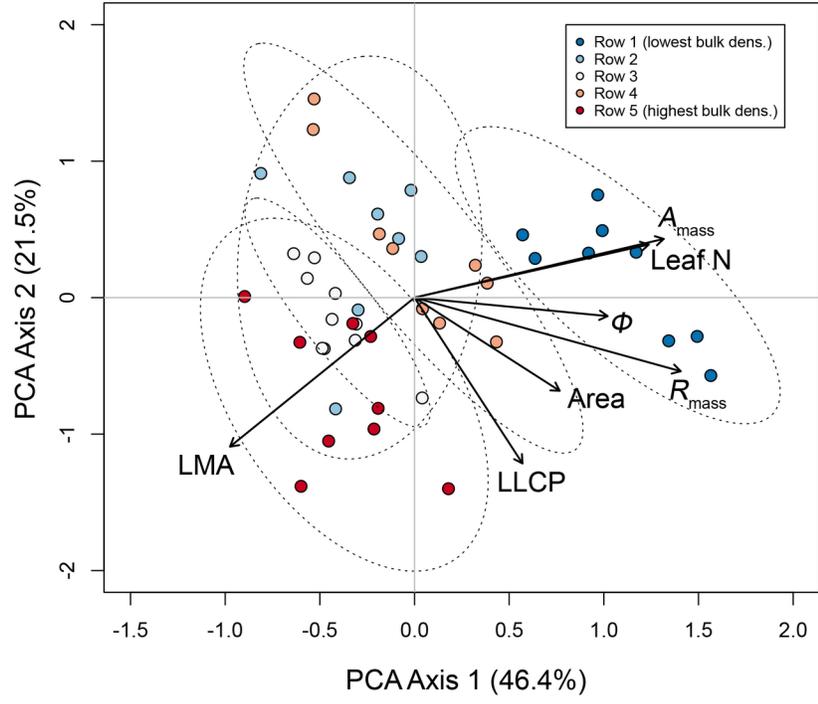


Figure 3

