Exploring Competitive Interactions Between Non-Crop Plants in a Coffee Agroecosystem and the Potential for Coexistence

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Abstract

Agroecosystems integrate ecological principles to balance food production with biodiversity conservation. Despite efforts to use sustainable practices, weeds are still seen as problematic due to common views on plant competition. Plant diversity is crucial for maintaining agrobiodiversity, supporting functions like pollination, soil erosion control, and habitats for beneficial insects, while also contributing to ecosystem stability and multifunctionality. Current literature on plant competition provides insight into how competition influences species composition, thereby structuring communities. By integrating Indigenous agricultural practices with agroecological principles, we can better manage non-crop plants that offer potential benefits. Sustainable management practices based on agroecological principles can support agrobiodiversity and ecosystem function. This study evaluates the effect of interspecific and intraspecific interactions combined with above and below-ground competition between two dominant native weed species (Ipomoea purpurea and Viquiera cordata) in a coffee agroecosystem in the Soconusco region of Chiapas, Mexico. Field experiments with 102 plants across six sites (15mx20m) and four treatments (control, root competition, shoot competition, and root and shoot competition) were conducted over 9 weeks in a 278-hectare organic shaded coffee farm. The findings from this study suggest that in this agroecosystem both intraspecific and interspecific competition are occurring simultaneously with the impact on growth varying across treatments. We find that the additive effects of root and shoot competition significantly reduce the height and number of leaves for both plant species. Promisingly, these findings suggest that competitive interactions between Ipomoea purpura and Viguiera cordata can contribute to their management and coexistence. Understanding plant coexistence can help develop weed management practices that enhance plant diversity, thereby providing ecosystem benefits that support mid-to-long term stability. This study lays the foundation for more extensive research on weed competition within the coffee agroecosystem and provides insights into the natural management of weed communities.

Introduction

Agroecosystems: Food Production, Biodiversity, and Traditional Agricultural Practices and Perceptions Agroecology seeks to bridge the gap between the provisioning of food for people and preserving biodiversity (Soley & Perfecto, 2021). By applying ecological principles to agronomy, we move beyond mere yield-focused outputs to consider the intricate and complex biological, physical, and chemical interactions sustaining long-term productivity (Gliessman 2004). Achieving equilibrium between food production and stable ecosystems is essential for sustaining biotic and abiotic processes that are crucial to food system longevity. Indigenous and local rural farmers offer valuable insights into ecologically sound food systems (Gliessman 1992, Perfecto et al. 1995, Moguel et al. 1998, Mason et al. 2020, Negi et al. 2020, Dawson et al. 2021). Research on agroecological land management highlights how Indigenous farmers design food systems that prioritize the continuation of biodiversity (biotic and abiotic) and ecosystem multifunctionality (Moguel et al. 1998, Gari 2000, Negi et al. 2020). Their knowledge is deeply rooted in traditional cultural practices, underpinned by a spiritual connection to landscapes and natural resources (Kimmere 2002). Land and resource management thus become integral components of food systems management, reflecting Indigenous peoples' close relationship with the natural world and its resources (Kimmere 2002). With approximately 370 million Indigenous individuals occupying nearly 22% of the Earth's landmass, their agricultural methods prioritize ecosystem preservation, biodiversity conservation, and sustainable food production (Kimmere 2002, Perroni 2017, I.P. Sharma et al. 2020). Indigenous agricultural practices, akin to principles of agroecology, contribute to habitat creation within food systems, underscoring their role in food security and biodiversity conservation.

An important component of biodiversity that is often overlooked within agroecology, despite their capacity to sustain complex ecological structures, is the importance of the herbaceous biodiversity within these systems (Gaba et al. 2016, Gliessman 2004, Archibald et al, 2021). Within the field of agroecology, a negative perception still remains with regards to non-crop herbaceous communities. Many studies report that non-crop plants, most commonly referred to as weeds, compete with crops for essential nutrients (e.g., light, water, soil nutrients, and space) (Ronchi & Silva 2006, Maxwell & Luschei 2008, Weiner et al. 2010, Gaba et al. 2016, Romillac et al. 2023) and are the most important biotic factor constraining crop production in organic, low-input, agriculture (Liebman et al. 1997, Gaba et al. 2016, Scavo & Mauromicale 2020). There is strong evidence showing competition between crop and non-crop herbaceous species but there is also growing recognition that non-crop plants provide invaluable ecosystem services to food systems, including erosion prevention, soil moisture retention, and habitats for beneficial insects (Blanckaert et al. 2006, Meylan et al. 2013, Gliessman 2014). Despite the growing body of research showing the benefits of a diverse herbaceous community within food systems, the ecology of non-crop herbaceous plants, especially their diversity, function, and ecological interactions remains understudied (Gaba et al. 2016, Archibald et al. 2021, Romillac et al. 2023). In order to maximize natural ecosystem processes in agroecosystems, we must understand the ecology of non-crop plants and their diversity. Since plant knowledge and perception held by farmers influence management,

interest arose in the perceptions and management strategies practiced by indigenous and local rural farmers.

Expanding on the inherent link between Indigenous communities and their environment, the parallels between Indigenous agricultural methods and agroecology raise the question: Do Indigenous practices offer unique insights into non-crop management within sustainable and organic food systems? The existing body of research on this question has shown a widely different perspective on weeds and their management compared to industrial agriculture and even to agroecology (Bach et al. 2019, Archibald et al. 2021). Previous research indicates that mainstream conservation and farming practices often ignore Indigenous contributions to weed management (Bach et al.2019). A multi-regional study on Aboriginal perspectives of weed plants consistently showed that despite their distinct viewpoints compared to mainstream land management agencies, Aboriginal peoples' insights are rarely integrated into management strategies, even when Aboriginal peoples' were employed through government agencies as rangers and implemented weed control (Bach et al., 2019). Additionally, a survey study done in a semi-arid region of Mexico found that unlike modern Western agricultural practices, traditional farmers acknowledge the supplementary worth of non-crop plants and implement management strategies according to their use and importance (Chacon & Gliessman 1982, Bye 1981, Blanckaert et al. 2006).

The additional value identified by local and Indigenous farmers in the states of Puebla and Oaxaca, Mexico guided management practices used for non-crop plants within diverse agricultural systems (Blanckaert et al. 2006). Findings of this study, acquired through free and structured interviews, developed a floristic inventory of weed species that identified 161 species, which out of those species, 148 species (91.9%) presents one or more uses to the inhabitants (Blanckaert et al. 2006). Further, findings from this study showed that weeds served various purposes in agricultural fields, with (76.4%) of weeds primarily used as fodder, as most weeds were herbaceous annuals, followed by medicinal (20.3%), edible (11.5%), and ornamental (6.1%) use (Blanckaert et al. 2006). The inhabitants of the Santa María Tecomavaca region in Mexico, with Mazatec backgrounds, also mentioned agroecological advantages of certain weeds. The dry materials of *Viguiera dentata* were often mixed with soil during field preparation for soil enrichment and structure improvement (Blanckaert et al. 2006).

The perceptions and knowledge that guide weed management techniques can impact our collective ability to promote food security and sovereignty for Indigenous and rural communities. As noted by Blanckaert (2006), the presence of edible and medicinal weeds contribute significantly to the daily diet and basic health of rural and Indigenous families. Therefore, indiscriminate eradication of weeds could not only reduce the availability of valuable resources for local residents but also jeopardizes local food security. Integrating Indigenous perspectives on weed management and agricultural practices aligns with the goals of agroecology, facilitating the promotion and preservation of biodiversity while addressing the nutritional needs of vulnerable populations facing food insecurity.

Furthermore, the integration of Indigenous knowledge and scientific knowledge is one of the pillars of agroecology (Vandermeer and Perfecto 2017). Therefore, there is a significant

opportunity to integrate Western ecological knowledge with Traditional Ecological knowledge to manage weeds in agroecological food systems. Liebman et al. (1997) suggest that combining various methods, or "little hammers," can achieve effective control through the synergistic and cumulative effects of tactics that work better together than individually. This approach also reduces the risk of crop failure by distributing the protective burden across several methods, which, in turn, decreases the likelihood of pests developing resistance to any single tactic. In ecological weed management, the additive effects of multiple, temporally varied stresses on weeds can enhance crop yield and quality. Integrating ecological weed management with Indigenous practices and knowledge allows for a better understanding of the potential benefits and functions of certain weed species, as well as plant phenology and traits, to minimize competition between weeds and crops

Coffee Agroecosystems

Food systems that allow natural interactions to occur amongst crop plants, soil organisms, soils, insect enemies, insects, environmental conditions and management actions, such as agroecosystems, are great study systems to understand how biodiversity and human needs can be achieved (Gliessman 2014). The coffee agroecosystem in Latin America is a particularly important place of interest because of the cultural significance and socioeconomic importance of coffee (Perfecto et al. 2014). Lin, Perfecto, and Vandeermer (2008) add that coffee agroecosystems provide the agricultural basis for many rural farmers throughout midelevation regions in the developing world. Others also claim that changes in coffee commodity chains and in management pressures have increased the economic vulnerability of farmers (Bacon 2005, Lin et al. 2008). Coffee itself is not an essential food source but it is an important economic means that supports farmers' ability to purchase food resources and maintain their livelihood. The study by Lin et al. (2008) also highlights the potential of coffee agroecosystems' resilience to climate change compared to agricultural systems with high intensification. Coffee agroecosystems not only harbor biodiversity within the tropics but they also contribute to the survivorship of farmers in developing countries (Perfecto et al.2003, Meylan et al.2013, Archibald et al. 2021). Coffee farms are also excellent model systems for ecological research, especially in the tropics in which coffee is cultivated using a varying abundance and diversity of shade trees, offering a gradient of diversity and complexity that share many structural attributes normally associated with forests (Perfecto & Snellin 1995, Perfecto et al. 2014). Due to the structural similarities shared with forest ecosystems, coffee agroecosystems present a unique opportunity for investigating complex ecological interactions, particularly those involving crop-weed and weed-weed interactions because these interactions occur naturally with or without human intervention.

Integrated Weed Management in Coffee Agroecosystems

Weed plants and weed communities form part of the ecology and overall biodiversity of any agroecosystem (Romillac et al.2023). Aside from providing a variety of additional food sources, medicinal, and agroecological benefits (Moguel et al.1998, Bye 1981, Blanckaert et al. 2006), weeds also provide ecosystem services such as providing habitat for beneficial insects, retaining soil moisture, and reducing soil erosion (Meylan et al. 2013). Integrating knowledge and practices from agroecology alongside of Indigenous practices may enhance the beneficial ecosystem functions provided by weeds when managed carefully. For instance, knowledge on whether a crop is an annual or a perennial can also help determine weed management practices. For instance, there is evidence that suggest that, in annual crop systems, weeds-crop competition may be stronger and reduce production than in perennial crop systems (Menalled et al. 2020). Coffee agroecosystems are a unique case for studying ecological weed management because, as perennial agroforestry systems, maintain a diverse understory can be beneficial. In perennial agroforestry systems there tends to be more diversity of soil microbial soil resources due to defoliation from long term crops and therefore weed-crop completion can be reduced due to an increased resource pool within the soil (Menalled et al. 2020).

Balancing the tradeoffs of competition and ecosystem services is representative of the principles of agroecology (Scavo & Mauromicale 2020) yet weed interactions within coffee agroecosystems are rarely studied in field experiments, even though they could provide ecosystem benefits (Gliessman 1992). A study by Archibald et al. (2022), conducted in the Central Valley of Costa Rica, looked at the taxonomic and functional diversity of the herbaceous community in organic agroforestry systems. They found 38 species from 20 taxonomic families present in the system. Their findings showed that the herbaceous communities were functionally diverse depending on the gradients of canopy cover, suggesting that farms that adopt agroforestry tend to have more functionally diverse herbaceous stratum and on-farm diversity (Archibald et al. 2022). Additionally, they found that farmer knowledge of plant traits in the herbaceous community was positively correlated with management practices (Archibald et al. 2022). These findings are similar to the study mentioned previously by Blanckaert et al. (2006), in which they also found that management practices were guided by farmers' perception and knowledge of the plant's traits and ecosystem services. Our growing understanding of weed management within agroecosystems, coupled with Indigenous techniques, suggest a variety of management practices that could be applied depending on the season, management history, cropping system type and the life stage of the farming system (Gliessman 1992, Gaba et al. 2016, Archibald et al. 2022). Management practices include using non-crop plants as spontaneous cover to prevent soil erosion and cutting them down before flowering (Gaba et al. 2016). Other studies have highlighted management practices within coffee agroecosystems that have varying levels of intensity and agrobiodiversity, by creating production-focused and conservation-focused areas (Meylan et al. 2013, Gaba et al. 2016) and, therefore, provide different ecosystem services. Weeds are key components of the biodiversity in agroecosystems (Romillac et al. 2023) as they support multifunctionality within food systems. Thus, weed management deserves to be further studied and understood to balance multiple needs of humans and biodiversity. Studies have shown that the degree of competition between weeds in the herbaceous community and coffee is highly variable (Ronchi & Silva, 2006, Scavo & Mauromicale 2020). This study aims to explore competitive interactions between two dominant native weed species in a tropical agroecosystem in Tapachula, Mexico, contributing to the growing research on competition and coexistence among non-crop plants. Understanding how competition, a mechanism of coexistence, influences plant growth can help to develop management practices that alleviate the trade-offs between weed-crop competition and the long-term ecosystem benefits weed diversity provides within a food system (Gaba et al. 2016)

Mechanisms of Coexistence: Competitive interactions and Niche differences

As sessile autotrophs, plants and plant communities undergo competition with neighboring plants for space, light, water, soil minerals and nutrients. A widely studied and understood principle from classical competition theory is that one species will inevitably face competitive exclusion because plants fundamentally share the same needs for the same resources (Weiner 1990, Goldberg 1990). The largest species is predicted to exclude smaller species (Weiner 1990), regardless of other traits such as competitive response traits or whether the species are native or invasive (Bengtsson 1994). Despite numerous studies on plant competition, ecologists are still unable to fully understand why competitive exclusion does not apply to ecosystems that are able to maintain local (alpha) diversity in plants that are competing for the same resources (Bengtsson et al. 1994, Wright 2001, Silvertown 2004). This becomes especially evident in tropical ecosystems, especially equatorial rainforests (Wright 2001), where tree alpha diversity is greater than in any other vegetation type. It is wellunderstood that competition among plants influences community composition (Goldberg, 1990) and is crucial for maintaining biodiversity. However, species must still coexist despite the pressures of competitive exclusion (Johnson, 2021). Given this understanding, why do we not apply rigorous ecological principles and questions about the possible mechanisms of coexistence to agroecosystems, which also prioritize biodiversity maintenance?

Classical coexistence theory states that in order for coexistence to occur between two species, intraspecific competition must be stronger than interspecific competition and that each species must occupy a different niche (Tilman 1982, Chesson 1986, Goldber & Barton 1992, Silvertown 2004, Barabás et al 2016). This means that competition must be stronger between plants of the same species (intraspecific) and weaker between plants of the different species (interspecific). The basic idea behind this is that plants of the same species share the same requirements regarding resources; therefore, each species depresses its own growth more than it depresses the growth of other species (Chesson 1986). Moreover, above-ground and belowground competition provide insights into the varying levels of resource acquisition by individual plants. Since roots and shoots are physically discrete and acquire different resources from the environment, numerous studies on plant competition have attempted to separate the effects of root and shoot competition (Weiner 1986, Weiner 1990, Dillenburg et al. 1992, Casper 1997, Thorsted et al. 2002, Murphy & Dudley 2007, Gottlieb & Gruntman 2022). Partitioning aboveground and below-ground interactions among plants allows researchers to compare four possible competition treatments: control, root competition, shoot competition, and root and shoot competition. This approach enhances our understanding of the potential effects of competition on the overall growth of individual plants.

Additionally, studies attempting to understand coexistence amongst plant species also included other mechanisms to consider (natural enemies, temporal fluctuations, spatial variations, resource gradients, etc.) that influence coexistence (Goldberg & Barton 1992, Bengtsson 1994, Chesson 2000, Silvertown 2004, Chesson 2019). In particular, studies conducted in tropical ecosystems or hyper-diverse ecological communities, look beyond predictions of asymmetric competition and competitive exclusion to try to understand how plants are able to coexist. Instead, Silvertown (2004) and Wright (2001), look towards other mechanisms like niche differentiation, spatio-temporal variations, and explore the hypothesis that in light suppressed understories, plants competition is rare (Wright 200, Silvertown 2004).

Chesson also acknowledged that in order for long-term coexistence to occur, stabilizing effects of niche differences must exceed fitness differences between species (Chesson 200). In contrast, Goldberg (1992) and Bengtsson (1994) suggest that resource partitioning may not be an important mechanism for coexistence. Bengtsson (1994) also argues that in order to see coexistence through niche segregation, environmental heterogeneity is required. Findings from Silvertown (2004) show evidence of niche differentiation between shrubs and herbs in arid environments. Furthermore, studies conducted in tropical forest ecosystems indicate that small guilds of species might partition light gradients through a trade-off between growth rate in better light conditions and survival in shade (Wright 2001). Wright also states that understory plants are suppressed by above- and below-ground competition, by canopy plants, suggesting further possibilities for the natural management of these understory species. Silvertown and Wright's studies are impactful in addressing the gap for in-field experiments that look at possible mechanisms of coexistence that go beyond intraspecific competition. To understand plant species coexistence, one must look at multiple possible mechanisms that might be at play in tropical forests.

Competition as a mechanism of coexistence is relevant to weed management because it reduces the potential proliferation of one dominant weed species while maintaining plant diversity and ecosystem function. The coexistence of non-crop plants within an agroecosystem is important, as these herbaceous communities provide ecosystem services that contribute to the long-term stability of both food production and agrobiodiversity.

Merging multiple lines of inquiry, this study examines the strength of intraspecific and interspecific competition across two niche axis (above and below ground) between two native plant species, *Ipomoea purpurea* and *Viguiera cordata*, within a coffee agroecosystem. Our goal is to determine if competitive interactions provide insights into possible coexistence strategies between these two common weed species, aiding farmers practicing agroecology in their management decisions. Specifically, we investigate how response variables (height and number of leaves) change with different treatments (root competition, shoot competition, root and shoot competition), and whether intraspecific competition is stronger than interspecific competition, and if there is any evidence of niche partitioning between these two dominant weed species.

To address these questions, we conducted a field experiment with minimal manipulation, randomly assigning plants to treatments involving interspecific and intraspecific competition with both above and below ground interactions. Our study aims to fill gaps in the knowledge of field experiments that combine multiple competitive interactions to provide evidence of coexistence in tropical ecosystems. Additionally, this study contributes new findings that support the management of agrobiodiversity and enrich the growing literature that integrates traditional ecological knowledge with Western ecology

Methods

Study Site and Study Species

The study was conducted in Finca Irlanda, a large (278 ha) organic shaded coffee farm in the Soconusco region of Chiapas Mexico (15.17358 N -92.3363 W). The study was conducted from June to August 2022. A location commonly known as "La Estacion" within Finca Irlanda was selected as the study site due to its minimal physical disturbance from workers, allowing for the setup of large plots. The main strategy for weed management in Finca Irlanda is through regular cutting with a machete (X. Perez personal observations). Resulting in varying stages of regrowth of non-crop vegetation.

Ipomoea Purpurea, the common morning glory (Fig. 1a) is a climbing vine in the family Convolvulaceae, with showy flowers, native to the highlands of central Mexico (Clegg & Durbin 2003). It is a short-lived perennial plant that is often grown as an annual. Germination occurs between mid-May and August, and flowers begin to bloom after six weeks of emergence. The flowers of *I. purpurea* are pollinated by bumblebees (Bombus pennsylvanicus and Bombus *impatiens*) as well as by other generalist species but are also capable of self-fertilization (Chaney & Baucom 2014). The roots of *I. purpurea* are shallow and tend to spread outward on the top levels of the soil (Scott & Oliver 1976, X. Perez personal observation). Viguiera is a genus of flowering plants in the family Asteraceae (Turner, 2013). Unfortunately, little is known about the specific species Viguiera cordata (Fig. 1.b) Information gathered from a floristic inventory published by Billy L. Turner (2013) describes V. cordata as a perennial, ranging from 30 to 80 cm in height, and arising from a corm-like taproot. The leaves are mostly 4-7 cm long and 2-4 cm wide, with petioles 2-6 mm long. The blades are broadly lanceolate with serrate margins and are sparsely pubescent on both sides (Turner, 2013). The roots of V. cordata plants observed on Finca Irlanda are long and able to access deeper portions of the soil, we also observed that the plants are clonal and shoot will emerge from the root (X.Perez personal observations). Due to the limited information on this species, further research into its biology and ecology is recommended.

Experimental Site



Study Species



V. cordata intraspecific root and shoot competition



I. Purpurea control treatment

Figure 1: Image at the top shows canopy cover in Finca Irlanda next to Finca Hamburgo which is a full sun coffee farm. Images on the bottom show Viguiera cordata (bottom left) and the image to the right of that shows Ipomoea purpurea.

Experimental design

A total of six experimental sites (referred to as blocks and treated as replicates in this study), each measuring 15m x 20m, were established in June 2022. Individual plants of both species were located within each block, and treatments were set up randomly. We selected plants that were already growing within each block. We did not plant or grow them from seed instead we searched for existing plants of both species in each location. To reduce the possibility of unequal advantages due to size (thereby minimizing potential effects of asymmetric competition), we ensured that the selected individual plants were relatively the same length (20-40cm) and had the same number of leaves (between 5-8). Both these plant species can be observed growing near one another. Therefore, we did not have to dig up or move the plants. We simply located both plant species in close proximity to each other (approximately within 30 to 50 cm depending on the assigned treatment). Once *I. purpurea* and *V. cordata* plants were identified, we began setting up the experiment (*Figure 2*).

Individual plants were arranged to compete both intraspecifically and interspecifically and were then further organized within their randomly assigned treatments (control, root competition, shoot competition, root and shoot competition) (Colom & Baucom 2020, Kiaer et al. 2013). The control treatment contained a single plant of each species growing under no completion with any other plant.

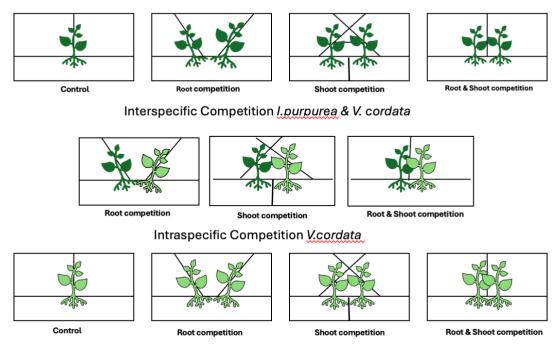
The experimental design for treatment 1(root competition), required the plants to be within proximity to each other to ensure that their roots will interact. We arranged two PVC

pipes (approximately 1.5-inch diameter, 3-foot tall) in a "V" shape directly behind the plants and with the use of flagging tape, gently tied the shoots of each plant away from one another to prevent above-ground competition. For treatment 2 (shoot competition), a 1.5-foot deep trench was dug between the two plants, and a metal sheet was inserted (Dillenburg et al. 1992, Thorsted et al. 2006, Kiaer et al. 2013). During the excavation, the topsoil was gently removed, a trench was dug using a garden trowel, the roots were untangled manually, and the metal sheet was inserted between the plants. The roots were then centered, and the topsoil was then added back. Shoots were guided by two PVC pipes forming an "X" shape, ensuring interaction as they grew. A wooden stick was also used at the base of the "X" shaped PVC pipes to further guide the tendrils of *I. purpurea* and further assist with above-ground competition. Lastly, treatment 3 (root and shoot competition), we selected plants that were growing very close to each other, allowing interaction of both root systems and shoots. The, one single PVC pipe was placed directly behind both plants to provide structural support.

We had three replicates (blocks 1-3) with the full set of treatment combinations, interspecific and intraspecific competition and all four treatments (control, root competition, shoot competition, and root and shoot competition) for both species. The remaining replicates (blocks 4-6) had all treatment combinations for *I.purpurea*, interspecific and intraspecific competition with all four treatments (control, root competitor, shoot competition, root and shoot competition) but V. cordata plants were only arranged into interspecific competition with I. pupurea plants and under all four treatments (control, root competition, shoot competition, and root and shoot competition). Meaning that in replicate blocks 4-6 we did not continue to test for intraspecific competition with V. cordata plants (Fig. 2). Data was collected once or twice a week (depending on weather conditions) for 9 weeks on a total of 102 plants. Data collected included plant height, number of leaves, and percent canopy cover. Plant height was measured using measuring tape and the number of leaves was counted by sight. The assessment of percent canopy cover in each block was conducted with the use of an application called CanopyApp (University of New Hampshire) downloaded to my own personal device. To obtain a canopy analysis for each block, pictures were taken of the canopy over each experimental plant, and then the percent canopy was averaged to get better representation of the canopy cover in a 15m x 20m block

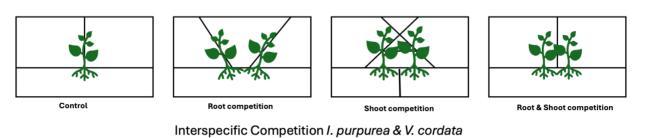
Representation of Blocks 1-3

Intraspecific Competition I. purpurea



Representation of Blocks 4-6

Intraspecific Competition I. purpurea



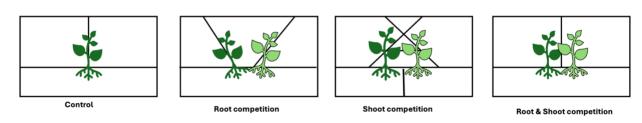


Figure 2: Representation of experimental design. Blocks 1-3 included intraspecific competition with Viguieia cordata, but that was not included in blocks 4-6.

Measure of competitive effects

To determine the effect of competition on the growth of neighboring plants, we examined multiple interaction types. Lotka-Volterra competition equations were utilized to estimate the competition coefficient of these interactions. In this study we focused on individual plants competing with each other rather than population or community dynamics. Therefore, we used a modified Lotka-Volterra competition equation. Microsoft Excel (Microsoft® Excel for Mac Version 16.86) was used to conduct these calculations. The data was arranged and separated by treatment (root, shoot, root and shoot) and by species, for example: *I. purpurea_root competition*, and then further narrowed down by replicate block (1-6).

Competition coefficient equation for Intraspecific competition:

$$\frac{dB1}{B1dt} = r1 (1 - \alpha_1 B_1)$$

Competition coefficient equation for Interspecific competition:

$$\frac{dB_1}{B_1dt} = r1(1 - a_{12} - B_2)$$

Equation to solve for α_{12}

$$\alpha_{12} = \frac{\frac{dB_1}{B_1d_1} + r_1}{r_1 * B_2}$$

In the equation, B1 denotes the dependent variable (height or number of leaves) of plant 1, and B2 represents the dependent variable (height or number of leaves) of plant 2. The rate of growth without competition is represented by r1. To calculate dB1/B1dt, we gathered the natural log of the height and number of leaves at time 1 through time 9. We then subtracted the natural log of height, for example, at time 1 from the natural log of height at time 2 ($lnB1_{(t2)}$ - $lnB1_{(t1)}$), and then continued until we went through all the time point. The averages of these values were then calculated and used in the equation as dB1/B1dt. B1B1 was estimated by calculating the average of the values (height and number of leaves) without the natural log, ($B1_{(t1)}+B1_{(t2)}$)/2. Once we had all the values for each plant, we calculated the competition coefficients for intraspecific and interspecific competition. Finally, we calculated the overall strength of intraspecific and interspecific competition by dividing the interspecific competition coefficients by the intraspecific competition coefficients to obtain α_{12} and α_{21} .

Statistical analysis

All statistical analyses were conducted using R Studio (Version 2022.12.0+353). It is important to state that competition type (interspecific and intraspecific competition) and treatment (control, root, shoot, and root and shoot) were tested separately. We did this to be able to compare the values for the dependent variables (height and number of leaves) from these competitive interactions to the values from the control plants. We also conducted a mixed model that included all of the interaction terms, treatments (root, shoot, and root and shoot) and competition types (interspecific and intraspecific competition), without the values for the control plants. This was done to see if there was a statistically significant difference between the competition interaction combination.

To test the effects of competition types (interspecific and intraspecific competition) and treatments (control, root, shoot, root & shoot) on the dependent variables (height and number of leaves), we used generalized linear mixed-effects models (GLMER). First, we employed linear mixed-effects regression (Imer) through the 'Ime4' package to test both fixed (day 1-9) and random effects (height, number of leaves, and canopy cover), as our data included repeated measures for each plant. In this case our predictors are the random effects because our data includes multiple height values for each individual plant across time (nine days). We also included interactions in the Imer models that included day, canopy cover, treatment or number of leaves. We then checked for normality of the residuals using the Shapiro-Wilk test, with the null hypothesis assuming normality. Since our data did not have a normal distribution, we could not assume normality. Since the residuals were not normally distributed, we used a generalized linear mixed-effects model. For height, we used the Gamma distribution family with a log link function ('Gamma(link = "log")') because height is a continuous response variable, and the log link function ensured positive values. For the number of leaves, we used the Poisson distribution family because the number of leaves is count data, where the counts are nonnegative integers. Lastly, we used the 'emmeans' package to conduct pairwise comparisons and clarify the significant effects found in the 'glmer' models.

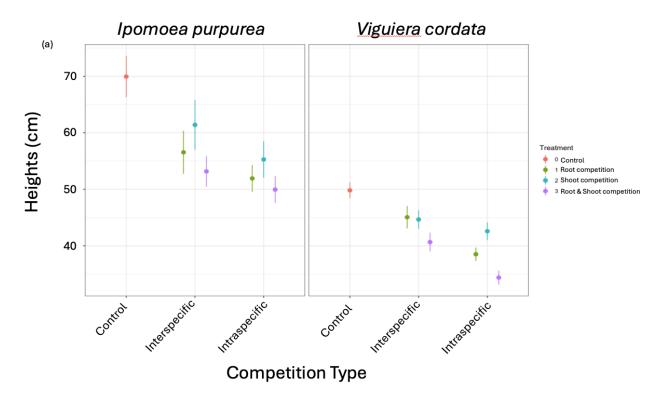
Results

Ipomoea purpurea height response

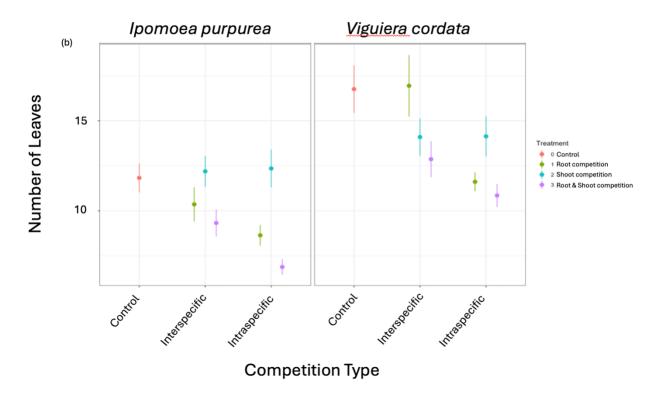
The overall effect of the treatments (root competition, shoot competition, and root and shoot competition) on the height of *I. purpurea* plants showed a strong response (P = 0.0389) to treatment 3 (root and shoot competition). The effect of treatment 2 (shoot competition) on height also showed moderate significance (P = 0.0615). Both treatments 1 (root competition) and 3 (root and shoot competition) reduced the height of *I. purpurea* plants more than when *I. purpurea* was not competing with another plant (Fig. 3a). All treatments reduced the height of *I. purpurea* plants. *I. purpurea* plants under treatment 1 (root competition) were approximately 35.95% smaller than those in the control treatment. Plants that experienced treatment 2 (shoot competition) were approximately 48.24% smaller than those in the control treatment. Treatment 3 (root and shoot competition) also reduced the height of *I. purpurea* plants, which were 50.76% smaller than control plants without any treatment manipulations (Fig. 3a). While these results from the overall effects of the interactions were significant

according to the 'glmer' model, the pairwise post hoc test did not find significant differences between the specific treatments.

Intraspecific competition had a significant effect in the heights of *I. purpurea* plants (P = 0.0274). Overall, both interspecific and intraspecific competition reduced the height of *I. purpurea plants*. *I. purpurea* plants competing with *V. cordata* were 32.18% smaller than those with no competition. Additionally, *I. purpurea* plants competing with plants of the same species exhibited a height reduction of 49.96% compared to those without any competition (Fig. 3a). The pairwise post hoc test indicated that intraspecific competition was moderately significantly stronger compared to the control (P = 0.0702). Results of the statistical analyses can be found in Appendix 1.1.



Mean Heigh Measurements



Mean Count for Number of Leaves

Figure 3: Mean height measurement plot (a) and mean count for number of leaf count plot (b) for Ipomoea purpurea and Vigueria cordata.

Ipomoea purpurea number of leaves response

The number of leaves produced by *I. purpurea* plants was negatively impacted by the treatments (root, shoot, root and shoot) imposed on them. The overall effects of the interactions from the 'glmer' model showed statistical significance (P = 0.0145) for treatment 3 (root and shoot competition) compared to plants of the same species without any treatment (Fig. 3b). All treatments (root, shoot, root and shoot) reduced the number of leaves on *I. purpurea* plants. Treatment 1 (root competition) reduced the number of leaves by 22.58%, while treatment 2 (shoot competition) reduced the number of leaves by 16.75%. Treatment 3 (root and shoot competition) resulted in a 42.24% reduction in the number of leaves compared to the control plants (Fig. 3b). The pairwise post hoc test further showed that treatment 3 (root and shoot competition) was moderately significantly different from the control treatment (P = 0.0678).

The overall effects of intraspecific competition had a statistically significant impact (P = 0.0242) on the leaf production of *I. purpurea* plants compared to those in the control treatment (no competition). Both intraspecific and interspecific competition led to a decrease in the number of leaves produced by *I. purpurea*. Specifically, plants under interspecific competition had 8.61% fewer leaves compared to the control, while those under intraspecific competition showed a reduction of 33.73% (Fig. 3b). Pairwise post hoc analysis further supported these findings, indicating a moderately significant effect of intraspecific competition

(P = 0.0624) compared to the control. Results of the statistical analyses can be found in Appendix 1.1.

Viguieia cordata height response

The statistical analysis using 'glmer' revealed significant interactive effects of treatments (root, shoot, root and shoot) on the height of *V. cordata* plants. Specifically, treatment 1 (root competition) (P = 0.0122) and treatment 3 (root and shoot competition) (P = 0.0122) significantly influenced plant height. Treatments 1, 2, and 3 (root, shoot, and root and shoot competition) all resulted in decreased height of *V. cordata* plants compared to those in the control treatment (no competition). Treatment 1 reduced height by 19.37%, treatment 2 (shoot competition) by 13.02%, and treatment 3 (root and shoot competition) by 28.67% relative to control plants of the same species (Fig. 3a). Pairwise post hoc analysis further confirmed that treatment 3 (root and shoot competition) had a nearly stronger effect on plant height (P = 0.0591) compared to the control, whereas neither treatment 1 nor treatment 2 had a significant effect on plant height.

Intraspecific and interspecific competition had differing effects on the height of *V*. cordata plants. Intraspecific competition showed a stronger impact (P = 0.0283) on plant height compared to interspecific competition when compared to plants without competition (control) (Fig. 3a). Pairwise post hoc analysis supported this finding, indicating a marginally significant effect of intraspecific competition on plant height (P = 0.0723).

Viguiera cordata number of leaves response

The overall effects of the treatment interactions (root, shoot, root and shoot) on the number of leaves produced by *V. cordata* indicate that treatment 3 (root and shoot competition) approached statistical significance (P = 0.0553) compared to *V. cordata* plants without competition. Additionally, all treatments (root, shoot, root and shoot) led to reductions in leaf production by *V. cordata* plants. Treatment 1 resulted in 11.60% fewer leaves than the control, treatment 2 led to 6.9% fewer leaves, and treatment 3 resulted in 27.78% fewer leaves than the control (Fig. 3b). Pairwise post hoc tests did not reveal specific effects from the treatments.

The effect of intraspecific and interspecific competition on the number of leaves of *V. cordata* showed that interspecific competition was marginally significant compared to the control treatment (P = 0.0862). Overall, both interspecific and intraspecific competition decreased leaf production in *V. cordata*. Plants under interspecific competition had 14.18% fewer leaves than the control, and plants under intraspecific competition had 13.42% fewer leaves than those without competition (Fig. 3b). Interestingly, pairwise tests indicated that neither intraspecific nor interspecific competition reached statistical significance, thus failing to reject the null hypothesis.

Interactions between treatments and type of competition: Ipomoea purpurea

To assess the effect of the treatment (root, shoot, root and shoot) and the type of competition (intra versus inter), we conducted a 'glmer' analysis without the control data. However, it is important to note that these results do not include comparisons with control

plants. This is because we wanted to see if there was statistical significance between the treatments and competition type without the comparison to the control plants.

The statistical analysis revealed no significant effects for the heights of *I. purpurea* when considering both competition type (intraspecific and interspecific) and above- and belowground competition (root, shoot, root and shoot) together. Furthermore, a pairwise post hoc test confirmed that none of the specific combinations significantly influenced plant height. On the other hand, when testing competition type (inter vs. intra) and treatment (root, shoot, root and shoot) out results showed statistical significance in the pairwise post hoc test when collectively analyzed for their effects on the number of leaves in *I. purpurea*. Specific comparisons revealed that Treatment 3 (root and shoot competition) and intraspecific competition had a stronger effect (P = 0.0277) in reducing the number of leaves. Results of the statistical analyses can be found in Appendix 1.2.

Interactions between treatments and type of competition: Viguiera cordata

The results of the statistical analysis indicated no statistically significant interactions on the height and number of leaves in *V. cordata* plants. It is important to note that these models were conducted without including control plants, focusing solely on assessing the interactions among different competition conditions.

Competition Coefficients

Treatment 1 (root competition) results for height and number of leaves

The competition coefficient estimates (Fig. 5a.)indicated that interspecific competition had a stronger effect on the height of *I. purpurea* plants when competing below ground (treatment 1). However, the statistical analysis did not show any significant effects of treatment 1 (root competition) and showed that intraspecific competition had a stronger effect on *I. purpurea* plant heights. Thus, indicating contradictory results between the statistical analysis and these estimates. Regarding the number of leaves, intraspecific competition had a stronger impact on *I. purpurea* plants when competing for below-ground resources (treatment 1). These results align with the findings from the statistical analysis. For *V.cordata* plants, the competition coefficients (Fig. 5a.) indicate that intraspecific competition was stronger when combined with root competition. These findings are consistent with the statistical analysis, which showed that treatment 1 and intraspecific competition had an overall negative effect on the height of *V. cordata* plants. For the number of leaves, interspecific competition seemed to have a stronger effect on the number of leaves for *V. cordata*.

Treatment 2 (shoot competition) results for height and number of leaves

The competition coefficient estimates indicate that interspecific competition had a stronger effect on the height of *I. purpurea* plants when under shoot competition (Fig. 5b.) However, statistical analysis showed that intraspecific competition had a stronger negative effect on the height of *I. purpurea* plants. When considering the number of leaves, the competition coefficient estimates suggest that intraspecific competition is stronger when *I. purpurea* plants compete for above-ground resources only (Fig. 5b.). These findings are

supported by the statistical analysis, which indicates that intraspecific competition had a stronger effect with a P-value of 0.0242.

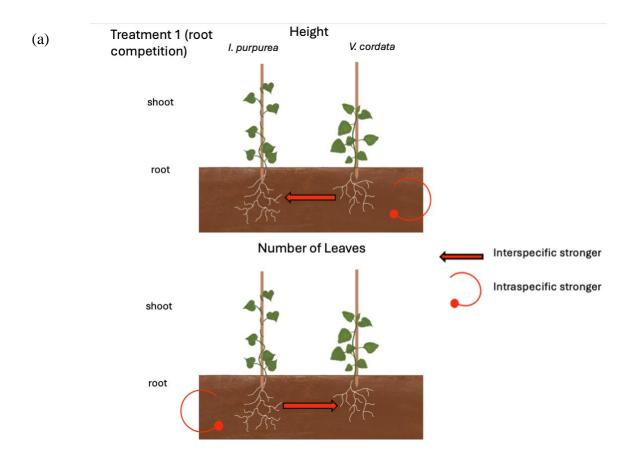
In the case of *V. cordata*, interspecific competition had a stronger effect on height (Fig. 5b.) when also competing above ground (treatment 2). These findings contradict the results from the statistical analysis, which showed that intraspecific competition had an overall stronger effect on the height of *V. cordata* plants. According to the observed trend of the competition coefficient estimates, interspecific competition had a stronger negative effect on the number of leaves produced by *V. cordata* plants when also competing above ground. These results align with our findings from the statistical analysis

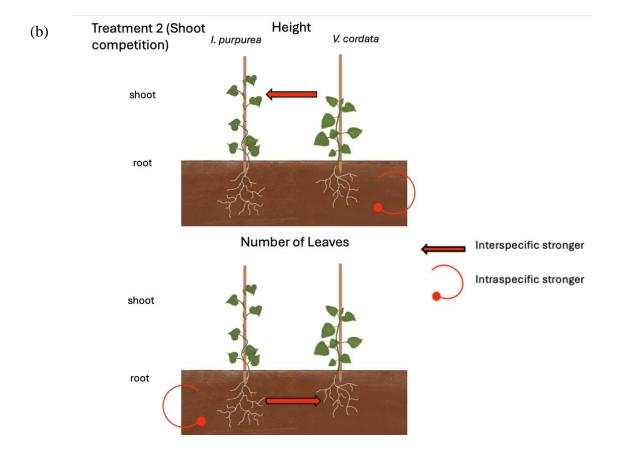
Treatment 3 (root and shoot competition) results for height and number of leaves

The competition coefficient estimate indicated that interspecific competition had a stronger effect on the height of *I. purpurea* plants (Fig. 5c.) when competing for both above and below ground resources (treatment 3). This contrasts with the statistical analysis, which showed a stronger negative effect on height from intraspecific competition (P = 0.0242). However, intraspecific competition did have a stronger effect on the number of leaves for *I. purpurea* plants compared to interspecific competition. These findings align with the statistical analysis, which indicated that intraspecific competition had a stronger effect in reducing the number of leaves in *I. purpurea* plants.

In the case of *V. cordata*, intraspecific competition had a stronger effect on plant height compared to interspecific competition when competing for both above and below ground resources (Fig. 5c.). This supports the statistical analysis, which found a stronger negative effect of intraspecific competition on the height of *V. cordata*. Conversely, the number of leaves was more impacted by interspecific competition than intraspecific competition when plants were competing for both above and below ground resources (Fig. 5c.). This aligns with the statistical analysis, which demonstrated a stronger effect on the number of leaves when *V. cordata* was competing with plants from a different species for both above and below ground resources.

In summary, the observed trends from the competition coefficient estimates differed from our predictions but provided moderate support for the results of the statistical analysis. The variation between the results of the statistical analysis and the competition coefficient estimates could be due to several factors, primarily the inability to simultaneously analyze the effects of above- and below-ground interactions with the type of competition (intraspecific and interspecific). This limitation suggests that the competition coefficient estimates might offer a clearer insight into the combined effects of these interactions. Due to data constraints, it was not possible to run the treatment and competition type, without removing data for control plants.





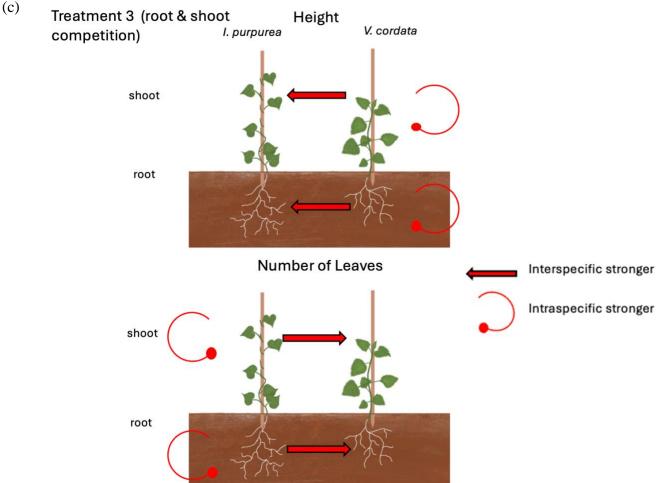


Figure 5: Representation of the competition coefficient estimates. (a) shows the coemption coefficient estimates for treatment 1 (root competition). (b) shows the competition coefficient estimates for treatment 2 (shoot competition). (c) shows the competition coefficient estimates for treatment 1 (root competition).

Discussion

In this study, we tested the competitive interaction between two common weed species, *I. purpurea* and *V. cordata*, in a coffee agroecosystem in Southern Mexico. We hypothesized that for coexistence to occur, intraspecific competition will have a stronger negative effect on plant growth than interspecific competition for both species across above-ground and below-ground interactions. Our findings suggest that both intraspecific and interspecific competition occur for both species but that above and below ground competition differ between the two species. Although there were discrepancies between the trends observed in the competition coefficient calculations, which are estimates that are utilized to compliment the experimental results, and the statistical analysis results, some general conclusions can be made.

In summary, the competition coefficient calculation estimates suggested that interspecific competition (the competition of *V. cordata* against *I. purpurea*) had a greater effect on the heights of *I. purpurea* plants across treatments (root, shoot, and root and shoot)

than the effect of intraspecific competition. This contrasts with the statistical analysis, which demonstrated a stronger overall effect of intraspecific competition on the heights of *I. purpurea* plants. Regarding the second response variable, number of leaves, both the competition coefficient estimates, and the statistical analysis consistently indicated that intraspecific competition had a stronger effect in reducing leaf count of *I. purpurea* plants above and below ground.

For *V. cordata* plants, there were notable discrepancies between the trends observed from the competition coefficient estimates and those obtained from the statistical analysis. Root competition and shoot competition, both demonstrated that intraspecific competition had a greater impact on the height of *V. cordata* plants than interspecific competition. Both, the competition coefficient estimates, and the statistical analysis indicated that intraspecific competition had a stronger effect on the heights of *V. cordata* plants. However, shoot competition showed conflicting results: competition coefficient estimates indicated a stronger effect from interspecific competition on the height of *V. cordata* plants, whereas the statistical analysis indicated that intraspecific competition was more influential. The results for the number of leaves were a lot more straightforward and both the competition coefficient estimates and the statistical analysis findings suggest that intraspecific competition, interspecific competition and root and shoot competition, interspecific competition was more intense. Thus, suggesting that the number of leaves produced by *V. cordata* plants are reduced more when competing for shoot and root and shoot resources in the presence of *I. purpurea*.

Interspecific and Intraspecific competition

These findings, although surprising, are congruent with past studies and attempts to understand the full spectrum of competition interactions and their effects on plants(Goldberg 1992, Aguiar et al. 2001, Gustafsson and Ehrlén 2003, Kiaer 2013, Romillac 2023). Previous studies looking at coexistence between shortgrass species, found evidence of intense competition but no difference between intraspecific and interspecific competition (Aguiar et al. 2001). Their findings showed that the intensity of competition fluctuated over the plants' life cycles, with interspecific and intraspecific competition affecting the response variables differently over time (Aguiar et al. 2001). Taking into consideration the fact that this study took place over a three-year experimental period, the findings of our study, align with their observations. Furthermore, a study examining the response of population growth on interspecific and intraspecific competition decrease found that vegetative growth of established individuals were not significantly affected by the removal of interspecific or intraspecific competition. Gustafsson & Ehrlen (2003) suggest there was no competition or a delayed response to competition. Moreover, their findings indicated that a decrease of both intraspecific and interspecific competition increased population growth of their target species, but when interspecific competition was reduced alone it led to a decrease in population growth (Gustafsson and Ehrlén 2003). These studies and our findings suggest that interspecific and intraspecific competition alone may not determine coexistence. Instead, the interactions occurring at various life stages (Aguiar et al. 2001, Gustafsson and Ehrlén 2003) and environmental fluctuations likely contribute to maintaining stable coexistence (Chesson 1992).

Above and below ground competition and niche segregation

Despite the variability in our findings, some of our results are consistent with previous findings that root competition (treatment 1) and the additive effects of treatment 3 (root and shoot competition) may have a stronger influence on plant growth (Casper 1997, Kiaer 2013). Casper (1997) argues that below-ground competition has a stronger influence on plants because below-ground plants compete for a broad range of soil resources, whereas aboveground competition primarily involves a single resource which is sunlight. However, other studies suggest that above-ground competition for light may reduce below-ground plant responses (Gottlieb & Gruntman 2022), highlighting the importance of investigating the combined effects of above- and below-ground competition. It is important to note that, despite the lack of statistical significance in the effects of treatment 2 (shoot competition), this does not accurately reflect a common interaction observes between these two plant species. In unmanaged areas of our study site, it is common to observe the vine *I.Purpurea* wrapped around a V. cordata plant and obstructing sunlight (X.Perez observations). A longer study may be required to accurately capture the effects for treatment 2 (shoot competition) with these two species. Additionally, although we did not study root architecture, morphology (Colom & Baucom 2020), or soil nutrient gradients (Gottlieb & Gruntman 2022), we observed potential niche segregation due to root architecture (X.P field observations). I. purpurea, a vine capable of growing horizontally across the soil, has greater mobility, while V. cordata does not. We noted that the roots of *I. purpurea* were shallow, potentially accessing nutrients in the topsoil, whereas V. cordata had longer, thicker roots, possibly accessing soil nutrients at deeper levels. Whether these observations on root architecture are a response to competition (Colom & Bauco 2020) are beyond the scope of this study and warrant further investigation, as they may constitute another mechanism enabling coexistence.

Limitations

The interpretation of results from this study is significantly constrained by the limited data collection period of nine weeks during a single field season. Within this short timeframe, critical transitional events such as *I. purpurea* tendrils wrapping around *V. cordata*, eventually choking the plant and leveraging its height to latch onto nearby trees or coffee plants, were not observed or captured in the data. This limitation may also explain why shoot competition did not yield significant results in this study, suggesting that the effects of shoot competition could potentially have a delayed response. Moreover, a comprehensive evaluation of all competition combinations across seasons could have provided a more holistic understanding of plant competition dynamics. Additionally, resource constraints in a remote field setting prevented the assessment of biomass, which is typically used in plant competition studies to evaluate treatment effects on roots, leaves, and stems, potentially enhancing result confidence and statistical power. Furthermore, the material used as stakes may have further impacted *I. purpurea* plants ability to climb up on to *V. cordata* and affect above-ground competition (Kiaer 2013). The smooth PVC pipes used may not have provided adequate grooves for *I. purpurea* to

grip onto. Lastly, we faced a challenge in analyzing the effect of both competition type (inter vs. intra) and the treatments (root, shoot, root and shoot) due to the set-up of the control data. Having both, a treatment and competition type labeled as "control" in the data we would get an error message when running the analysis. We were able to test the combined effects of competition type (inter vs. intra) and the treatments (root, shoot, root and shoot), after when removing the data for the control plants.

Weed Management Implication

Further evaluation is needed to understand the above- and below-ground competitive interactions, including interspecific and intraspecific competition, between crop and non-crop plants in agroecosystems, especially in agroecological and low input systems where herbicides are not used. This approach is critical for assessing competition's broader impacts and dynamics on food systems and biodiversity conservation. While not offering definitive management recommendations, this study suggests that competition may enable non-crop plant coexistence in tropical agroecosystems, as evidenced by below-ground and the cumulative effects of above and below ground competition, and management by reducing plant growth. In Finca Irlanda, elements of integrated weed management are already in practice. Though these plants are not used for food or medicine, three key management practices were observed: implementing canopy cover, maintaining a mosaic of vegetation growth levels, and mulching using cut weeds to retain moisture and enrich soil nutrients (X.Perez observations). Thus, showing that weeds (intentionally or not) are valuable to this agroecosystem. The suppressive effect of weeds in shaded coffee agroecosystems is well-documented, although its significance was not observed in this study (see supplemental material). Future research should continue to investigate competition dynamics across tropical agroecosystems along with management practices by rural and Indigenous farmers.

Conclusion

In general, our results do not fully support the classical predictions that in order for two species with similar requirements to achieve coexistence, intraspecific competition must be greater than interspecific competition (Tilman 1982). Nonetheless, our findings are significant as few field experiments have explored intra- and interspecific competition alongside above and below-ground interactions in tropical agroecosystem, particularly with native weed species. The observed pattern may perhaps contribute to overall stable coexistence facilitated by these complex competition interactions. Depending on whether competition occurs above or below ground, different competitive types (inter vs. intra) may exhibit varying strengths. This study suggests that coexistence might not solely depend on intraspecific competition but rather on the combination of competitive interactions over time and space, including the influence of canopy cover in reducing weed growth. Viewing coexistence mechanisms holistically captures the dynamic interactions and relative strengths of these variables. This research contributes to the understanding of competition mechanisms and their role in enabling coexistence and natural weed management in agroecosystems. Further ecological research in tropical field experiments is necessary to safeguard biodiversity conservation within food systems.

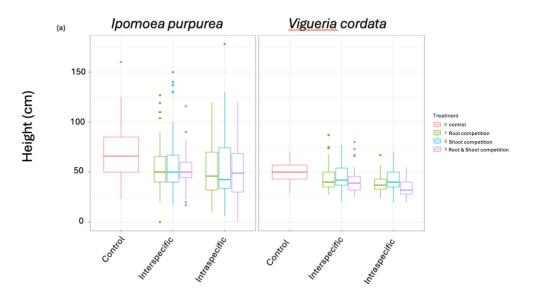
This study aims to provide further evidence that competition mechanisms can be utilized for managing weeds in low-input food systems. It also underscores the role of

Indigenous land management practices, which leverage plant knowledge and ecological interactions to sustain multifunctional natural systems and promote their longevity.

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Supplementary Material



Final Height Measurements

Competition Type

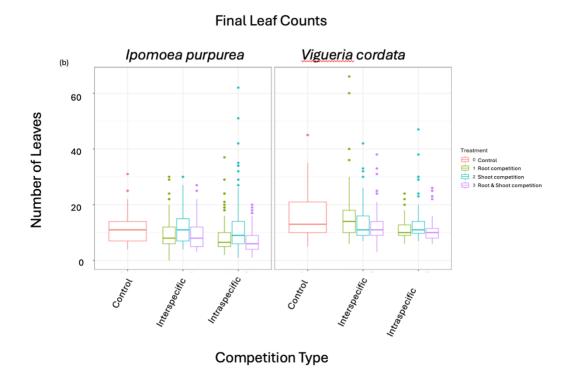
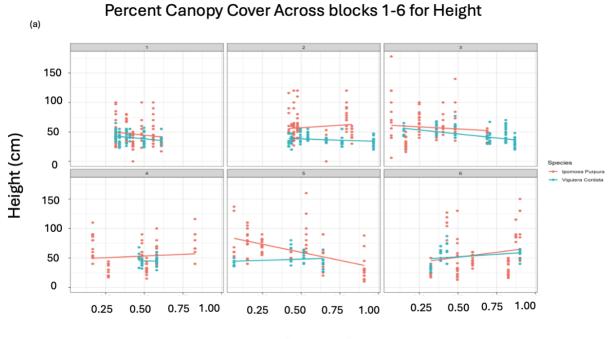
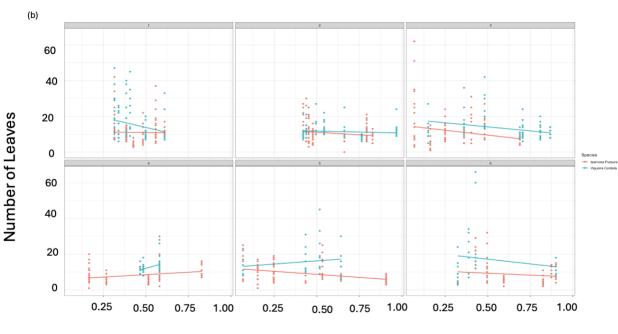


Figure 5: Boxplots of the final height measurements (a) and the final count for the number of leaves for Ipomoea purpurea and Viguiera cordata.



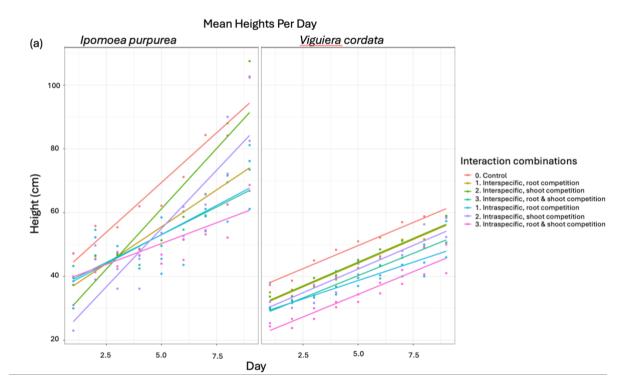
Percent Canopy Cover



Percent Canopy Cover Across Blocks 1-6 for Number of Leaves

Percent Canopy Cover

Figure 6: Percent canopy cover across all six blocks. Here we separated the two response variables to determine if there was a significant effect from canopy cover on number of leaves (a) and height (b).



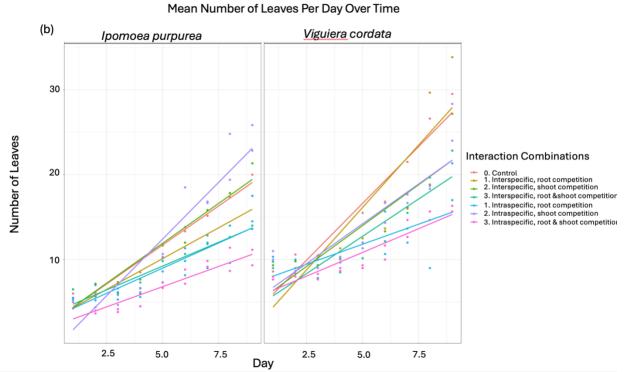


Figure 7: Linear regression of the average heights per day (a) for all interaction combinations and linear regression of the average leaf count per day (b) for all interaction combinations.

Literature Cited

Aguiar, Martín R. ; Lauenroth, William K. ; Peters, Debra P. "Intensity of Intra- and Interspecific Competition in Coexisting Shortgrass Species." The Journal of Ecology, vol. 89, no. 1, Oxford, UK: British Ecological Society, 2001, pp. 40–47, doi:10.1046/j.1365-2745.2001.00523.x.

Archibald, Sarah ; Allinne, Clementine ; Cerdán, Carlos R. ; Isaac, Marney E. "From the Ground up: Patterns and Perceptions of Herbaceous Diversity in Organic Coffee Agroecosystems." Ecological Solutions and Evidence, vol. 3, no. 3, Hoboken: John Wiley & Sons, Inc, 2022, doi:10.1002/2688-8319.12166.

Bach, Thomas M. ; Kull, Christian A. ; Rangan, Haripriya. "From Killing Lists to Healthy Country: Aboriginal Approaches to Weed Control in the Kimberley, Western Australia." Journal of Environmental Management, vol. 229, England: Elsevier Ltd, 2019, pp. 182–92, doi:10.1016/j.jenvman.2018.06.050.

Bacon, Christopher. "Confronting the Coffee Crisis: Can Fair Trade, Organic, and Specialty Coffees Reduce Small-Scale Farmer Vulnerability in Northern Nicaragua?" World Development, vol. 33, no. 3, Oxford: Elsevier Ltd, 2005, pp. 497–511, doi:10.1016/j.worlddev.2004.10.002. Barabás, György ; Michalska-Smith, Matthew J. ; Allesina, Stefano. "The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities." The American Naturalist, vol. 188, no. 1, United States: The University of Chicago Press, 2016, pp. E1–12, doi:10.1086/686901.

Bengtsson, Jan ; Fagerström, Torbjörn ; Rydin, Håkan. "Competition and Coexistence in Plant Communities." Trends in Ecology & Evolution (Amsterdam), vol. 9, no. 7, Oxford: Elsevier Ltd, 1994, pp. 246–50, doi:10.1016/0169-5347(94)90289-5.

Blanckaert, Isabelle ; Vancraeynest, Koenraad ; Swennen, Rony L. ; Espinosa-García, Francisco J. ; Piñero, Daniel ; Lira-Saade, Rafael. "Non-Crop Resources and the Role of Indigenous Knowledge in Semi-Arid Production of Mexico." Agriculture, Ecosystems & Environment, vol. 119, no. 1, Amsterdam: Elsevier B.V, 2007, pp. 39–48, doi:10.1016/j.agee.2006.06.015.

Casper, Brenda B., and Robert B. Jackson. "Plant Competition Underground." *Annual Review of Ecology and Systematics*, vol. 28, 1997, pp. 545–70. *JSTOR*, http://www.jstor.org/stable/2952504. Accessed 27 June 2024.

Clegg, Michael T ; Durbin, Mary L. "Tracing Floral Adaptations from Ecology to Molecules." Nature Reviews. Genetics, vol. 4, no. 3, London: Nature Publishing Group, 2003, pp. 206–15, doi:10.1038/nrg1023.

Chacón, J.C. ; Gliessman, S.R. "Use of the 'Non-Weed' Concept in Traditional Tropical Agroecosystems of South-Eastern Mexico." Agro-Ecosystems, vol. 8, no. 1, Elsevier B.V, 1982, pp. 1–11, doi:10.1016/0304-3746(82)90010-5.

Chaney, Lindsay ; Baucom, Regina S. "THE COSTS AND BENEFITS OF TOLERANCE TO COMPETITION IN IPOMOEA PURPUREA, THE COMMON MORNING GLORY." Evolution, vol. 68, no. 6, United States: Blackwell Publishing Ltd, 2014, pp. 1698–709, doi:10.1111/evo.12383.

Charudattan, R. "Biological Control of Weeds by Means of Plant Pathogens: Significance for Integrated Weed Management in Modern Agro-Ecology." BioControl (Dordrecht, Netherlands), vol. 46, no. 2, Dordrecht: Springer Nature B.V, 2001, pp. 229–60, doi:10.1023/A:1011477531101.

Chesson, Peter. "Chesson's Coexistence Theory: Comment." Ecology (Durham), vol. 101, no. 11, United States: John Wiley and Sons, Inc, 2020, pp. 1–7, doi:10.1002/ecy.2851.

Chesson, Peter. "Updates on Mechanisms of Maintenance of Species Diversity." The Journal of Ecology, vol. 106, no. 5, Oxford: John Wiley & Sons Ltd, 2018, pp. 1773–94, doi:10.1111/1365-2745.13035.

Chesson, Peter. "Updates on Mechanisms of Maintenance of Species Diversity." The Journal of Ecology, vol. 106, no. 5, Oxford: John Wiley & Sons Ltd, 2018, pp. 1773–94, doi:10.1111/1365-2745.13035.

Chesson, P. "Multispecies Competition in Variable Environments." Theoretical Population Biology, vol. 45, no. 3, Elsevier Inc, 1994, pp. 227–76, doi:10.1006/tpbi.1994.1013.

Dawson, Neil M. ; Coolsaet, Brendan ; Sterling, Eleanor J. ; Loveridge, Robin ; Gross-Camp, Nicole D ; Wongbusarakum, Supin ; Sangha, Kamaljit K. ; Scherl, Lea M. ; Phan, Hao Phuong ; Zafra-Calvo, Noelia ; Lavey, Warren G. ; Byakagaba, Patrick ; Idrobo, C. Julián ; Chenet, Aude ; Bennett, Nathan J. ; Mansourian, Stephanie ; Rosado-May, Francisco J. "The Role of Indigenous Peoples and Local Communities in Effective and Equitable Conservation." Ecology and Society, vol. 26, no. 3, Ottawa: Resilience Alliance, 2021, pp. 1-, doi:10.5751/ES-12625-260319.

Dillenburg, L.R ; Whigham, D.F ; Teramura, A.H ; Forseth, I.N. "Effects of Below- and Aboveground Competition from the Vines Lonicera Japonica and Parthenocissus Quinquefolia on the Growth of the Tree Host Liquidambar Styraciflua." Oecologia, vol. 93, no. 1, Berlin: Springer-Verlag, 1993, pp. 48–54, doi:10.1007/BF00321190.

Francis, Charles A. "Integrated Weed Management for Sustainable Agriculture." Agroecology and Sustainable Food Systems, vol. 43, no. 3, Philadelphia: Taylor & Francis, 2019, pp. 358–60, doi:10.1080/21683565.2018.1515800.

Gaba, Sabrina ; Reboud, Xavier ; Fried, Guillaume. "Agroecology and Conservation of Weed Diversity in Agricultural Lands." Botany Letters, vol. 163, no. 4, Taylor & Francis, 2016, pp. 351–54, doi:10.1080/23818107.2016.1236290.

Goel, Reeta ; Soni, Ravindra ; Suyal, Deep Chandra. Indigenous Agricultural Practices: A Supreme Key to Maintaining Biodiversity. Singapore: Springer Singapore Pte. Limited, 2020, pp. 91–112, doi:10.1007/978-981-15-1902-4_6.

Goldberg, Deborah E. 3 - Components of Resource Competition in Plant Communities. Elsevier Inc, 1990, pp. 27–49, doi:10.1016/B978-0-12-294452-9.50007-2.

Goldberg, Deborah E. ; Barton, Andrew M. "Patterns of Consequences of Interspecific Competition in Natural Communities: A Review of Field Experiments with Plants." The American Naturalist, vol. 139, no. 4, Chicago, IL: University of Chicago Press, 1992, pp. 771–801, doi:10.1086/285357.

Gottlieb, Ruth ; Gruntman, Michal. "Can Plants Integrate Information on Above-Ground Competition in Their Directional Responses below Ground?" Annals of Botany, vol. 130, no. 5, England: Oxford University Press, 2022, pp. 763–71, doi:10.1093/aob/mcac106. Gustafsson, Christel ; Ehrlén, Johan. "Effects of Intraspecific and Interspecific Density on the Demography of a Perennial Herb, Sanicula Europaea." Oikos, vol. 100, no. 2, Copenhagen: Munksgaard International Publishers, 2003, pp. 317–24, doi:10.1034/j.1600-0706.2003.11493.x.

H. D. Scott, and L. R. Oliver. "Field Competition between Tall Morningglory and Soybean. II. Development and Distribution of Root Systems." *Weed Science*, vol. 24, no. 5, 1976, pp. 454–60. *JSTOR*, http://www.jstor.org/stable/4042644. Accessed 15 June 2024.

Johnson, Christopher A. "How Mutualisms Influence the Coexistence of Competing Species." Ecology (Durham), vol. 102, no. 6, United States: John Wiley and Sons, Inc, 2021, pp. 1–8, doi:10.1002/ecy.3346.

Kiær, Lars Pødenphant ; Weisbach, Anne Nygaard ; Weiner, Jacob. "Root and Shoot Competition: A Meta-Analysis." The Journal of Ecology, vol. 101, no. 5, Oxford: Blackwell Publishing, 2013, pp. 1298–312, doi:10.1111/1365-2745.12129.

Kimmerer, Robin Wall. "Weaving Traditional Ecological Knowledge into Biological Education: A Call to Action." Bioscience, vol. 52, no. 5, Circulation, AIBS, 1313 Dolley Madison Blvd., Suite 402, McLean, VA 22101. USA: American Institute of Biological Sciences, 2002, pp. 432–38, doi:10.1641/0006-3568(2002)052[0432:WTEKIB]2.0.CO;2.

Liebman, Matt ; Gallandt, Eric R. 9 - Many Little Hammers: Ecological Management of Crop-Weed Interactions. Academic Press, 1997, pp. 291–343, doi:10.1016/B978-012378260-1/50010-5.

Lin, Brenda B ; Perfecto, Ivette ; Vandermeer, John. "Synergies between Agricultural Intensification and Climate Change Could Create Surprising Vulnerabilities for Crops." Bioscience, vol. 58, no. 9, Circulation, AIBS, 1313 Dolley Madison Blvd., Suite 402, McLean, VA 22101. USA: American Institute of Biological Sciences, 2008, pp. 847–54, doi:10.1641/B580911.

Mason, Rachel E. ; White, Alissa ; Bucini, Gabriela ; Anderzén, Janica ; Méndez, V. Ernesto ; Merrill, Scott C. "The Evolving Landscape of Agroecological Research." Agroecology and Sustainable Food Systems, vol. 45, no. 4, Philadelphia: Taylor & Francis, 2021, pp. 551–91, doi:10.1080/21683565.2020.1845275.

Maxwell, B.D ; Luschei, E. "Ecology of Crop-Weed Interactions: Towards a More Complete Model of Weed Communities in Agroecosystems." Journal of Crop Improvement, vol. 11, no. 1– 2, Taylor & Francis Group, 2004, pp. 137–51, doi:10.1300/J411v11n01_07.

Menalled, Uriel D. ; Bybee-Finley, K. Ann ; Smith, Richard G. ; DiTommaso, Antonio ; Pethybridge, Sarah J. ; Ryan, Matthew R. "Soil-Mediated Effects on Weed-Crop Competition: Elucidating the Role of Annual and Perennial Intercrop Diversity Legacies." Agronomy (Basel), vol. 10, no. 9, Basel: MDPI AG, 2020, pp. 1373-, doi:10.3390/agronomy10091373. Meylan, Louise ; Merot, Anne ; Gary, Christian ; Rapidel, Bruno. "Combining a Typology and a Conceptual Model of Cropping System to Explore the Diversity of Relationships between Ecosystem Services: The Case of Erosion Control in Coffee-Based Agroforestry Systems in Costa Rica." Agricultural Systems, vol. 118, Elsevier Ltd, 2013, pp. 52–64, doi:10.1016/j.agsy.2013.02.002.

Moguel, P. (Universidad Michoacana de San Nicolas de Hidalgo, Michoacan, Mexico.) ; Toledo, V.M. "Biodiversity Conservation in Traditional Coffee Systems of Mexico." Conservation Biology, vol. 13, no. 1, Boston, MA, USA: Blackwell Science Inc, 1999, pp. 11–21, doi:10.1046/j.1523-1739.1999.97153.x.

MURPHY, GUILLERMO P ; DUDLEY, SUSAN A. "Above- and below-Ground Competition Cues Elicit Independent Responses." The Journal of Ecology, vol. 95, no. 2, Oxford, UK: Oxford, UK : Blackwell Publishing Ltd, 2007, pp. 261–72, doi:10.1111/j.1365-2745.2007.01217.x.

Perfecto, Ivette ; Snelling, Roy. "Biodiversity and the Transformation of a Tropical Agroecosystem: Ants in Coffee Plantations." Ecological Applications, vol. 5, no. 4, Ecological Society of America, 1995, pp. 1084–97, doi:10.2307/2269356

Perfecto, Ivette ; Vandermeer, John. "Agroecological Matrix as Alternative to the Land-Sparing/Agriculture Intensification Model." Proceedings of the National Academy of Sciences - PNAS, vol. 107, no. 13, United States: National Academy of Sciences, 2010, pp. 5786–91, doi:10.1073/pnas.0905455107.

Perfecto, Ivette, et al. "Complex Ecological Interactions in the Coffee Agroecosystem." *Annual Review of Ecology, Evolution, and Systematics*, vol. 45, 2014, pp. 137–58. *JSTOR*, http://www.jstor.org/stable/24810175. Accessed 27 June 2024.

Ronchi, C.P.(Instituto Capixaba de Pesquisa) ; Silva, A.A.(Universidade Federal de Viçosa Departamento de Fitotecnia). "Effects of Weed Species Competition on the Growth of Young Coffee Plants." Planta Daninha, vol. 24, no. 3, Sociedade Brasileira da Ciência das Plantas Daninhas, 2006, pp. 415–23, doi:10.1590/S0100-83582006000300001.

Romillac, Nicolas ; Piutti, Séverine ; Slezack-Deschaumes, Sophie ; Gaba, Sabrina. "Intraspecific Functional Trait Variation in Weeds: A Strategy in Response to Competition with Crop and Weed Plants." Weed Research, vol. 63, no. 5, Oxford: Wiley Subscription Services, Inc, 2023, pp. 283–96, doi:10.1111/wre.12592.

Scavo, Aurelio ; Mauromicale, Giovanni. "Integrated Weed Management in Herbaceous Field Crops." Agronomy (Basel), vol. 10, no. 4, MDPI AG, 2020, pp. 466-, doi:10.3390/agronomy10040466. Silvertown, Jonathan. "Plant Coexistence and the Niche." Trends in Ecology & Evolution (Amsterdam), vol. 19, no. 11, Oxford: Elsevier Ltd, 2004, pp. 605–11, doi:10.1016/j.tree.2004.09.003.

Soley, Fernando G. ; Perfecto, Ivette. "A Way Forward for Biodiversity Conservation: High-Quality Landscapes." Trends in Ecology & Evolution (Amsterdam), vol. 36, no. 9, Elsevier Ltd, 2021, pp. 770–73, doi:10.1016/j.tree.2021.04.012.

Tilman, David. Resource Competition and Community Structure. Princeton University Press, 1982.

Thorsted, Marian D. ; Weiner, Jacob ; Olesen, Jørgen E. "Above- and Below-Ground Competition between Intercropped Winter Wheat Triticum Aestivum and White Clover Trifolium Repens." The Journal of Applied Ecology, vol. 43, no. 2, Oxford, UK: Blackwell Science Ltd, 2006, pp. 237–45, doi:10.1111/j.1365-2664.2006.01131.x.

Tscharntke, Teja ; Clough, Yann ; Bhagwat, Shonil A. ; Buchori, Damayanti ; Faust, Heiko ; Hertel, Dietrich ; Hölscher, Dirk ; Juhrbandt, Jana ; Kessler, Michael ; Perfecto, Ivette ; Scherber, Christoph ; Schroth, Götz ; Veldkamp, Edzo ; Wanger, Thomas C. "Multifunctional Shade-Tree Management in Tropical Agroforestry Landscapes — a Review." The Journal of Applied Ecology, vol. 48, no. 3, Oxford, UK: Blackwell Publishing, 2011, pp. 619–29, doi:10.1111/j.1365-2664.2010.01939.x.

Umaña, María Natalia ; Zhang, Caicai ; Cao, Min ; Lin, Luxiang ; Swenson, Nathan G ; Suding, Katharine. "Commonness, Rarity, and Intraspecific Variation in Traits and Performance in Tropical Tree Seedlings." Ecology Letters, vol. 18, no. 12, England: Blackwell Science, 2015, pp. 1329–37, doi:10.1111/ele.12527.

Vandermeer, J. and Perfecto, I., 2017. Ecological complexity and agroecology. Routledge.

Weiner, Jacob. "Asymmetric Competition in Plant Populations." Trends in Ecology & Evolution, vol. 5, no. 11, England: Elsevier Ltd, 1990, pp. 360–64, doi:10.1016/0169-5347(90)90095-U.

Weiner, Jacob. "How Competition for Light and Nutrients Affects Size Variability in Ipomoea Tricolor Populations." Ecology (Durham), vol. 67, no. 5, Washington, DC: The Ecological Society of America, 1986, pp. 1425–27, doi:10.2307/1938699.

Wright, S. Joseph. "Plant Diversity in Tropical Forests: A Review of Mechanisms of Species Coexistence." Oecologia, vol. 130, no. 1, Berlin: Springer-Verlag, 2002, pp. 1–14, doi:10.1007/s004420100809.

Appendix

Appendix 1.1. Summary table for the statistical results for the generalized linear mixed-effects models (GLMER) relating plant height and number of leaves to interspecific and intraspecific competition, as well as, root competition, shoot competition, and root and shoot competition. Boldface indicates significant effect p<0.05.

| Plant Species | Predictor | Competition | Coefficient | Std. error | Confidence Interval 95% | P-value |
|---------------------|---------------------|---|-------------|------------|----------------------------|---------|
| Ipomoea purpurea | Height | Treatment 3 (root and shoot competition) | -0.50796 | 0.24595 | 0.990022± 0.025898 | 0.0389 |
| | | Treatment 2 (shoot competition) | -0.48243 | 0.25795 | 0.023152± -0.988012 | 0.0615 |
| | | Intraspecific competition | -0.4996 | 0.2265 | -0.05566± -0.94354 | 0.0274 |
| | Number of leaves | Treatment 3 (root and shoot competition) | -0.42242 | 0.17278 | -0.0837712± -0.7610688 | 0.0145 |
| | | Intraspecific competition | -0.33733 | 0.14963 | -0.0440552± -0.6306048 | 0.0242 |
| Viguiera cordata | Height | Intraspecific competition | -0.2632 | 0.1200 | -0.028± -0.4984 | 0.0283 |
| | | Treatment 3 (root and shoot competition) | -0.2867 | 0.1145 | -0.06228± -0.51112 | 0.0122 |
| | Number of leaves | Interspecific competition | -0.14185 | 0.08268 | 0.0202028± -0.3039028 | 0.0862 |
| | | Treatment 3 (root and | -0.27785 | 0.14500 | 0.00635± -0.56205 | 0.0553 |

| shoot | |
|--------------|--|
| competition) | |

Appendix 1.2. Summary table for the statistical results from the pairwise post hoc test for the combined effects on plant height and number of leaves from interspecific and intraspecific competition, as well as, root competition, shoot competition, and root and shoot competition. Boldface indicates significant effect p<0.05

| Plant Species | Predictor | Combined competition | Coefficients | Std. error | Confidence Interval 95% | P-value |
|---------------------|---------------------|---|--------------|------------|-------------------------------|---------|
| lpomoea purpurea | Number of leaves | Intraspecific and treatment 3 (root and shoot competition) | 0.3716 | 0.169 | 0.70284± 0.04036 | 0.0277 |