

Examining the Effects of Traits on Early-Establishment Tree Communities Under Different Soil

Water Conditions

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Studies have demonstrated the existence of a positive relationship between species richness and productivity in forests around the world. This positive relationship is thought to be explained by two mechanisms: complementarity effects and selection effects. Both mechanisms rely on species' traits, whereby the diversity of traits (under complementarity effects) or the presence of specific trait values (under selection effects) can increase productivity. However, while it has been clearly established that species richness increases productivity, few studies have tested the implicit assumption that traits underpin the established species richness-productivity relationship. To address this gap, this study examined which traits are responsible for the species-productivity relationship in temperate tree communities during the early stages of stand development, and whether they act via complementarity effects or selection effects. In addition, this study aims to determine how the observed relationship and its underlying traits change in environments with different water availabilities by assessing which traits are associated with productivity in each environment.

These questions were answered using an experimental plantation of temperate tree communities in the early stages of stand development, in which water exclusion treatments were implemented. Six temperate tree species were planted in this experiment, either in a monoculture or in a three-species mixed community. To separate the effects of species and trait diversity, the mixed tree communities had a fixed species richness but varied in trait diversity. The species compositions of the mixes were selected to create a trait diversity gradient. Leaf area, leaf mass per area, stomatal density, chlorophyll concentration, specific root length, root tissue density, and root diameter were measured in each community.

Community productivity was measured both as aboveground biomass and as belowground biomass.

The most consistent pattern of selection in the press treatment was for leaf area, as it was under selection in combination with leaf mass per area and with stomatal density. Pairs of traits including specific root length were also under selection in the pulse and the control treatments. Selection for these traits resulted in three to fivefold increases in aboveground biomass. These results demonstrate that selection effects are the driving force of community productivity during stand establishment. Here, selection acted upon traits related to tree architecture, thermoregulation, photosynthetic rate, and water use, which illustrate the mechanisms by which selection effects drive increases in the productivity of early-establishment communities across varying soil water conditions.

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Table of Contents

Author's Declaration.....	<i>ii</i>
Abstract	<i>iii</i>
Acknowledgements	<i>v</i>
List of Figures	<i>x</i>
List of Tables	<i>xvi</i>
List of Abbreviations.....	<i>xviii</i>
1. General Introduction	1
1.1 History of Biodiversity-Ecosystem Function Studies.....	1
1.2 Traits and Biodiversity-Ecosystem Function	3
1.3 Trait Choices	4
1.3.1 Leaf Area.....	4
1.3.2 Leaf Mass per Area	5
1.3.3 Chlorophyll Concentration.....	6
1.3.4 Stomatal Density	6
1.3.5 Specific Root Length	7
1.3.6 Root Tissue Density	8
1.3.7 Root Diameter	8
1.4 Responses to Drought	10
1.4.1 Plant Responses to Drought	10
1.4.2 Stand Responses to Drought	11
1.5 Life History of Studied Species	12
1.5.1 <i>Quercus rubra</i>	12
1.5.2 <i>Acer saccharum</i>	13
1.5.3 <i>Betula alleghaniensis</i>	13
1.5.4 <i>Larix laricina</i>	14

1.5.5 <i>Pinus resinosa</i>	14
1.5.6 <i>Picea glauca</i>	15
1.6 Research Objectives	15
2. Examining the Effects of Traits on Early-Establishment Tree Communities Under Different Soil Water Conditions	17
2.1 Introduction	17
2.2 Methods	21
2.2.1 Study Site	21
2.2.2 Experimental Design	23
2.2.3 Water Exclusion Treatment	24
2.2.4 Leaf Trait Measurements	26
2.2.5 Root Trait Measurements	29
2.2.6 Biomass Measurements	31
2.2.7 Testing Complementarity Effects	32
2.2.8 Testing Selection Effects	33
2.2.9 Statistical Analyses	34
2.3 Results	36
2.3.1 Trait Values of the Most Productive Species	36
2.3.2 Effects of Water Exclusion Treatments	39
2.3.3 Which Traits and Mechanisms Affect Community-Level Biomass?	45
2.4 Discussion	49
2.4.1 Selection for Trait Combinations with Leaf Area	49
2.4.2 Selection for Trait Combinations with Specific Root Length	52
2.4.3 Presence of Complementarity and Selection in Early-Establishment Forests	53
2.4.4 Effects of Water Availability	55
2.4.5 Conclusion	56
3. General Discussion.....	57

3.1 Summary and Key Findings.....	57
3.2 Implications	58
3.3 How Should Selection and Complementarity Effects Change Over Time?	59
3.4 Future Work.....	60
References	63
Appendices	84
Appendix 1. Sampling Locations	84
Appendix 2. Species Differences in Aboveground Biomass.....	85
Appendix 3. Effects of Plot Composition on Trait Values	87
Appendix 4. Exploration into the Effects of the Water Exclusion Treatments	90
Appendix 5. Significant Regressions That Did Not Provide Evidence of Complementarity or Selection Effects	98
Appendix 6. Principal Component Analysis for Gymnosperm and Angiosperm Traits.....	100

List of Figures

Figure 1. Aerial view of the IDENT-Outaouais plantation in September 2024. 22

Figure 2. Three-species and monoculture temperate tree communities established along a functional diversity gradient in the IDENT-Outaouais experiment. The functional diversity gradient was established based on trait values from the TRY dataset (Kattge et al., 2011). Three-species mix compositions are as follows: Mix 1, *L. laricina*, *Q. rubra*, *A. saccharum*; Mix 2, *B. alleghaniensis*, *Q. rubra*, *A. saccharum*; Mix 3, *P. glauca*, *P. resinosa*, *L. laricina*; Mix 4, *B. alleghaniensis*, *P. glauca*, *A. saccharum*; Mix 5, *Q. rubra*, *P. resinosa*, *L. laricina*; Mix 6, *P. glauca*, *A. saccharum*, *L. laricina*; Mix 7, *B. alleghaniensis*, *Q. rubra*, *P. resinosa*. 24

Figure 3. Spatial distribution of tree communities in the IDENT-Outaouais experiment. Replicates were applied in three blocks of 36 plots, delineated by black lines. Each combination of community composition and water exclusion treatment is repeated once within each block. Plots in the control treatment are indicated in purple, plots in the press treatment are indicated in pink, and plots in the pulse treatment are indicated in green. In total, the experiment is composed of 108 plots. 25

Figure 4. Differences in trait values across individuals of each species and water exclusion treatments. The angiosperms and the gymnosperms were included in the same panel when scales were comparable and in separate panels when scales were not comparable. The dominant species for each clade are identified by triangles. Trait differences are illustrated in

panels a to g: Panel a) chlorophyll concentration (mg/m^2), panel b) root diameter (mm), panel c) stomatal density (stomata/ mm^2), panel d) root tissue density (g/cm^3), panel e) leaf area (cm^2), panel f) specific root length (m/g), and panel g) leaf mass per area (g/cm^2). 39

Figure 5. Differences in the percent volumetric water content of each treatment over the 2024 summer. All volumetric water content measurements taken at least three days after a rain event were included in the comparisons. For each day of measurement, percent volumetric water content within a community plot was averaged. Plot volumetric water content therefore represents the mean amount of soil water content in each plot. Across all plots, the average volumetric water contents were significantly different between the pulse and the press treatments ($p = 0.020$), marginally different between the pulse and the control treatments ($p = 0.1$), and not different between the press and the control treatments ($p = 0.785$). 40

Figure 6. Change in percent volumetric soil water content during the growing season, by treatment. All treatments followed the same temporal trends and maintained consistent percent volumetric water content differences throughout the growing season. The percent volumetric soil water content in the pulse treatment was consistently lower than in the control and the press treatments ($p < 0.001$). 41

Figure 7. Differences in plot biomass across treatments. Panel a) illustrates the effects of the pulse, press, and control treatments on aboveground biomass, in kilograms. Aboveground biomass for each tree was calculated as $\text{height} \times \text{diameter}^2 \times \text{wood density}$. The total

aboveground biomass of the trees in 2024 did not differ across treatments ($F(2, 969) = 0.531$, $p = 0.588$). Panel b) illustrates the effects of the pulse, press, and control treatments on belowground biomass, in grams. Belowground biomass for each plot was calculated as the total dried weight of tree roots collected from three soil cores. The belowground biomass of the trees in 2024 did not differ across treatments ($F(2, 699) = 1.314$, $p = 0.27$)......43

Figure 8. Differences in trait values of monoculture communities where trait plasticity was observed. The trait values of monocultures were grouped by treatment for comparisons. Three-species communities were not included, to isolate the effects of the water exclusion treatments from those of neighbouring species. In *B. alleghaniensis* monocultures, chlorophyll concentration was higher in the pulse treatment than in the press and the control treatments (Press: $p = 0.009$, Control: $p = 0.007$). In *P. resinosa* monocultures, root tissue density was lower in the press treatment than in the pulse and the control treatments (Pulse: $p = 0.002$, Control: $p = 0.002$)......44

Figure 9. Linear regressions of aboveground biomass, in kilograms, against the selection metrics. Panel a) illustrates the linear regression of aboveground biomass against the modified Functional Dispersion index (FDisc_{WD}) calculated using species-level leaf area and leaf mass per area trait values for plots in the press treatment ($R^2 = 0.45$, $p = 0.027$). Panel b) illustrates the linear regression of aboveground biomass against the modified Functional Dispersion index (FDisc_{WD}) calculated using species-level leaf area and stomatal density values for the press treatment ($R^2 = 0.46$, $p = 0.027$). The original Functional Dispersion index (FDis) was modified

into FDis_{CWD} which calculates the community weighted mean distance to the best trait value, instead of to the distance to the mean trait value. Plots with smaller community weighted distances to the best trait values produced four times more aboveground biomass, thus showing evidence of selection effects.....47

Figure 10. Linear regressions of aboveground biomass, in kilograms, against the modified Functional Dispersion index (FDis_{CWD}) of trait pairs including specific root length. Panel a) illustrates the linear regression of aboveground biomass against FDis_{CWD} calculated using species-level chlorophyll concentration and specific root length values for plots in the pulse treatment ($R^2 = 0.60$, $p = 0.039$). Panel b) illustrates the linear regression of aboveground biomass against FDis_{CWD} calculated using species-level stomatal density and specific root length values for plots in the control treatment ($R^2 = 0.53$, $p = 0.049$). The original Functional Dispersion index (FDis) was modified into FDis_{CWD} which calculates the community weighted mean distance to the best trait value, instead of to the distance to the mean trait value. Plots with smaller community weighted distances to the best trait values produced four times more aboveground biomass, thus showing evidence of selection effects. 48

Figure A 1. Sampling locations in each plot. The white square delineates the nine central individuals from which leaf traits and aboveground biomass were measured. The white circles indicate the three locations where soil cores were collected. Trait measurements were not taken for individuals in the outer two rows, as they served as a buffer for edge effects. 84

Figure A 2. Differences in average aboveground biomass (kg) across species, in each water exclusion treatment. For *L. laricina*, aboveground biomass was averaged across all individuals for each treatment. For all other species, aboveground biomass was averaged across individuals growing in monoculture for each treatment. Across all species, aboveground biomass was highest in *L. laricina* and *B. alleghaniensis*. 85

Figure A 3. Plot of daily precipitation and mean volumetric water content (VWC%) from May to October 2024. Green bars represent mean VWC% across all treatments and blue bars represent daily precipitation (mm). 91

Figure A 4. Differences in the percent volumetric water content (VWC%) based on community composition. VWC% was first averaged within a plot, then VWC% based on community composition was compared across all treatments. Mix compositions are as follows: Mix 1, *L. laricina*, *Q. rubra*, *A. saccharum*; Mix 2, *B. alleghaniensis*, *Q. rubra*, *A. saccharum*; Mix 3, *P. glauca*, *P. resinosa*, *L. laricina*; Mix 4, *B. alleghaniensis*, *P. glauca*, *A. saccharum*; Mix 5, *Q. rubra*, *P. resinosa*, *L. laricina*; Mix 6, *P. glauca*, *A. saccharum*, *L. laricina*; Mix 7, *B. alleghaniensis*, *Q. rubra*, *P. resinosa*. Mixes 1, 3, 5, and 6, which had the lowest VWC% values are plots which contained *L. laricina*. 92

Figure A 5. Change in percent volumetric water content (VWC%) with hours since the last rain event greater than 5 mm. Each datapoint represents the mean VWC% of a single plot at a given time. 93

Figure A 6. Change in relative extractable soil water during the growing season, based on treatment. Each datapoint represents the relative extractable water of a single plot on a given day. A threshold level of 0.4 was used to determine periods of water stress, indicated by the black dotted line. All treatments followed the same pattern over time, with drops in REW in July and September. The pulse treatment was the only treatment in which the REW trendline drops below threshold level of 0.4 in July. The average REW in the pulse treatment was consistently lower than in the control and press treatments. 96

Figure A 7. Change in relative extractable water with hours since the last rain event greater than 5 mm. Each datapoint represents the relative extractable water of a single plot at a given time. A threshold level of 0.4 was used to determine periods of water stress indicated by the black dotted line. In each treatment, the threshold of 0.4 was reached ~125 hours after a rain event.....97

Figure A 8. Principal Component Analysis for traits of a) gymnosperms and b) angiosperms. In panel a), principal component 1 explains 83.8% of the variation in traits and principal component 2 explains 16.2% of the variation in traits. In panel b), principal component 1 explains 62.1% of the variation in traits and principal component 2 explains 37.9% of the variation in traits. These Principal Component Analyses were done using the trait values measured at the IDENT-Outaouais plantation in 2024.....100

List of Tables

Table 1. Summary of measured leaf and root traits.	9
Table 2. Summary of significant and marginally significant results. Results in italics are marginally significant.....	45
Table A 1. Comparisons of trait values for each species based on plot composition. T-tests were performed between the trait values of each species in monoculture and their trait values across all mixes, for each trait and each treatment. A false discovery rate correction was applied. Significant adjusted p-values and the difference in trait values between the monoculture and the mixes are presented below.	87
Table A 2. Summary statistics of the percent volumetric water content (VWC%) across plots in the press, pulse, and control water exclusion treatments. These summary statistics were calculated using the mean VWC% for each plot and represent the mean, minimum, maximum, and the variance in VWC% across plots over the whole summer.	90
Table A 3. Characterization of the water stress in each treatment based on relative extractable water. Start date represents the first date on which relative extractable water dropped below 0.4 in each treatment. Days below 0.4 represents the number of days where the relative extractable water stayed below 0.4 for at least one plot. Days majority below 0.4 represents the number of days where the relative extractable water stayed below 0.4 for more than half the plots in a treatment.....	95

Table A 4. List of regressions that were significant or marginally significant (*italics*) but did not provide evidence of either complementarity or selection effects. In cases in black, biomass decreased with functional dispersion (FDis), the metric used to calculate multivariate trait complementarity. This indicates that productivity was lower in communities that had a high trait diversity of a given group of traits. In cases in red, biomass increased with the community weighted distance to best (CWD). This indicates that productivity was higher in communities that had trait values that diverged from the traits of the most productive species. 98

List of Abbreviations

ANOVA	Analysis of variance
CHL	Chlorophyll concentration
CWD	Community weighted distance to the ‘best’ trait value
CWM	Community weighted mean
D	Diameter
EMM	Estimated marginal means
IDENT	International diversity experiment network with trees
FDis	Functional dispersion index
FDis_{CWD}	Multivariate equivalent to the community weighted distance from the ‘best’ trait
H	Height
LA	Leaf area
LMA	Leaf mass per area
LME	Linear mixed-effects model
PCA	Principal component analysis
SD	Stomatal density
SRL	Specific root length
VWC%	Percent volumetric water content
WD	Wood density

1. General Introduction

The ecological field of biodiversity-ecosystem function has been based on investigating the effects of biodiversity on ecosystem functioning (van der Plas, 2019). Early biodiversity-ecosystem function research has often quantified biodiversity at the species level, under the assumption that species richness is correlated to the functional diversity of the species present (Naeem & Wright, 2003; Balvanera et al., 2006). As a result, more studies into the direct effects of traits, are needed to directly quantify the functional diversity of a community (Díaz & Cabido, 2001).

This study is conducted in an experimental plantation of early-establishment temperate tree communities. Seven traits were studied in six temperate tree species to investigate how trait diversity and composition influences community productivity under varying water availability conditions.

1.1 History of Biodiversity-Ecosystem Function Studies

Biodiversity-ecosystem function studies became prevalent in the context anthropogenic environmental change, where concerns for ecosystem functions arose in the face major changes in the structure and composition of ecosystems (Hooper et al., 2005). Biodiversity-ecosystem function studies have since aimed to investigate whether biodiversity can drive ecosystem functions (e.g., productivity, carbon storage, hydrology, nutrient cycling), as well as how environmental factors affect the biodiversity-ecosystem function relationship (Hooper et al., 2005; van der Plas, 2019).

The link between biodiversity and ecosystem function has been of interest to researchers for the last three decades (van der Plas, 2019). Initially, the field was dominated by grassland experiments, such as works led by Tilman, Loreau, and Hector, where the effects of simulated species loss on ecosystem functioning was observed (Tilman et al., 1996; Hector et al., 1999, Loreau & Hector, 2001). Within the first decade of biodiversity-ecosystem function research, 48% (44 of 91) of studies had an experimental component and 48% (40 of 91) of studies were conducted in a grassland system (Naeem & Wright, 2003). Conceptual, review, and model studies were also prominent at this time, making up another 43% of the literature (Naeem & Wright, 2003). In contrast, less than 10% of studies at this time were observational and less than 10% were conducted in a forest system (Naeem & Wright, 2003).

In recent years, observational studies have become more prevalent. Temperate grasslands have remained a focus of biodiversity-ecosystem function research (16%; 42 of 258 studies), but research in forest systems has largely increased (van der Plas, 2019). Temperate and boreal forests make up 18% (47 of 258 studies) of biodiversity-ecosystem function studies conducted in natural systems, and tropical or subtropical forests make up another 16% (40 of 258 studies) (van der Plas, 2019).

Although studies in natural forest systems are well represented, experimental studies on forests remain rare (Nadrowski et al., 2010). This issue is tackled by the International Diversity Experiment Network with Trees (IDENT), a network of tree-based experiments. First established in 2009, the IDENT network provides an ideal system for the study of the biodiversity-ecosystem function relationship in early tree communities (Tobner et al., 2014).

1.2 Traits and Biodiversity-Ecosystem Function

Most early biodiversity-ecosystem function work has quantified biodiversity as species diversity, by manipulating the identity and the number of species included in experimental assemblages (Naeem & Wright, 2003; Balvanera et al., 2006). The prevalence of these practices is highlighted in a meta-analysis by Balvanera et al., which found that 88% (393 of 446) of biodiversity-ecosystem function studies measured biodiversity as species richness (2006). In these studies, species richness is often assumed to be correlated to the functional diversity, i.e., the diversity of traits of the species present (Diaz & Cabido, 2001; Naeem & Wright, 2003). However, studies based on species richness cannot directly test the mechanisms of biodiversity effects because they do not link species to the roles they fill (Diaz & Cabido, 2001).

The development of diversity metrics has allowed for the use of trait values to directly quantify the functional diversity of a community (Villéger et al., 2008; Laliberté & Legendre, 2010). By using these metrics of functional diversity, studies can gain new insights into the mechanisms underlying the relationships between biodiversity and ecosystem functions. For the relationship between species richness and productivity, two underlying mechanisms have been proposed: complementarity effects and selection effects. Complementarity effects arise from positive interactions among species, such as niche complementarity and facilitation, whereby the diversity of traits across species allows each species to perform better, thus collectively increasing the productivity of the community (Grime, 1974; Grime 1998a; Loreau, 2000; Diaz & Cabido, 2001; Loreau & Hector, 2001). Complementarity effects, which are driven by trait diversity, can be measured using the functional dispersion (FDis) index. FDis highlights the complementarity effects in a community, as it represents the mean distance in

multidimensional trait space of individual species to the abundance-weighted central trait value of all species (Loreau, 2000; Laliberté & Legendre, 2010). In contrast, selection effects occur when species with specific traits outperform others in a given environment, driving the productivity of a community (Loreau, 2000). Here, greater richness increases productivity because highly productive species are more likely to be present in a community with a high initial richness (Loreau, 2000). Selection effects, which are driven by trait identity, are often measured using the community weighted means (CWM) of single traits (Loreau, 2000; Casanoves et al., 2011). The CWM of a trait is used to measure selection effects because it weighs the trait values of the species present based on their relative abundance. This method is based on the biomass ratio hypothesis proposed by Grime, which proposes that ecosystem function should be driven by the trait values of the major contributors to plant biomass (Garnier et al., 2004; Grime, 1998a).

1.3 Trait Choices

Four leaf traits and three root traits that affect the resource acquisition, growth, and architectural strategies of trees were measured for this study.

1.3.1 Leaf Area

Leaf area is an architectural trait, which varies along a spectrum of leaf size, branch size, and branching distance (Olson et al., 2009). This spectrum, known as Corner's Rules, reflects two patterns observed in the shape and structure of trees: individuals with large leaves require thicker branches, and individuals with thicker branches ramify less frequently (Corner, 1949;

White, 1983; Olson et al., 2009). In contrast, individuals with small leaves have many thin branches (White, 1983; Olson et al., 2009). The observed patterns in branching frequency likely arose to reduce self-shading, whereas those observed in branching size likely resulted to meet the greater conductive and mechanical demands of larger leaves (White, 1983; Olson et al., 2009).

In addition to its relation to total light capture, leaf area is related to other functions such as water loss and thermoregulation. The boundary layer of a leaf, which affects how much heat and gas can be diffused from the leaf to the air, varies in size depending on leaf width (Givnish 1979; Lambers et al. 2008). As the thickness of the boundary layer increases, convective and evaporative cooling become more difficult (Givnish & Vermeij, 1976). Small leaves are therefore less prone to overheating due to their thinner air boundary layers (Parkhurst & Loucks 1972; Givnish 1979). The thickness of the boundary layer also affects the rate of transpiration, with larger leaves losing more water through transpiration than smaller leaves due to their higher temperatures (Givnish 1979; Lambers et al. 2008).

1.3.2 Leaf Mass per Area

Leaf mass per area can be used to describe leaf growth strategies, as it reflects the cost of light interception at the leaf level (Westoby et al., 2002; Wright et al., 2004; Poorter et al., 2009). Leaf mass per area correlates to the leaf economic spectrum, which describes the trade-off between maximum leaf photosynthetic rate, and leaf lifespan, the period of photosynthetic return on investment (Westoby et al., 2002; Wright et al., 2004). This trade-off is based on the principle that longer leaf lifespans require stronger leaf structures, such as thicker laminae and

denser tissues (Westoby et al., 2002). Species with high leaf mass per area also tend to have lower photosynthetic rates, resulting in a slower growth rate (Lambers et al., 1998; Westoby et al., 2002; Wright et al., 2004).

1.3.3 Chlorophyll Concentration

Chlorophyll concentration is correlated with photosynthetic capacity (Lambers et al., 2008). Chlorophyll pigments in the leaves capture light during photosynthesis and transfer its excitation energy to electrons (Lambers et al., 2008). Through linear or cyclic transport, these electrons produce NADPH and energy in the form of ATP which are used for photosynthesis during the Calvin-Benson cycle (Lambers et al., 2008). Light capture increases with chlorophyll concentration, thus increasing the potential for photosynthetic capacity in leaves with higher chlorophyll concentrations (Evans, 1996).

1.3.4 Stomatal Density

Stomatal density relates to the transpiration and photosynthetic rates of plants, as stomata control the diffusion of CO₂ into the leaf for photosynthesis, and the resulting diffusion of water out of the leaf (Evans & Loreto, 2000; Lambers et al., 2008). During photosynthesis, CO₂ diffuses from the air into the mesophyll cells due to the partial pressure gradient created by the use of CO₂ during photosynthesis (Evans & Loreto, 2000). Simultaneously, water diffuses out of the leaves (Evans & Loreto, 2000). This loss of water from transpiration results in decreases in leaf temperature and water potential (Farquhar & Sharkey, 1982; Lambers et al., 2008). Transpiration rate decreased by half in plants where stomatal density was genetically

reduced by 35%, thus demonstrating the effect of stomatal density on transpiration rate (Hepworth et al., 2015).

Furthermore, at high irradiance levels, photosynthetic rate is positively related to stomatal conductance, which is determined by stomatal size and density (Lambers et al., 2008; Haworth et al., 2018). Photosynthetic rate is related to stomatal conductance because CO₂, which is assimilated into the leaf through the stomata, is required for the completion of the Calvin-Benson cycle during photosynthesis (Evans & Loreto, 2000; Lambers et al., 2008). Low quantities of CO₂ in the leaf limit the rate of functioning of Rubisco, the main enzyme of the Calvin-Benson cycle (Lambers et al., 2008). Although both stomatal size and density can affect stomatal conductance, the isolated effects of stomatal density on photosynthetic rate are highlighted in a study by Tanaka et al., where genetically increasing stomatal density increased photosynthetic rate by 30% in plants grown under constant light conditions (2013).

1.3.5 Specific Root Length

Specific root length, the investment in root length per unit of root dry mass in absorptive roots, represents the belowground resource acquisition strategies of trees (Eissenstat, 1991; Comas & Eissenstat, 2004). Variation in specific root length can result from variation in either root diameter or root tissue density, but in trees, most of the variation in specific root length results from variation in root diameter (Comas et al., 2002; Freschet et al., 2021a).

Along the collaborative gradient of root trait trade-offs, resource uptake strategies range from increasing self-acquisition by producing cheap roots for rapid soil exploration to

increasing investments into mycorrhizal symbionts (Bergmann et al., 2020). In species with ectomycorrhizal symbionts, specific root length tends to be higher, in part because the symbiosis with ectomycorrhizal fungi is less dependent on cortex area (Bergmann et al., 2020). Fast-growing species generally have a higher specific root length, as this improves self-resource acquisition by increasing the amount of soil that can be explored for resources per unit cost (Eissenstat, 1991; Comas & Eissenstat, 2004; Holdaway et al., 2011; Freschet et al., 2021b).

1.3.6 Root Tissue Density

Root tissue density, measured as root dry weight per root volume, can be used to describe aspects of root anatomy such as cell size, cell wall thickness, and the proportion of vascular tissue to parenchyma (Ryser, 1996; Freschet et al., 2021a). Root tissue density increases with cell wall stabilization, which in turn results in a lower root nitrogen content (Bergmann et al., 2020).

Root tissue density is also associated to root growth strategies (Ryser, 1996; Freschet et al., 2021a). The root tissue density of fine roots tends to be higher in slow-growing species, reflecting the slow expansion and long lifespan of their roots, and a slow resource return on investment from longer lived and well protected roots (Kramer-Walter et al., 2016; Freschet et al., 2021a; Freschet et al., 2021b; Bergmann et al., 2020).

1.3.7 Root Diameter

Root diameter is also correlated with plant growth, with fine roots of fast-growing species having smaller diameters (Comas et al., 2002; Comas & Eissenstat, 2004). Root diameter

also reflects resource acquisition strategies along the collaboration axis of trait root trade-offs (Bergmann et al., 2020). Along the collaboration axis, species which offset nutrient acquisition to their mycorrhizal symbionts have larger root diameters (Bergmann et al., 2020). These thick roots also have a higher mycorrhizal colonization percentage than thin roots (Bergmann et al., 2020). In contrast, smaller root diameters allow trees to explore more soil per investment into biomass, thus improving self-resource acquisition (Comas & Eissenstat, 2004; Bergmann et al., 2020). Root hydraulic conductivity is also higher in thinner roots, possibly due to the shorter path length for water moving into the xylem (Eissenstat, 1992).

1.3.8 Trait Summary

The traits measured for this project are summarized below (Table 1).

Table 1. Summary of measured leaf and root traits.

Trait	Definition	Units
Leaf area	Size of photosynthetic area of individual leaves	cm ²
Leaf mass per area	Carbon cost of light interception at the leaf level	g/cm ²
Chlorophyll concentration	Quantity of chlorophyll pigment present in leaf tissues	mg/m ²
Stomatal density	Number of stomata per unit of leaf area	stomata/mm ²
Specific root length	Root length investment per unit of root dry mass	m/g
Root tissue density	root dry weight per fresh root volume	g/cm ³
Root diameter	root dry weight per root volume	mm

1.4 Responses to Drought

1.4.1 Plant Responses to Drought

Reduced water availability can be lethal to trees due to its impacts on root interactions with the soil and leaf interactions with the atmosphere (Bréda et al., 2006). Plants respond to drought through structural or physiological changes, which either increase water availability or reduce water loss (Bréda et al., 2006). Plants can respond to a reduction in water availability by increasing their higher root:shoot ratio or by producing a deeper rooting system, thereby increasing water supply (Marron et al., 2002; Bréda et al., 2006; Aubin et al., 2016). Water loss can also be reduced through multiple mechanisms including, but not limited to, stomatal closure, osmotic adjustment, and increases in leaf mass per area (Abrams et al., 1994; Marron et al., 2002; Bréda et al., 2006; Poorter et al., 2009; Aubin et al., 2016).

Plants can be broadly categorized based on their responses to drought, either as drought avoidant species or drought tolerant species (Augé et al., 1998). During periods of reduced water availability, drought avoidant species can avoid tissue water deficits by reducing evaporative water losses from the stomata and increasing water uptake from the roots (Augé et al., 1998; Marron et al., 2001; Bréda et al., 2006). In doing so, drought avoidant species can maintain photosynthesis and continue to grow, however at a slower rate (Monclus et al., 2005). Drought avoidant species are also characterized by plant tissues that are sensitive to drought (Augé et al., 1998). In contrast, the plant tissues of drought tolerant species can resist periods of dehydration (Augé et al., 1998). While drought tolerant species are able to survive and recover from periods of water stress, their ability to avoid dehydration is limited (Augé et al., 1998; Bréda et al., 2006).

1.4.2 Stand Responses to Drought

While much is known on the impacts of drought on individual trees, much less is known on the effects of drought on forest stands (Clark et al., 2016). The effects of drought on forest stands are difficult to predict as multiple interacting factors, which change over time, modulate the responses of forests to drought (Skubel et al., 2015; Clark et al., 2016; Xu et al., 2018). Such factors include stand age, stand density, tree size, and tree resource allocation, which affect water uptake and water use (Klos et al., 2009; Clark et al., 2016; Xu et al., 2018).

Large trees have been found to be more vulnerable to drought stress in forests worldwide, primarily due to an increase in vulnerability with tree height (Bennett et al., 2015). Given that taller trees must transport water from the roots to the leaves along a longer transportation path, they face greater hydraulic challenges than smaller trees (Phillips et al., 2003; Bennett et al., 2015). In addition, the greater evaporative demands in the upper canopy of large trees further contribute to their vulnerability to drought (McDowell et al., 2011; Bennett et al., 2015). During periods of drought, large trees may not be able to access enough water to maintain growth, hydraulic safety, and regulate leaf temperature (Bennett et al., 2015). In mature forests, where more large trees are found, the effects of drought on tree growth and mortality are greater (Klos et al., 2009; Xu et al., 2018).

Tree mortality due to drought also appears to be more likely for seedlings and smaller trees (Condit et al., 1995; Lloret et al., 2004; Rice et al., 2004; Guarín & Taylor, 2005; Mueller et al., 2005). In these smaller trees, smaller and shallower root systems likely contribute to an increase in water stress (Rice et al., 2004; Padilla & Pugnaire, 2007). However, in contrast to a mature forest stand, juvenile plantations can maintain a more conservative water balance, a

more stable soil moisture content, and wetter soils during drought due to the lower water uptake requirements of young trees (Rabbai et al., 2020).

1.5 Life History of Studied Species

1.5.1 *Quercus rubra*

Quercus rubra (red oak) is a native semi-determinate broadleaf species, which undergoes multiple cycles of growth within a single year (Burns & Honkala, 1990; Heuret et al, 2003). These bouts of growth coincide with favourable light, water, and temperature conditions (Burns & Honkala, 1990). Each leaf flush is followed by a period of rest, during which *Q. rubra* extends its roots (Burns & Honkala, 1990; Heuret et al, 2003). The root network of *Q. rubra* is characterized by a deep taproot, providing escape from water stress (Abrams, 1990; Sander, 1990). *Q. rubra* can resprout from its root network and can therefore have stems 10-15 years younger than its root system (Burns & Honkala, 1990).

Q. rubra is classified as moderately drought and shade tolerant (Burns & Honkala, 1990; Ninemets & Valladares, 2006; Gustafson & Sturtevant, 2013; Peters et al., 2015). During drought, *Quercus rubra* exhibits smaller decreases in photosynthetic rate, a later onset of stomatal closure, and a higher water use efficiency than co-occurring tree species (Abrams, 1990; Barry et al., 2024). The water use efficiency of *Q. rubra* is likely enhanced by its thick leaves and small stomata guard cells (Abrams, 1990). The deep roots, high stomatal density, and ring-porous xylem anatomy of *Q. rubra* further contribute to its success in dry, open sites (Abrams, 1990).

1.5.2 *Acer saccharum*

Acer saccharum (sugar maple) is a native broadleaf species (Burns & Honkala, 1990). The growth of *Acer saccharum* is classified as determinate, because its shoot elongation ends once its leaves are fully developed (Gaucher et al., 2004). *A. saccharum* is very shade tolerant, with seedlings capable of surviving long periods of suppression in the understory (Burns & Honkala, 1990). In drier sites, seedling survival depends on shade as the root system needs time to develop (Burns & Honkala, 1990). Young seedlings have shallow root systems, making them sensitive to soil moisture conditions near the surface (Burns & Honkala, 1990).

A. saccharum is a drought sensitive species (Ninemets & Valladares, 2006; Gustafson & Sturtevant, 2013; Peters et al., 2015). To maximize water and nutrient uptake capacity when water availability is reduced, *A. saccharum* has been shown to increase its investment into root production, maintain a larger root biomass, and prioritize the sustenance of roots with a greater abundance of arbuscular mycorrhizal fungi (Raczka et al., 2023). Leaf shedding was also observed in *A. saccharum* following a spring drought in central Ontario in May 2010 (Stangler et al., 2016). Following this drought event, leaves from the second leaf flush were smaller, lighter, and had a lower nutrient content than the leaves initially produced (Stangler et al., 2016).

1.5.3 *Betula alleghaniensis*

Betula alleghaniensis (yellow birch) is a native broadleaf that grows continuously throughout the growing season and until leaf abscission (Burns & Honkala, 1990; Gaucher et al., 2004). While generally being considered intermediate in shade and drought tolerance, *B. alleghaniensis* requires high amounts of light, crown expansion space, soil moisture, and

nutrients to compete with its co-occurring species (Burns & Honkala, 1990; Ninemets & Valladares, 2006; Gustafson & Sturtevant, 2013; Peters et al., 2015). Under water limited conditions *B. alleghaniensis* seedlings produce significantly less biomass, highlighting its need for copious amounts of water for regeneration (Rasheed & Delagrange, 2016). *B. alleghaniensis* seedlings also have a lower photosynthetic rate when water is limited, resulting from a reduction in stomatal conductance and chlorophyll content (Rasheed & Delagrange, 2016).

1.5.4 *Larix laricina*

Larix laricina (tamarack) is a native deciduous conifer that can handle a range of unfavourable growth conditions such as moist, acidic, and cold soils (Burns & Honkala, 1990). *L. laricina* is drought intolerant and extremely shade intolerant (Burns & Honkala, 1990; Ninemets & Valladares, 2006; Gustafson & Sturtevant, 2013; Peters et al., 2015). *L. laricina* seedlings require abundant light and constant water levels for growth (Burns & Honkala, 1990). When light is abundant, *L. laricina* is one of the fastest growing conifers in northern forests (Burns & Honkala, 1990). When water availability is reduced, the stomatal conductance and the aboveground biomass production of *L. laricina* has been shown to decrease (MacDonald & Lieffers, 1990).

1.5.5 *Pinus resinosa*

Pinus resinosa (red pine) is a native evergreen conifer, which becomes established following fires (Burns & Honkala, 1990). It is a species of determinate growth, considered shade intolerant and intermediate in drought tolerance (Becker, 1987; Burns & Honkala, 1990; Jones

et al., 1991; Ninemets & Valladares, 2006; Peters et al., 2015). Water limiting conditions increase *Pinus resinosa* seedling mortality, decrease seedling growth, and decrease the rate of needle elongation (Larson, 1962; Becker, 1987). Cyclic patterns of drought and re-watering decrease the rate of needle elongation, with more severe reductions in needle growth and longer periods of recovery following the second drought cycle (Larson, 1962). In addition, extended periods of drought can reduce root production in *P. resinosa* seedlings (Becker et al., 1987).

1.5.6 *Picea glauca*

Picea glauca (white spruce) is a native evergreen conifer (Burns & Honkala, 1990). Seedlings of *P. glauca* can grow continuously when optimal growth conditions are maintained, but shoot growth becomes determinate after a few years (Burns & Honkala, 1990). *P. glauca* is considered shade tolerant, and often remains in the understory for long periods of time due to its slower growth rate relative to co-occurring species (Burns & Honkala, 1990; Ninemets & Valladares, 2006). *P. glauca* also has an intermediate tolerance to drought (Ninemets & Valladares, 2006; Gustafson & Sturtevant, 2013; Peters et al., 2015). In drier conditions, *P. glauca* produces less aboveground biomass and smaller needles (Merlin & Landhäusser, 2019).

1.6 Research Objectives

Biodiversity-ecosystem function research has largely focused on studying the relationships between biodiversity and biomass stocks or productivity (Balvanera, 2006; van der Plas, 2019). This relationship between biodiversity and productivity has been found to be

positive in forests worldwide, when biodiversity is measured as species richness (Zhang et al., 2012). The positive relationship between biodiversity and productivity is especially common in temperate forests, being observed in more than half of the studies conducted in natural temperate forests (van der Plas, 2019).

Complementarity effects and selection effects, the mechanisms thought to explain the positive species richness-productivity relationship, are based on the traits of the species present in a community. Despite this, few studies have tested which specific traits, or combinations of traits, underpin the established species richness-productivity relationship.

In addition, environmental conditions may affect when complementarity and selection effects for particular traits are at play, as well as the relative importance of the two mechanisms. The effects of environmental conditions on the species richness-productivity relationship are not well understood, as previous studies have yielded mixed results (Paquette & Messier, 2011; Zhang et al., 2012; Ratcliffe et al., 2017; Zheng et al., 2025).

For my thesis, I studied an experimental plantation of early-establishment temperate tree communities to investigate how trait diversity and composition influences community productivity under varying water availability conditions. I measured seven leaf and root traits to test which traits are responsible for the species richness-productivity relationship in temperate tree communities during stand development, and to test whether they act via the complementarity or the selection effect. I then compared the trait-productivity relationships observed in three water availability treatments to determine how the traits responsible for an increase in productivity change under different environmental conditions.

2. Examining the Effects of Traits on Early-Establishment Tree Communities Under Different Soil Water Conditions

2.1 Introduction

Global anthropogenic change is affecting the richness, composition, and abundance of co-occurring tree species in ecosystems across a range of forest types (Hooper et al., 2005; Allen et al., 2010; Vellend et al., 2013; Dornelas et al., 2014). As these changes occur, growing concern for their impact on forests has prompted research into the negative effects of species loss on forest ecosystem functions (Díaz & Cabido, 2001; Balvanera et al., 2006). One such ecosystem function, primary productivity, may be particularly impacted by the loss of species richness, as it has been shown to increase with species richness in forests around the world (Zhang et al., 2012).

Two mechanisms can explain the positive relationship between species richness and productivity: complementarity effects and selection effects. Complementarity effects arise from positive interactions among species, such as niche complementarity and facilitation, whereby the diversity of traits across species allows for more efficient resource use (Grime, 1974; Grime 1998a; Díaz & Cabido, 2001; Loreau & Hector, 2001). By using resources more efficiently, each species performs better, thus collectively increasing the productivity of the community (Loreau, 2000; Loreau & Hector, 2001). In contrast, selection effects occur when species with specific traits outperform others in a given environment, leading to the dominance of these species (Loreau, 2000). In such a case, the disproportionate dominance of highly productive species drives the productivity of a community (Loreau, 2000). Here, greater richness increases

productivity because the dominant species are more likely to be present in a community with a high initial richness (Loreau, 2000). Based on measures of species abundances, both mechanisms have been shown to occur in forests.

While both of these mechanisms relate to the species richness of a community, they are more directly linked to the traits of the species present in the community (Diaz & Cabido, 2001). Under complementarity effects, the diversity of traits across species increases community productivity, whereas under selection effects, the presence of specific trait values increases community productivity. Despite the fundamental role of traits in our understanding of these mechanisms, to our knowledge, few studies have tested the implicit assumption that traits underpin the established species richness-productivity relationship. Here, we address that gap by examining which traits drive the species richness-productivity relationship in temperate tree communities during the early stages of stand development, and whether they act via the complementarity or the selection effect.

In addition, environmental conditions may affect when complementarity and selection effects for particular traits are at play. First, the nature of the interactions among species within a community can change with environmental stress (He et al., 2013). For example, the Stress-Gradient Hypothesis postulates that interactions between species should become more facilitative and less competitive with increasing environmental stress (Lortie & Callaway, 2006; He et al., 2013). Under the Stress-Gradient Hypothesis, complementarity effects should therefore be stronger in stressful environments than in non-stressful environments. However, evidence for the stress gradient hypothesis has been mixed, with some studies reporting decreases in competitive interactions with increasing resource stress and others reporting no

changes in the interactions among species (He et al., 2013). If complementarity effects are at play in our system, the Stress-Gradient Hypothesis predicts that they will be more important in more stressful environments.

Second, environmental conditions along a stress gradient can shape species composition, as different species may be better suited for different environments (Grime, 1998b). CSR theory states that in low stress environments, highly competitive species should perform better. Here, traits that provide efficient resource capture and utilization allow these competitive species to maximize their growth and outperform neighbouring species (Grime, 1974; Grime, 1998b). In high stress environment, stress-tolerant species should perform better. Here, the growth of highly competitive species is restricted by a lack of resources, thus allowing the establishment of slower growing, stress-tolerant, species (Grime, 1974; Grime, 1998b). As environmental conditions may change which trait values are optimal, different species should therefore perform better in environments of varying stress levels, based on their traits. We thus expect the trait values underpinning selection effects to vary in different environments. However, studies examining the effects of environmental stress on the species richness-productivity relationship have yielded mixed results, and the effects of environmental stress on the traits underlying this relationship has not been investigated (Paquette & Messier, 2011; Zhang et al., 2012; Ratcliffe et al., 2017; Zheng et al., 2025).

To address these gaps, this study uses an experimental plantation of temperate tree communities in the early stages of stand development to investigate how trait diversity and composition influence community productivity under varying environmental conditions. Monocultures and three-species communities of temperate trees were established along a trait

diversity gradient to separate the effects of species richness from those of traits. To establish an environmental stress, water availability was reduced by 25% annually and 50% biennially in two-thirds of the tree communities. In each tree community, four leaf traits and three root traits known to influence plant productivity and survival under drought conditions were measured. Community productivity was estimated using measures of aboveground and belowground biomass.

The objectives of this study are twofold. First, we ask which traits are responsible for the species richness-productivity relationship in temperate tree communities during the early stages of stand development, and whether they act via the complementarity or the selection effect. If trait diversity underlies the species-richness productivity relationship, then biomass will increase with trait diversity in the three-species communities. If trait composition underlies the species-richness productivity relationship, communities with a high abundance of specific trait values associated with increased productivity will have a higher biomass. Second, we ask how do complementarity and selection effects and their underlying traits change in environments with different water availabilities by assessing which traits are associated with productivity in each environment.

Climate models for eastern Canada project an increase in temperature, while precipitation will remain constant (IPCC, 2023). Under these conditions, plant productivity will be limited as a result of increased respiration costs and decreased water availability (Bréda et al., 2006). Here, we focus on forest stands during the establishment period because mortality rates are often high during the seedling phase of tree growth (Fenner, 1987). As a result, the early years of stand development can modify future rates of nutrient cycling or biomass

accumulation, and shape future forest structure, composition and function (Lutz & Halpern, 2006; Williams et al., 2017). Understanding how traits act to promote and maintain the productivity of forest communities during stand establishment in environments with different water availabilities will help inform the development of forest conservation and management in a time of changing climate (van Mantgem et al., 2009).

2.2 Methods

2.2.1 Study Site

This study was conducted at the IDENT-Outaouais plantation, established in 2020, near Notre-Dame-de-la-Paix, Qc, Canada (45.7742, -75.0066). This site is a repurposed agricultural field, characterized by average temperatures of 16 °C and total precipitations of 578 mm during the growing season (May to October), and a sandy loam soil (Fig. 1).



Figure 1. Aerial view of the IDENT-Outaouais plantation in September 2024.

Following the initial establishment of the experiment, seedlings were watered for two years, before the implementation of a water exclusion system. To further help the establishment of the seedlings, herbaceous vegetation was manually removed during the growing season from 2020 until the end of 2024, and the study area was fenced to reduce mammalian herbivory.

2.2.2 Experimental Design

Following a similar design to other plantations in the IDENT network, this study site is composed of replicated high-density tree communities. Each community contains a 7x7 assemblage of temperate trees, planted as seedlings at regular intervals of 0.5 m. The close-proximity design was implemented to promote interactions among individuals at early stages of their development.

Six native temperate tree species (*Acer saccharum* Marsh, *Betula alleghaniensis* Britton, *Larix laricina* (Du Roi) K. Koch, *Picea glauca* (Moench) Voss, *Pinus resinosa* Ait., and *Quercus rubra* L.) from local provenances in Maniwaki, Qc, and in Berthierville, Qc, were planted in seven three-species mixes. The community compositions of the three-species mixes were selected to form a gradient of functional diversity using traits from the TRY dataset, with communities where species have similar traits at the low-diversity end of the gradient and those where species have the most dissimilar traits at the high-diversity end (Fig. 2) (Kattge et al., 2011). Later, the local trait values were used to determine the realized diversity gradient among mixtures. By maintaining a functional diversity gradient while keeping species richness fixed, the effects of trait diversity could be separated from the effects of species richness. Reference monoculture communities for five of the listed species were also included in the study. Due to a limited supply of *L. laricina* seedlings at the time of planting, it could not be planted in monoculture. Overall, 12 unique communities (7 three-species mixes and 5 monocultures) were planted in this experiment (Fig. 2).

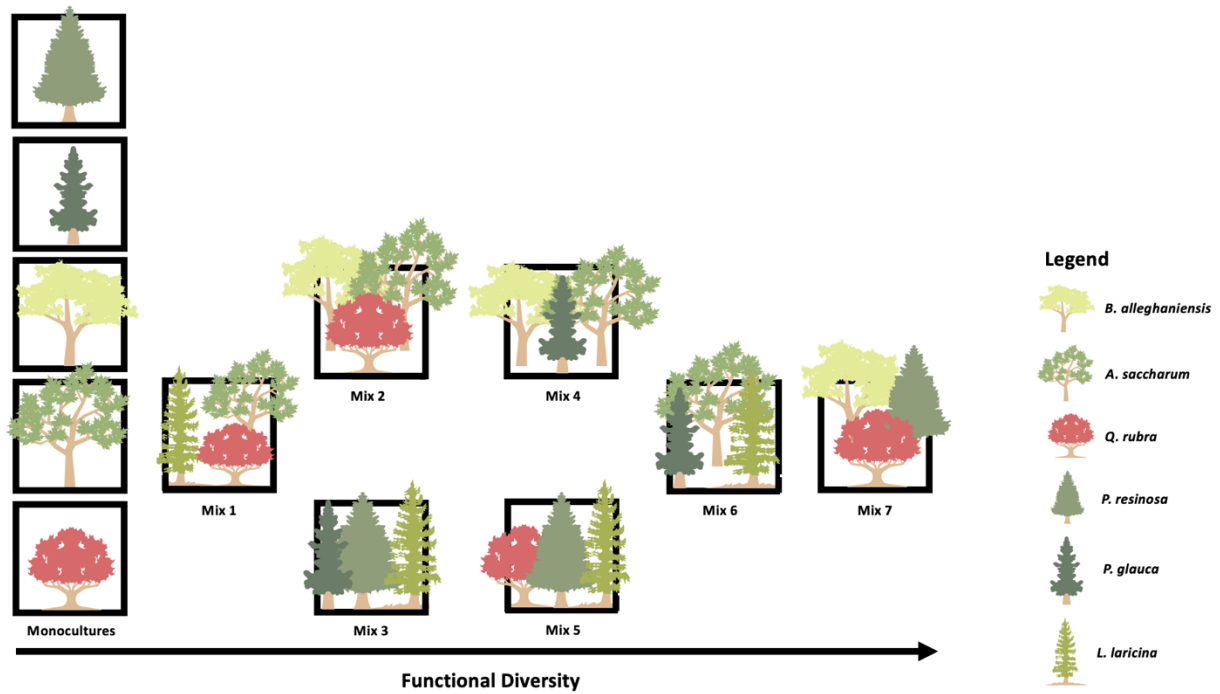


Figure 2. Three-species and monoculture temperate tree communities established along a functional diversity gradient in the IDENT-Outaouais experiment. The functional diversity gradient was established based on trait values from the TRY dataset (Kattge et al., 2011). Three-species mix compositions are as follows: Mix 1, *L. laricina*, *Q. rubra*, *A. saccharum*; Mix 2, *B. alleghaniensis*, *Q. rubra*, *A. saccharum*; Mix 3, *P. glauca*, *P. resinosa*, *L. laricina*; Mix 4, *B. alleghaniensis*, *P. glauca*, *A. saccharum*; Mix 5, *Q. rubra*, *P. resinosa*, *L. laricina*; Mix 6, *P. glauca*, *A. saccharum*, *L. laricina*; Mix 7, *B. alleghaniensis*, *Q. rubra*, *P. resinosa*.

2.2.3 Water Exclusion Treatment

A water availability gradient was implemented using ground level gutters placed between trees to remove rainwater. Three water availability treatments were applied: a control (no precipitation removal), a press water removal stress (25% precipitation removal annually), and a pulse water removal stress (50% precipitation removal biennially). The press treatment

simulates a low but persistent water limitation scenario, whereas the pulse treatment represents a stronger but annually variable water limitation scenario. Over time, the cumulative amount of water removed in each treatment is the same (50% removed over two years). Each combination of community composition and treatment was replicated three times and spatially arranged into blocks, forming a total of 108 communities (36 control, 36 press, 36 pulse) (Fig. 3).

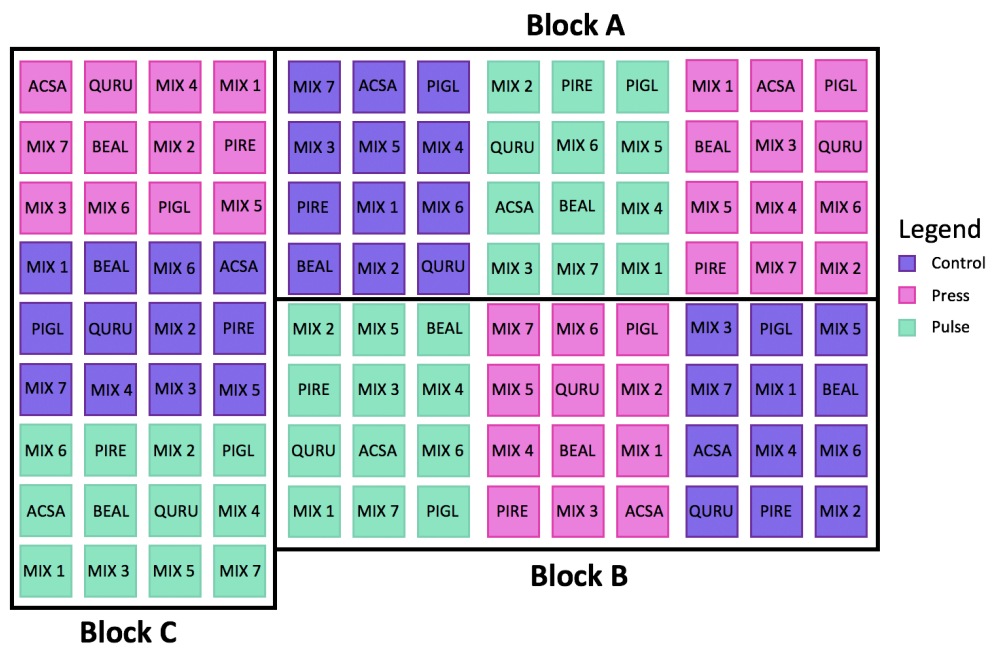


Figure 3. Spatial distribution of tree communities in the IDENT-Outaouais experiment.

Replicates were applied in three blocks of 36 plots, delineated by black lines. Each combination of community composition and water exclusion treatment is repeated once within each block. Plots in the control treatment are indicated in purple, plots in the press treatment are indicated in pink, and plots in the pulse treatment are indicated in green. In total, the experiment is composed of 108 plots.

To quantify the effects of the water exclusion treatments, soil moisture content was measured weekly from June to October 2024. These measurements were taken at least three days after a precipitation event to allow the soil to return to field capacity. Soil moisture content was recorded in nine locations per community to account for spatial variability within plots, with three measurements taken under the water exclusion gutters, three measurements taken along the water exclusion gutters, and three measurements taken away from the gutters. All soil moisture content measurements were taken integrating the top 5 cm of soil, using a FieldScout TDR 350 soil moisture meter.

2.2.4 Leaf Trait Measurements

Leaf trait measurements were collected from the nine centrally located trees in each community (n=972) between July 3rd, 2024 and August 15th, 2024 (Appendix 1). From these individuals, a sun exposed lateral branch was randomly selected and cut from the top third of the tree crown. When individuals were shaded, one of the most sun exposed branches was cut. Branches were collected in the morning and stored on ice in plastic bags with damp paper towels, until processing the same afternoon.

Four leaf traits were measured on each branch: Leaf area, leaf mass per area, chlorophyll concentration, and stomatal density. These traits were chosen as they are known to reflect the resource acquisition and the architectural strategy of trees and have been shown to be affected by drought conditions. Leaf area is related to the light capture, water loss, and thermoregulation of trees (Givnish 1979; Lambers et al. 2008; Olson et al., 2009). In response to drought, some tree species have been shown to produce smaller leaves (Graves, 1994; Timbal

& Lefebvre, 1995; Merlin & Landhäusser, 2019). Leaf mass per area, which reflects the carbon cost of light interception at the leaf level (Wright et al., 2004), has been shown to be higher among species in water limited environments (Wright & Westoby, 2002; Poorter et al., 2009). Chlorophyll concentration affects light capture and is therefore correlated with photosynthetic capacity (Lambers et al., 2008). In *B. alleghaniensis*, chlorophyll concentration decreases during drought (Rasheed & Delagrang, 2016). Stomatal density affects gas exchange, which then affects transpiration and photosynthetic rates (Evans & Loreto, 2000; Lambers et al., 2008). Within an individual, stomatal density has been shown to be lower in leaves produced in dry conditions than in leaves produced when soil moisture was high (Metwally et al., 1971).

Leaf trait measurements were collected differently for broadleaf species and conifer species. On broadleaf species, leaf area (cm^2) and leaf mass per area (g/cm^2) were measured without the petiole on three intermediate sized and relatively intact leaves, which were selected at random. Leaves were scanned on an Epson Perfection V850 Pro scanner at 300 dpi. The leaf area was determined from these scans in WinFolia (Version: 2020a Pro; Regent Instruments Inc., 2020). After scanning, leaves were dried at 60 °C until their dry weight stabilized. The dried leaves were then weighed using an ME403 precision balance (Mettler Toledo). Leaf mass per area was obtained by dividing the dry weight (g) of the leaves by the fresh leaf area (cm^2).

The chlorophyll concentration (mg/m^2) and stomatal density (stomata/ mm^2) of broadleaves were measured on a second set of three randomly selected leaves. On each of the three leaves, chlorophyll concentration was recorded using a CCM-300 chlorophyll content

meter from the chlorophyll fluorescence ratio F_{735}/F_{700} (Opti-Sciences; Gitelson et al., 1999) in four places (top left, top right, bottom left, bottom right) on the adaxial side of the leaf. A chlorophyll concentration value was obtained for each individual by averaging the 12 measurements. Following chlorophyll concentration measurements, a stomatal density imprint was made on the abaxial side of each leaf using clear nail polish and clear tape (n=3; Grant & Vatnick, 2004). To account for spatial variability within the leaf, imprints were taken in the top right, bottom left, and in the middle of the leaves. The stomatal density imprints were later photographed at x100 magnification (Leica DM1000 LED; Teledyne Lumenera INFINITY1-1M digital camera). On each stomatal density image, ImageJ was used to delineate a fixed area ($0.03 \text{ mm}^2 \times 0.04 \text{ mm}^2$) in a random location where stomata were clearly identifiable, and all stomata within the area were counted. For each individual, stomatal density was measured as the average number of stomata of the three imprints divided by the size of the fixed area (mm^2).

On conifer species, all leaf traits were measured on twenty needles taken, at random, from the top side of the branch. First, five bunches of four needles were formed to measure chlorophyll concentration. The needles were positioned so chlorophyll concentration could be measured on the adaxial side of the needles. Chlorophyll concentration was recorded once per set of needles using a CCM-300 chlorophyll content meter (Opti-Sciences; Gitelson et al., 1999). Next, the abaxial side of the needles was scanned at 300 dpi to measure leaf area, and a subset was scanned again at 4800 dpi to measure stomatal density, using an Epson Perfection V850

Pro scanner. The rest of the protocol for measuring leaf area and leaf mass per area on conifers was the same as described above for broadleaves.

Stomatal density scans were processed in ImageJ (Version 1.53), where a fixed area was delineated ($0.05 \text{ mm}^2 \times 0.05 \text{ mm}^2$) and all stomata within were counted. The fixed area was positioned near the mid-length of the needle and where stomata were clearly identifiable. For each individual, stomatal density was measured as the average number of stomata across three counts, divided by the fixed area (mm^2).

2.2.5 Root Trait Measurements

For each species three root traits were measured: specific root length, root tissue density, and root diameter. These traits were chosen as they are known to describe the important aspects of the architectural, growth, and resource acquisition strategies of trees (Comas & Eissenstat, 2004; Comas et al., 2013). Specific root length, the investment in root length per unit of root dry mass, is generally higher in fast-growing species (Eissenstat, 1991; Comas & Eissenstat, 2004; Holdaway et al., 2011; Freschet et al., 2021b). These species produce cheap roots for rapid soil exploration and generally invest less carbon into their mycorrhizal symbionts (Bergmann et al., 2020). Root diameter is negatively correlated to specific root length, with thin roots being associated to high specific root lengths (Comas et al., 2002; Comas & Eissenstat, 2004). As a result, fast-growing species tend to have smaller root diameters (Comas et al., 2002; Comas & Eissenstat, 2004). Along the collaboration axis of root trait trade-offs, species which acquire nutrients themselves have smaller root diameters (Bergmann et al., 2020). Root tissue density, the root dry weight per root volume (Freschet et al., 2021a), varies

along a fast-slow growth axis (Bergmann et al., 2020). Slow growing species typically have higher root tissue densities, reflecting a slow resource return on investment from longer lived and well protected roots (Kramer-Walter et al., 2016; Freschet et al., 2021a; Freschet et al., 2021b; Bergmann et al., 2020).

High specific root lengths are associated with the maintenance of plant productivity during drought (Eissenstat, 1991; Comas et al., 2013). Likewise, thin roots and high root tissue densities have been observed in plants growing in dry conditions, and following periods of drought (Ryser, 1996; Comas et al., 2002; Comas et al., 2013; Lozano et al., 2022; Holdaway et al., 2011). However, the responses of root traits to drought are highly variable and species dependent (Brunner et al., 2015; Lozano et al., 2020).

Root traits were measured at the species level in each community. Within the area delineated by the central 9 trees, three soil cores ($\varnothing$ 10 cm x 14 cm) were collected between July 23rd, 2024 and August 13th, 2024. Soil cores were taken at the center point between four adjacent trees, so that each species was equally represented across the three cores (Appendix 1). After collection, soil cores were bagged and kept frozen at -60 °C until processing.

Before being processed, soil cores were thawed for 12 hours at 4 °C. Thawed soil cores were soaked in a bucket of water for up to three hours to gently remove some of the soil. Next, the root water was poured through a series of sieves. First, over a 5 mm sieve, then over a 2 mm sieve. Roots retained in the sieves were gently hosed to remove more soil and debris, then resuspended in a bucket of clean water. Once the roots were mostly clean, they were transferred to a tray of water for further cleaning and sorting. Organic matter, debris, and grass

roots were removed using tweezers, and the tree roots were sorted by species based on their morphology.

For trait measurements, ten sets of live fine roots from 1st to 3rd order were selected at random for each species. These roots were scanned in a clear tray of deionized water at 1200 dpi on a backlit Epson Perfection V850 Pro scanner to avoid shadows. The fine roots were dried at 60 °C until their dry weight stabilized and weighed using an XSR205DU analytical scale (Mettler Toledo).

Root scans were then processed in Rhizovision (Version 2.0.3), to obtain measurements of average root diameter (mm), root length (mm), and root volume (mm³). From the measurements obtained, root tissue density was calculated as the dry weight divided by the volume of fresh root (g/cm³), and specific root length was calculated as the length of root divided by its dry weight (m/g).

2.2.6 Biomass Measurements

At the end of the 2024 growing season, the height (cm) and basal diameter (cm) of each tree was measured. Using these values, aboveground biomass was estimated following allometric equations for temperate tree species, where biomass is calculated as the square of the basal diameter multiplied by height and by wood density ($D^2 \times H \times WD$) (Tobner et al., 2016; Williams et al., 2017). Wood density values specific to Montreal were obtained from Belluau et al., (2021) and used in the calculations of aboveground biomass.

The total aboveground biomass of each community was measured as the sum of the aboveground biomasses of the nine central trees. The total belowground biomass of each

community was measured as the sum of the dry weight of all tree roots across the three soil cores collected in each community.

2.2.7 Testing Complementarity Effects

Univariate and multivariate measures of complementarity effects were obtained for each community. For single traits, the variance in trait values within a community was used as the metric for complementarity effects. Here, complementarity increases with variance. For multiple traits, Functional Dispersion (FDis) values was used as the metric of complementarity. FDis was calculated for each community as:

$$\mathbf{FDis} = \frac{\sum a_j z_j}{\sum a_j} \quad \text{Eqn. 1}$$

where a_j is the abundance of species j and z_i is the Euclidean distance of species j to the community's weighted trait centroid (Laliberté & Legendre, 2010). In turn, the weighted centroid of each community is the abundance-weighted mean multivariate trait value, calculated as:

$$\mathbf{centroid} = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j} \quad \text{Eqn. 2}$$

where a_j is the abundance of species j , and x_{ij} is the trait value of species j for trait i (Laliberté & Legendre, 2010). Calculations were done using the FD package in R (Laliberté & Legendre, 2010; Laliberté et al., 2014). In each community, FDis was calculated using all seven measured traits, as well as with each possible combination of trait pairs. Here, complementarity increases with FDis.

2.2.8 Testing Selection Effects

Univariate and multivariate measures of selection effects were obtained for each community. To quantify selection effects for a single trait, community weighted distance to the ‘best’ trait values (CWD) was measured following this equation:

$$\text{CWD} = \sum_{j=1}^n p_j |b_j - x_j| \quad \text{Eqn. 3}$$

where p_j is the relative abundance of species j , b_j is the reference trait value from the most productive species in the monocultures of the experiment, and x_j is the trait value of species j .

This equation was derived from the calculation of community weighted mean presented in Lavorel et al. (2008). The CWD metric allowed us to compare the trait values in the community to those of the most productive conifers and broadleaves in the system, thus indicating selection for that particular trait value.

Given the strong life history, anatomical, and physiological differences between angiosperms and gymnosperms, a different ‘best’ trait value was selected for each taxa. The ‘best’ trait values for broadleaves were taken from *B. alleghaniensis*, as this was the most productive broadleaf in monoculture (Appendix 2). To determine the ‘best’ value for each trait, an average was taken across *B. alleghaniensis* individuals in monoculture for each treatment. The ‘best’ trait values for conifers were taken from *L. laricina*, as this was the most productive conifer in the experiment (Appendix 2). Since there were no *L. laricina* monocultures, the ‘best’ trait values were obtained by averaging the traits of all *L. laricina* individuals in each treatment. This was possible because the mean trait values of *L. laricina* did not differ based on community composition. This method was not used for *B. alleghaniensis* because some of its traits varied with community composition (Appendix 3).

To quantify selection effects for multiple traits, the Functional Dispersion index was modified to be centered around the weighted community best trait value rather than the weighted trait centroid of the community. This provided us with a multivariate equivalent (FDis_{CWD}) to the community weighted distance from the ‘best’ trait value used previously. We calculated FDis_{CWD} in the following way:

$$\text{best trait centroid} = [c_{bi}] = \frac{\sum a_j b_{ij}}{\sum a_j} \quad \text{Eqn. 4}$$

$$\text{FDis}_{CWD} = \frac{\sum a_j z_{bj}}{\sum a_j} \quad \text{Eqn. 5}$$

where a_j is the abundance of species j , b_{ij} is the best trait value of species j for trait i , and z_{bj} is the Euclidean distance of species j to the multivariate ‘best trait’ centroid. In each community, FDis_{CWD} was calculated using all seven measured traits, as well as with each possible combination of trait pairs. Here, lower FDis_{CWD} values represent convergence towards the traits of the most productive species. Thus, selection increases as FDis_{CWD} decreases.

2.2.9 Statistical Analyses

All statistical analyses were performed in R (Version 4.5.1; R Core Team, 2025). To determine which angiosperm and gymnosperm planted in the experiment were most productive in monoculture, a two-way ANOVA was conducted to test the effects of species, treatment, and their interaction on aboveground biomass (Appendix 2). When significant effects were detected, a post-hoc TukeyHSD was used to identify pairwise differences among groups. Two-way ANOVAs with post-hoc TukeyHSD tests were also conducted to examine the effects of species, treatment, and their interaction on trait values.

To determine if water availability differed across water exclusion treatments, differences in the mean, minimum, maximum, and variance in percent volumetric water content (VWC%) across communities in each treatment was tested using one-way ANOVAs. Using the lme4 and emmeans packages in R, changes in percent volumetric water content through time were compared using a linear mixed-effects model (LME) with a post-hoc estimated marginal means test (EMM), predicting VWC% as a function of treatment, date, and their interaction, and with plot ID specified as a random effect to account for repeated measures within plots (Bates et al., 2015; Lenth, 2025). The mean aboveground and belowground biomass produced in each treatment was compared using a one-way ANOVA. One-way ANOVAs and post-hoc TukeyHSD tests were also used to assess whether the treatments had an effect on species traits. More tests used to describe the water exclusion treatments, including ANOVA and post-hoc TukeyHSD tests comparing the mean VWC% based on community composition and calculations of the relative extractable soil water to quantify drought intensity, are outlined in the supplementary materials (Appendix 4).

To determine if biomass increased with diversity due trait complementarity in each treatment, we tested whether aboveground and belowground biomass increased with the variance of each trait and with FDis using linear regressions. To determine if biomass increased with diversity due to selection for the ‘best’ traits in each treatment, we tested whether aboveground and belowground biomass increased with CWD and with FDis_{CWD}. We verified model assumptions using the procedure described in Zurr & Ieno (2016). When model assumptions of homoscedasticity were not met, independent variables were log-transformed or square root transformed as needed to produce homoscedasticity. The Benjamini-Hochberg

procedure was used to control the experiment-wide false discovery rate and calculate adjusted p-values.

2.3 Results

2.3.1 Trait Values of the Most Productive Species

Of the broadleaves, *B. alleghaniensis* was the most productive in monoculture in all treatments (Appendix 2). Compared to *A. saccharum*, *B. alleghaniensis* consistently had a lower stomatal density and smaller leaves (Two-way ANOVA & TukeyHSD post-hoc, SD-All: $p < 0.001$, LA-All: $p < 0.001$), and had lower chlorophyll concentrations in the press and the pulse treatments (Press: $p = 0.002$, Pulse: $p < 0.001$, Control: $p = 0.143$; Fig. 4). Compared to *Q. rubra*, *B. alleghaniensis* had a lower stomatal density in all treatments (All: $p < 0.001$), and smaller leaves in the control treatment (Press: $p = 0.983$, Pulse: $p = 0.135$, Control: $p = 0.011$; Fig. 4). Chlorophyll concentration in *B. alleghaniensis* was lower than in *Q. rubra*, but this difference was not significant in any treatments (Press: $p = 0.360$, Pulse: $p = 0.694$, Control: $p = 1.000$; Fig. 4). *B. alleghaniensis* also had smaller leaf mass per area values than *A. saccharum* and *Q. rubra* but this difference was not significant in any treatments (Press: $p = 0.863$, Pulse: $p = 0.661$, Control: $p = 0.923$; Fig. 4).

For root traits, *B. alleghaniensis* had intermediate-sized, but relatively small, root diameters, which were smaller than in *A. saccharum* in all treatments (All: $p < 0.001$) and larger than in *Q. rubra* in the press and pulse treatments (Press: $p = 0.002$, Pulse: $p = 0.017$, Control: $p = 0.076$; Fig. 4). The root tissue density of *B. alleghaniensis* was higher than *A. saccharum* in the pulse and the control treatments (Press: $p = 0.154$, Pulse: $p < 0.001$, Control: $p < 0.001$), and

lower than *Q. rubra* in all treatments (Press: $p = 0.025$, Pulse: $p < 0.001$, Control: $p < 0.001$; Fig. 4). *B. alleghaniensis* also had relatively high, but intermediate-sized specific root lengths, which were greater than in *A. saccharum* across all treatments (All: $p < 0.001$), and lower than in *Q. rubra* in the press treatment (Press: $p = 0.004$, Pulse: $p = 0.562$, Control: $p = 1.000$; Fig. 4).

Of the conifers, *L. laricina* was the most productive in all treatments (Appendix 2). *L. laricina* had a higher chlorophyll concentration (Press: $p = 0.013$, Pulse: $p < 0.001$, Control: $p < 0.001$), stomatal density (All: $p < 0.001$), and root diameter than *P. glauca* in all treatments (All: $p < 0.001$; Fig. 4). Compared to *P. resinosa*, *L. laricina* had a higher chlorophyll concentration in the press and the pulse treatments (Press: $p = 0.001$, Pulse: $p < 0.001$, Control: $p = 0.073$), greater stomatal density in all treatments (All: $p < 0.001$), and larger root diameters in the press and the control treatments (Press: $p = 0.029$, Pulse: $p = 0.399$, Control: $p < 0.001$; Fig. 4). *L. laricina* had a lower leaf mass per area than both *P. glauca* and *P. resinosa* in all treatments (All: $p < 0.001$). Root tissue density of *L. laricina* was lower than *P. glauca* in the pulse and in the control treatments (Press: $p = 0.262$; Pulse: $p = 0.052$, Control: $p = 0.007$; Fig. 4). *L. laricina* had relatively small, intermediate-sized needles relative to the other conifers, although needle size did not differ significantly among treatments (All: $p = 1.000$).

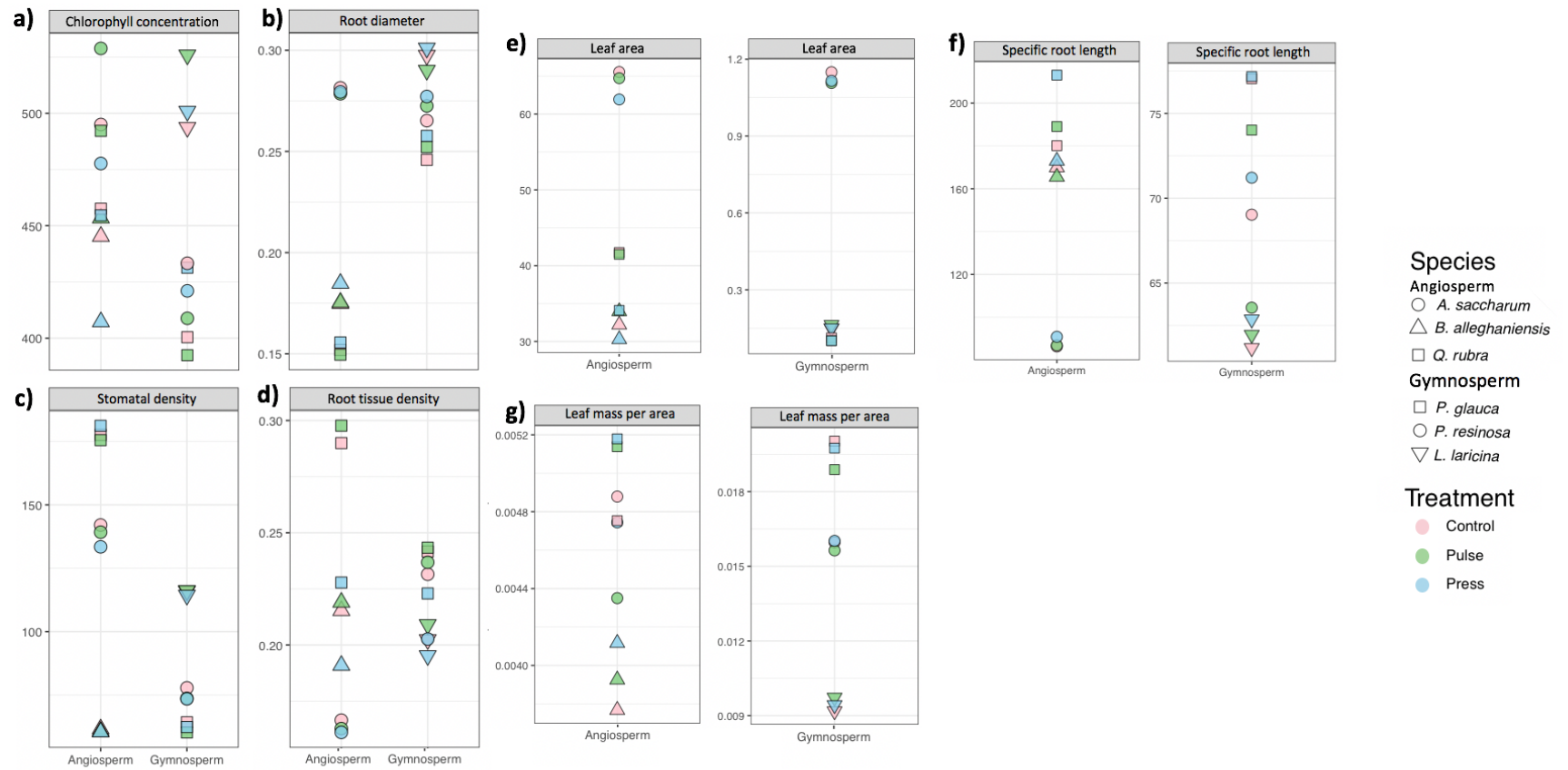


Figure 4. Differences in trait values across individuals of each species and water exclusion treatments. The angiosperms and the gymnosperms were included in the same panel when scales were comparable and in separate panels when scales were not comparable. The dominant species for each clade are identified by triangles. Trait differences are illustrated in panels a to g: Panel a) chlorophyll concentration (mg/m^2), panel b) root diameter (mm), panel c) stomatal density ($\text{stomata}/\text{mm}^2$), panel d) root tissue density (g/cm^3), panel e) leaf area (cm^2), panel f) specific root length (m/g), and panel g) leaf mass per area (g/cm^2).

2.3.2 Effects of Water Exclusion Treatments

Of the water exclusion treatments, only the pulse treatment was drier than the control, although this difference was marginal. On average, percent soil volumetric water content (VWC%) in the pulse treatment was 14.86%, which is 20% and 16% drier than the press (mean VWC% = 18.16%) and the control treatments (mean VWC% = 17.36%) (ANOVA & TukeyHSD post-hoc, Press: $p = 0.020$, Control: $p = 0.1$; Fig. 5). VWC% in the press and the control treatments were similar, with soils in the press treatment containing 5% more water than the control ($p = 0.785$; Fig. 5). Overall, all treatments followed the same temporal trends and maintained consistent VWC% differences during the growing season (LME & EMM post-hoc, $p < 0.001$; Fig. 6). Throughout the summer, the pulse treatment maintained a mean VWC% between 2.30 and 4.92 percentage points lower than the mean of the wettest treatment recorded on a given day ($p < 0.001$; Fig. 6). On average, this represents a 26% difference in VWC% between the pulse and the wettest treatment, whereas the press and the control consistently did not differ ($p < 0.001$; Fig. 6).

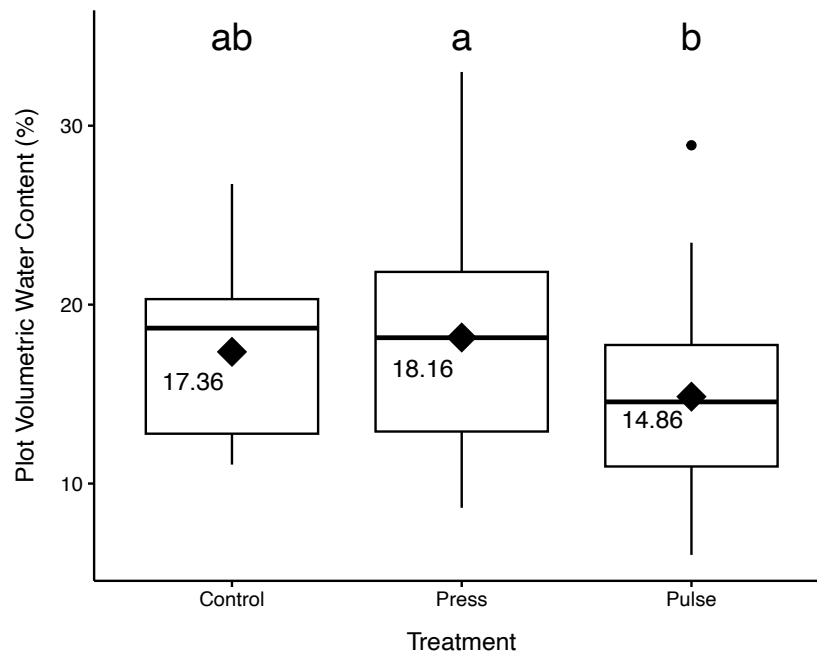


Figure 5. Differences in the percent volumetric water content of each treatment over the 2024 summer. All volumetric water content measurements taken at least three days after a rain event were included in the comparisons. For each day of measurement, percent volumetric water content within a community plot was averaged. Plot volumetric water content therefore represents the mean amount of soil water content in each plot. Across all plots, the average volumetric water contents were significantly different between the pulse and the press treatments ($p = 0.020$), marginally different between the pulse and the control treatments ($p = 0.1$), and not different between the press and the control treatments ($p = 0.785$).

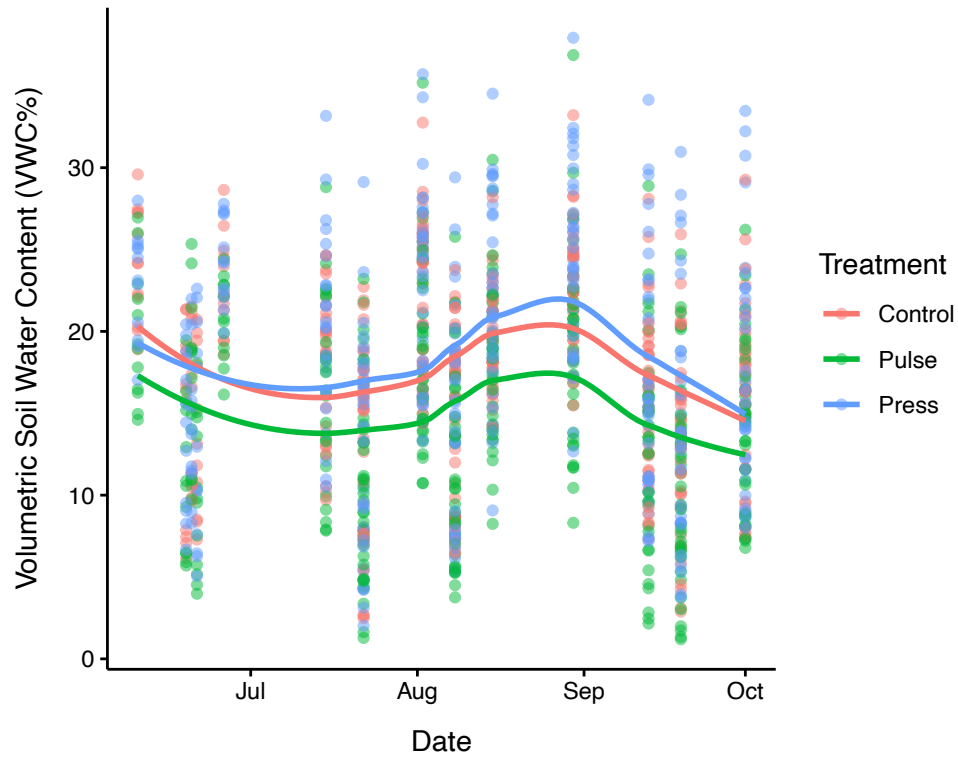


Figure 6. Change in percent volumetric soil water content during the growing season, by treatment. All treatments followed the same temporal trends and maintained consistent percent volumetric water content differences throughout the growing season. The percent volumetric soil water content in the pulse treatment was consistently lower than in the control and the press treatments ($p < 0.001$).

The water exclusion treatments did not affect the amount of aboveground and belowground biomass produced by trees (ANOVA, aboveground: $F(2, 969) = 0.531$, $p = 0.588$, belowground: $F(2, 699) = 1.314$, $p = 0.27$; Fig. 7). However, there was an effect of treatment on certain trait values, which varied among species. Following a Benjamini-Hochberg correction to control the false discovery rate, chlorophyll concentration values differed across treatments in *B. alleghaniensis* monocultures, with chlorophyll concentration being higher in the pulse treatment than in the press and the control treatments (ANOVA & Tukey post-hoc, Press: $p = 0.009$, Control: $p = 0.007$; Fig. 8). Root tissue density values differed across treatments in *P. resinosa* monocultures, with root tissue density being lower in the press treatment than the pulse and the control treatments (ANOVA & TukeyHSD post-hoc, Pulse: $p = 0.002$, Control: $p = 0.002$; Fig. 8). These differences in trait values reflect the plastic response of the species to the treatments.

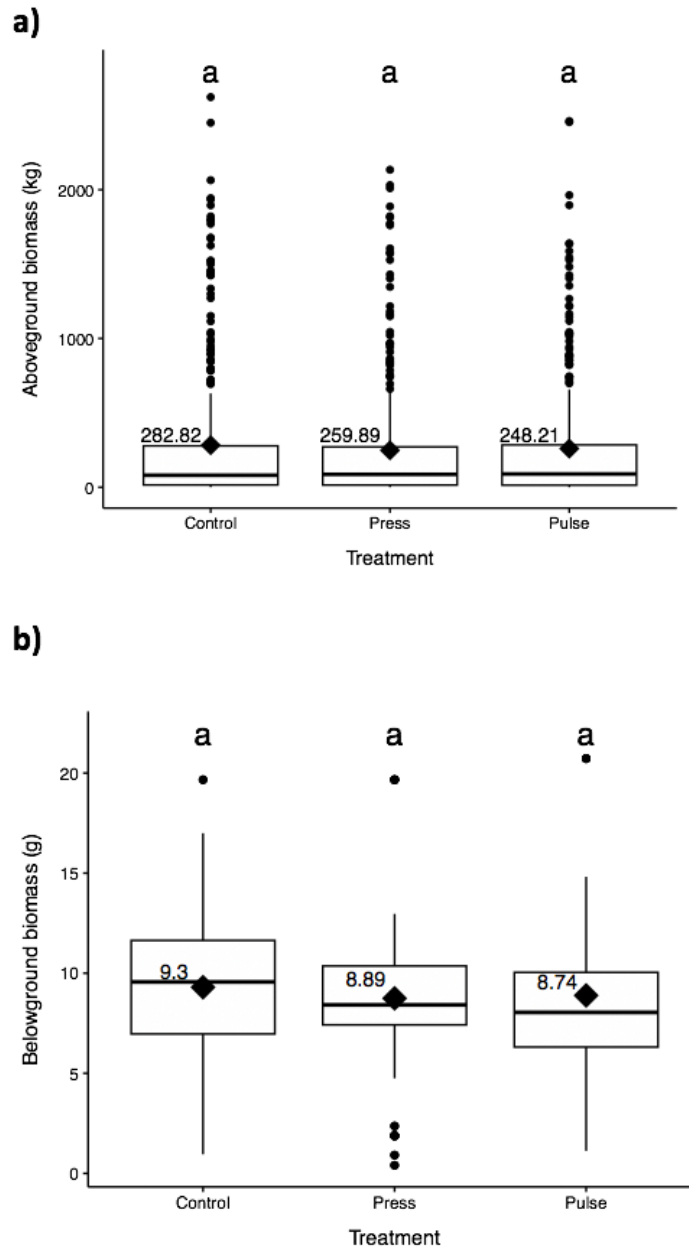


Figure 7. Differences in plot biomass across treatments. Panel a) illustrates the effects of the pulse, press, and control treatments on aboveground biomass, in kilograms. Aboveground biomass for each tree was calculated as height x diameter² x wood density. The total aboveground biomass of the trees in 2024 did not differ across treatments ($F(2, 969) = 0.531$, $p = 0.588$). Panel b) illustrates the effects of the pulse, press, and control treatments on

belowground biomass, in grams. Belowground biomass for each plot was calculated as the total dried weight of tree roots collected from three soil cores. The belowground biomass of the trees in 2024 did not differ across treatments ($F(2, 699) = 1.314$, $p = 0.27$).

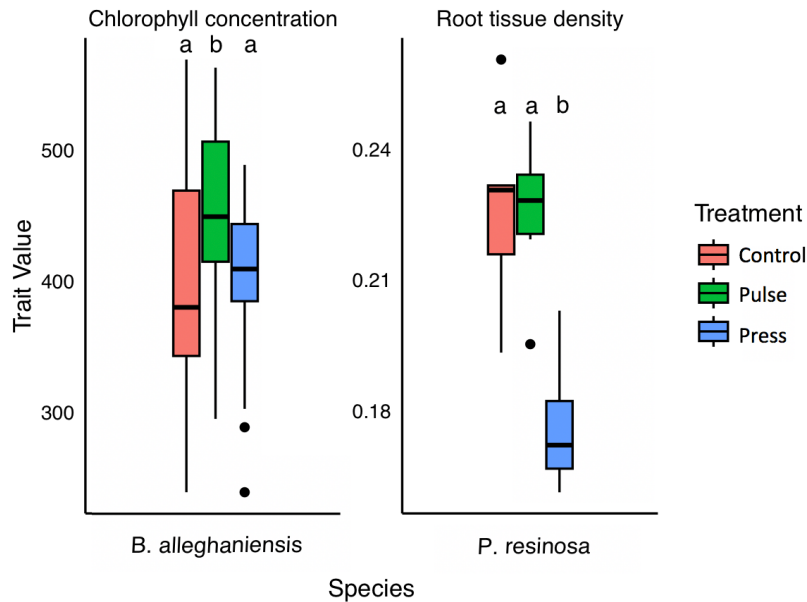


Figure 8. Differences in trait values of monoculture communities where trait plasticity was observed. The trait values of monocultures were grouped by treatment for comparisons. Three-species communities were not included, to isolate the effects of the water exclusion treatments from those of neighbouring species. In *B. alleghaniensis* monocultures, chlorophyll concentration was higher in the pulse treatment than in the press and the control treatments (Press: $p = 0.009$, Control: $p = 0.007$). In *P. resinosa* monocultures, root tissue density was lower in the press treatment than in the pulse and the control treatments (Pulse: $p = 0.002$, Control: $p = 0.002$).

2.3.3 Which Traits and Mechanisms Affect Community-Level Biomass?

We found no evidence of complementarity effects in this system because neither metric of community productivity increased with community trait variance or with FDis. We also found no evidence of univariate selection effects in this system because neither metric of community productivity decreased with CWD. In contrast, multivariate analyses with aboveground biomass provided evidence of selection effects (Table 2).

Table 2. Summary of significant and marginally significant results. Results in italics are marginally significant.

Treatment	Trait	Biomass metric	R ²	Adjusted p-value
Press	FDis _{CWD} Leaf area & Leaf mass per area	Aboveground biomass	0.45	0.027
Press	Log(FDis _{CWD} Leaf area & Stomatal density)	Aboveground biomass	0.46	0.027
Control	<i>Log(FDis_{CWD} Leaf area & Stomatal density)</i>	<i>Aboveground biomass</i>	0.35	0.055
Pulse	<i>Log(FDis_{CWD} Leaf area & Stomatal density)</i>	<i>Aboveground biomass</i>	0.32	0.075
Control	<i>Log(FDis_{CWD} Leaf mass per area & Stomatal density)</i>	<i>Aboveground biomass</i>	0.30	0.095
Pulse	FDis _{CWD} Chlorophyll concentration & Specific root length	Aboveground biomass	0.60	0.039

Control	Log(Stomatal density & Specific root length)	Aboveground biomass	0.53	0.049
Pulse	<i>Log(FDis_{CWD} All traits)</i>	<i>Aboveground biomass</i>	0.29	0.098

In multivariate analyses, aboveground biomass decreased with the community weighted distance to best of trait pairs that included leaf area in the press treatment. Here, aboveground biomass decreased threefold with multivariate distance to the best leaf mass per area and leaf area values (FDis_{CWD} for LA & LMA) (Linear model, $R^2 = 0.45$, $p = 0.027$; Fig. 9). Aboveground biomass also decreased threefold with the log of the distance to the best trait value for the combination of leaf area and stomatal density (log FDis_{CWD} for LA & SD) (Linear model, press: $R^2 = 0.46$, $p = 0.027$; Fig. 9).

In addition, other trait pairs which included specific root length were under selection. In the pulse treatment, communities where specific root length and chlorophyll concentration were closest to the best value, aboveground biomass was four times higher than in communities which diverged most from the best specific root length and chlorophyll concentration values (log FDis_{CWD} for CHL & SRL) (Linear model, $R^2 = 0.60$, $p = 0.039$; Fig. 10). In the control, aboveground biomass decreased fourfold with the log of the distance to the best stomatal density and specific root length values (log FDis_{CWD} for SD & SRL) (Linear model, $R^2 = 0.53$, $p = 0.049$; Fig. 10).

There was also weak evidence of selection for the trait pairs of leaf area and stomatal density, leaf mass per area and stomatal density, and for FDis_{CWD} calculated with all seven traits. Aboveground biomass decreased marginally with the log of the distance to the best trait

value for the combination of leaf area and stomatal density in the pulse and the control treatments ($\log \text{FDis}_{\text{CWD}}$ for LA & SD) (Linear model, Pulse: $R^2 = 0.32$, $p = 0.075$, Control: $R^2 = 0.35$, $p = 0.055$) and with the log of the distance to the best trait value for the combination of leaf mass per area and stomatal density in the control ($\log \text{FDis}_{\text{CWD}}$ for LMA & SD) (Linear model, $R^2 = 0.30$, $p = 0.095$). When calculated with all seven traits, the log transformed FDis_{CWD} had a weak effect on aboveground biomass in the pulse treatment ($\log \text{FDis}_{\text{CWD}}$ All) (Linear model, $R^2 = 0.29$, $p = 0.098$).

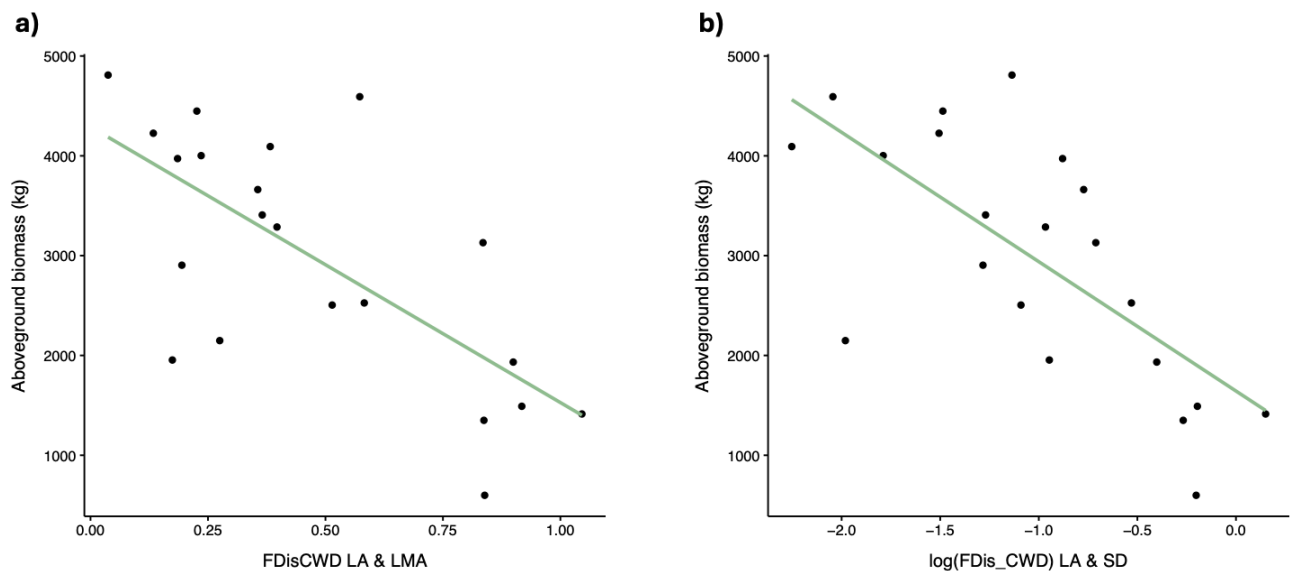


Figure 9. Linear regressions of aboveground biomass, in kilograms, against the selection metrics. Panel a) illustrates the linear regression of aboveground biomass against the modified Functional Dispersion index (FDis_{CWD}) calculated using species-level leaf area and leaf mass per area trait values for plots in the press treatment ($R^2 = 0.45$, $p = 0.027$). Panel b) illustrates the linear regression of aboveground biomass against the modified Functional Dispersion index (FDis_{CWD}) calculated using species-level leaf area and stomatal density values for the press

treatment ($R^2 = 0.46$, $p = 0.027$). The original Functional Dispersion index (FDis) was modified into FDis_{CWD} which calculates the community weighted mean distance to the best trait value, instead of to the distance to the mean trait value. Plots with smaller community weighted distances to the best trait values produced four times more aboveground biomass, thus showing evidence of selection effects.

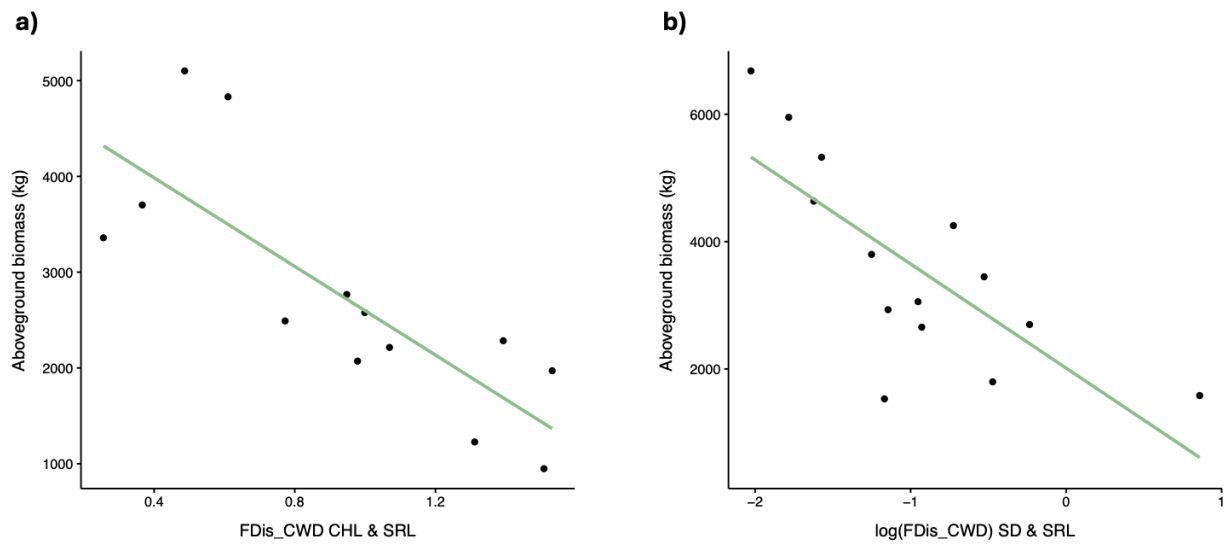


Figure 10. Linear regressions of aboveground biomass, in kilograms, against the modified Functional Dispersion index (FDis_{CWD}) of trait pairs including specific root length. Panel a) illustrates the linear regression of aboveground biomass against FDis_{CWD} calculated using species-level chlorophyll concentration and specific root length values for plots in the pulse treatment ($R^2 = 0.60$, $p = 0.039$). Panel b) illustrates the linear regression of aboveground biomass against FDis_{CWD} calculated using species-level stomatal density and specific root length values for plots in the control treatment ($R^2 = 0.53$, $p = 0.049$). The original Functional Dispersion index (FDis) was modified into FDis_{CWD} which calculates the community weighted

mean distance to the best trait value, instead of to the distance to the mean trait value. Plots with smaller community weighted distances to the best trait values produced four times more aboveground biomass, thus showing evidence of selection effects.

In some cases, the FDis of certain trait combinations were negatively correlated with community-level biomass. Here, communities with a lower trait diversity produced more biomass than those with high trait diversity. In other cases, the CWD of certain trait combinations were negatively correlated with community-level biomass. Here, communities with a higher community weighted distance to the best trait value produced more biomass than those with trait values close to the best. Because these relationships do not provide support for either mechanism, they are described in the supplementary materials (Appendix 5).

2.4 Discussion

2.4.1 Selection for Trait Combinations with Leaf Area

The trait combinations of leaf area with leaf mass per area and leaf area with stomatal density were under selection in the press treatment. In both cases, leaf area emerged as a target of selection. In these cases, communities with smaller leaf areas produced more aboveground biomass. Small leaves are characteristic of the dominant species in our system, *L. laricina* and *B. alleghaniensis*. Given the open nature of the canopy at the time of establishment, light conditions likely favoured the successful dominance of *L. laricina* and *B. alleghaniensis*, which depend on abundant light to compete and grow successfully (Burns &

Honkala, 1990). Under these high light conditions, small leaves are less prone to overheating due to their thinner air boundary layers (Parkhurst & Loucks 1972; Givnish 1979). In addition, the water costs associated with leaf temperature regulation are greater in these high light environments (Givnish & Vermeij, 1976; Westoby et al., 2002). Smaller leaves may therefore confer an advantage by decreasing the amount of water lost during cooling (Givnish & Vermeij, 1976). The physiological advantages provided by smaller leaves in a high light environment may explain the observed selection effects on leaf area in both trait pairs.

In addition to having smaller leaves, both the dominant conifer and broadleaf had a lower leaf mass per area. Low leaf mass per area values reflect a lower leaf dry-mass investment per unit of light-intercepting area produced at the leaf level (Wright et al., 2004). By investing less mass per unit area of leaf tissues, low leaf mass per area species benefit from a quicker photosynthesis return on investment, allowing them to grow faster (Wright, 2004; Poorter et al., 2009; Wright et al., 2010). Leaf mass per area is also related to water use efficiency, the rate of CO₂ uptake for a given rate of water loss (Cernusak, 2020). However, contrary to the selection for low leaf mass per area values observed in this system, previous studies have reported increases in water use efficiency with leaf mass per area (Poorter et al., 2009; Baird et al., 2017; Messier et al., 2018). This positive correlation between leaf mass per area and water use efficiency has been documented both within and among temperate tree species of the same population (Messier et al., 2018). Similar trends have also been observed at the global scale, as species in water limited environments produce higher leaf mass per area leaves as a result of lower leaf expansion rates and thicker cell walls (Poorter et al., 2009).

Within a species, water limited individuals have also been shown to produce higher leaf mass per area leaves than non-water limited conspecifics (Baird et al., 2017). Here, changes in leaf anatomy resulting in higher mesophyll surface area per leaf area ratios likely drove increases in leaf mass per area and water use efficiency (Baird et al., 2017).

In contrast, the best stomatal densities for conifers and broadleaves differed. While *L. laricina* has a higher stomatal density than *P. glauca* and *P. resinosa*, *B. alleghaniensis* has a lower stomatal density than *Q. rubra* and *A. saccharum* (Fig. 4). The high- and low- stomatal densities of *L. laricina* and *B. alleghaniensis* do not necessarily indicate high- and low- leaf gas exchange, as this property is also determined by other stomatal traits (Boardman, 1977). For example, gas exchange is also affected by stomatal size, with larger stomata providing faster evaporative cooling (Boardman, 1977; Abrams, 1990).

Gas exchange rates can also be affected by the opening and closing of stomata in response to environmental cues (Wolz et al., 2017). Intrinsic water use efficiency can be used to determine stomatal responsiveness, as species that close their stomata rapidly in response to environmental cues tend to have a high intrinsic water use efficiency (Farquhar & Richards, 1984; Brodribb et al., 2009; Cernusak, 2020; Ozeki et al., 2022). The environmental threshold at which trees reduce their stomatal conductance varies across species, therefore differences in the stomatal responses of *L. laricina* and *B. alleghaniensis*, reflected in their intrinsic water use efficiencies, may also explain why these species exhibited diverging stomatal densities (Wolz et al., 2017).

Based on the observed selection on leaf area and stomatal density, evapotranspirative and photosynthetic functions are likely the targets of selection during stand establishment. Future studies should focus on characterizing multiple aspects of gas exchange in these species to determine if these species have similar or distinct gas exchange strategies. Such work will provide a more comprehensive understanding of the traits under selection.

Given that leaf area, leaf mass per area, and stomatal density did not affect community productivity on their own, these traits are likely adaptive as pairs. In gymnosperms, leaf area was weakly correlated to leaf mass per area and had a weak negative correlation to stomatal density (LA-LMA R^2 : 0.11, LA-SD R^2 : -0.25; Appendix 6). In angiosperms, leaf area was moderately correlated to leaf mass per area and stomatal density (LA-LMA R^2 : 0.39, LA-SD R^2 : 0.38; Appendix 6). Since the correlations between these traits were mostly weak, these results are unlikely to be an artifact of trait correlations, indicating that there is indeed selection for these trait pairs.

2.4.2 Selection for Trait Combinations with Specific Root Length

The trait combination of chlorophyll concentration & specific root length was under selection in the pulse treatment, whereas the trait combination of stomatal density & specific root length was under selection in the control treatment. In both cases, specific root length emerged as a target of selection. In these cases, the best trait values for conifers and broadleaves differ as *L. laricina* has a low specific root length and high stomatal density and

chlorophyll concentrations, whereas *B. alleghaniensis* has a high specific root length and low stomatal density and chlorophyll concentrations (Fig. 4).

While these specific trait combinations increase community productivity, the biological reason why is unclear. Here, specific root length was strongly negatively correlated to chlorophyll concentration and stomatal density within gymnosperms (PCA, CHL-SRL R^2 : -0.89, SRL-SD R^2 : -0.93; Appendix 6). Within angiosperms, specific root length was strongly negatively related to chlorophyll concentration, but was not correlated to stomatal density (PCA, CHL-SRL R^2 : -0.73, SRL-SD R^2 : 0.04; Appendix 6). Given these strong correlations between traits, but the lack of strong selection for either trait, variation in another, unmeasured trait may be driving the observed variation in specific root length, chlorophyll concentration, and stomatal density. These results indicate that the mechanism of selection involves physiological functions and plant strategies related to these traits. Future work can explore additional traits related to nutrient acquisition (as suggested by specific root length), photosynthetic rate (as suggested by chlorophyll concentration), and gas exchange (as suggested by stomatal density).

2.4.3 Presence of Complementarity and Selection in Early-Establishment Forests

Although results show consistent evidence that selection increases community productivity, we did not find evidence of complementarity in our system. The lack of evidence for complementarity effects may be due to the young age of the system. This finding is consistent with existing literature, as previous studies have shown that selection effects are the main drivers of community productivity during stand establishment, whereas complementarity effects strengthen over time (Lasky et al., 2014; Grossman et al., 2017; Taylor et al., 2020;

Urgoiti et al., 2022). Complementarity effects are expected to be strongest during secondary succession, during which trait complementarity should improve species co-occurrence through niche partitioning, resulting in a more productive forest (Forrester et al., 2014; Taylor et al., 2020). In contrast, the effectiveness of trait complementarity is likely reduced in the early years of stand establishment because all seedlings can access abundant light and nutrients (Taylor et al., 2020). Given that this experiment was established in 2020, four years prior to our study, it is likely that complementarity effects have likely not had time to develop (Urgoiti et al., 2022). As our system ages, future work should study changes in the importance of selection and complementarity effects.

Future research should also investigate how the traits that underly complementarity and selection effects change as forests mature. First, the life stage of trees may affect which traits are targets of complementarity or selection, as traits that were important for trees as seedlings may not hold the same importance in mature trees. For example, leaf mass per area is a better predictor of growth rate in young trees than in mature trees (Wright et al., 2010). Because mature trees have more leaves, they are less impacted by the direct limitations on growth that result from producing high leaf mass per area leaves (Wright et al., 2010). Second, as the water and nutrient requirements of trees increase and resources become limiting, selection and complementarity effects may act upon different traits. Already, water availability in our system seems strongly affected by the aboveground biomass as plots with *L. laricina*, the most productive species overall, had lower amounts of surface water (Appendix 4). As these changes occur, new traits may arise as important targets of selection or complementarity.

2.4.4 Effects of Water Availability

Most evidence for selection was observed in the press treatment, which should represent a low but persistent reduction in water availability. Here, selection for smaller leaves in combination with leaf mass per area and stomatal density likely conferred an advantage by facilitating thermoregulation or by decreasing evaporative losses. The temperatures of small leaves are more closely coupled to the temperature of the atmosphere because of better convective heat dissipation (Parkhurst & Loucks, 1972). Convective heat dissipation allows small leaves to avoid overheating, which in turn, reduces the rate of transpiration (Givnish, 1979). This may provide a greater advantage in dry conditions, where trees cannot afford to lose as much water. Given that selection for these trait pairs was not observed in the pulse and the control treatments, belowground resources may have affected aboveground processes.

Notably, these trait combinations were not under selection in the pulse treatment, suggesting that the effect of the treatments may be cumulative. For example, shoot formation often occurs over two years, with bud development starting in the first year and bud elongation in the second year (Bréda et al., 2006). As a result, water availability can affect shoot formation in either or both years (Bréda et al., 2006). Since water availability was not reduced in the pulse treatment in 2023, selection from lower water availability in the second year alone may be harder to detect. Furthermore, if selection for these trait pairs in the press treatment resulted from reduced water availability in 2023, this could explain why the trait pair of leaf area and stomatal density had a marginally significant effect on aboveground biomass in the pulse and the control treatments.

Finally, different trait pairs were selected within each treatment, suggesting different dynamics in each environment. Thus, the water availability treatments impacted the community dynamics, albeit in unclear ways. While differences in surface soil water content across treatments were minimal as a result of the particularly wet growing season in 2024, the possibility that water availability the treatments impacted the observed selection effects cannot be ruled out. Future research should follow changes in each of these environments through time to clarify how each water availability treatment impacts community dynamics.

2.4.5 Conclusion

In conclusion, this study demonstrates that selection effects are the driving force of community productivity during stand establishment. Specifically, our results show that increases in productivity were determined by selection for smaller leaf areas in combination with low leaf mass per area and contrasting stomatal densities in angiosperms and gymnosperms in the press treatment. In contrast, increases in productivity were determined by selection for trait pairs which included specific root length in the pulse and control treatments. These traits, which relate to tree architecture, thermoregulation, photosynthetic rate, and water use, illustrate the mechanisms by which selection effects drive differences in community productivity across varying soil water conditions.

3. General Discussion

3.1 Summary and Key Findings

My thesis had two main objectives: First, to determine which traits are responsible for the species richness-productivity relationship in temperate tree communities during the early stages of stand development, and whether they act via the complementarity or the selection effect, and second, to examine how the species richness-productivity relationship and its underlying traits change in environments with different water availabilities.

In the second chapter of my thesis, I used an experimental plantation of early-establishment temperate tree communities to investigate to assess which traits, and which combinations of traits, were related to community productivity, while identifying whether biomass increased with trait diversity or composition. I then compared the trait-biomass relationships observed among three treatments differing in water availability.

My thesis highlighted the role of selection effects in shaping community productivity during stand development. Selection effects were prevalent in all water availability treatments, but the trait pairs under selection differed between treatments. While I observed selection for multiple combinations of leaf-leaf and leaf-root trait pairs, I found that in this system, increases in community productivity were most strongly driven by selection for trait pairs which included leaf area in the press treatment, whereas trait pairs which included specific root length were under selection in the pulse and control treatments.

3.2 Implications

Understanding the dynamics of selection and complementarity effects on early-establishment stands is important for forest management for many reasons. First, the successful development of a forest community depends on success at the early-establishment stage, as seedlings face high mortality rates at this stage of forest development. The outcome of this stage can have cascading effects for long-term forest development, by affecting future rates of nutrient cycling or biomass accumulation, and by shaping future forest structure, composition and function (Lutz & Halpern, 2006; Williams et al., 2017). From a management perspective, building an understanding of which traits are under selection at this stage is valuable. This knowledge can be used to identify the species that have the highest chance of successful establishment, thus guiding species selection for the reforestation and afforestation of sites.

Second, the environmental conditions at the early-establishment stage of forest development are unique from those at later stages of development. These conditions result mainly from the open nature of the canopy, which lead to increased sunlight exposure, higher ground and air temperatures, higher wind velocities, and lower soil and litter moisture (Swanson et al., 2011). These environmental conditions during establishment may favour certain species over others based on selection for particular traits. Targeting species which benefit from these conditions is especially valuable for the regeneration of species in clearcut, and some shelterwood systems, where >70% of full light is available during regeneration (Briennesse et al., 2015).

By showing that the trait pairs under selection varied across treatments, this work illustrates that different traits are better suited to different environments. The water limitation conditions implemented in this system have been designed to reflect future climate conditions, as climate models project decreases in water availability in eastern Canada (IPCC, 2023). As total biomass increases and water availability becomes more limiting, continued monitoring of this system will help further our understanding of which traits will be under selection and which species combinations will have complementary traits under future climate conditions. This can inform future forest management practices by guiding the selection of community compositions that can maintain productivity in a changing climate.

3.3 How Should Selection and Complementarity Effects Change Over Time?

The relative importance of selection and complementarity effects is expected to change throughout the lifespan of a forest. During early establishment, selection effects are more prominent than complementarity effects due to abundance of light and nutrients (Taylor et al., 2020). This is reflected in the results of my thesis, as we found strong evidence of selection and no evidence of complementarity in young tree communities.

In the early years of stand establishment, the need for trait complementarity is likely reduced because all seedlings can access abundant light and nutrients (Taylor et al., 2020). As the forest ages, light availability becomes heterogenous, resources become more limiting, competition increases, and slow-growing shade-tolerant species start to establish (White, 1979; Huston & Smith, 1987). Once this happens, trait complementarity is expected to improve species co-occurrence through niche partitioning, resulting in a more productive forest

(Forrester et al., 2014; Taylor et al., 2020). Complementarity effects are thought to be the most beneficial during this stage of secondary succession, as in the long term, forests can become dominated by functionally redundant late-succession species (Taylor et al., 2020).

3.4 Future Work

To build on the work accomplished for this thesis, changes in the complementarity and selection effects at play in the tree communities of the IDENT-Outaouais experiment should be monitored as the system ages. Forest dynamics will change with time, and as such, the results obtained here only provide a snapshot of the mechanisms at play during the early establishment phase of this system.

The traits underlying these mechanisms should also be followed over time, as they continue to change throughout a tree's life. My results indicate that in early-establishment tree communities, selection acts on traits related to photosynthesis and thermoregulation likely resulting from the abundance of light at this time. However, as the communities develop, changes in the environment may result in selection for a different suite of traits. For example, as the canopy closes, light availability and the temperature of the surrounding air will decrease (Swanson et al., 2011). In these new conditions, optimizing photosynthetic capacity and leaf thermoregulation may not confer the same advantages to productivity as it previously did.

In addition, traits that are complementarity or that are under selection may change as the water exclusion treatment becomes more stressful. Following the changes in the relative importance of these mechanisms, and in the traits underlying them, will provide important

insights into the effects of water availability on community dynamics which could inform management decisions in the context of climate change.

Future work should also explore how additional traits may affect community productivity in early-establishment forests. While I measured as many traits as possible, this subset of traits does not capture the full phenotypes of the individuals in this experiment.

The results of my thesis indicated evidence of selection for specific root length in combination with chlorophyll concentration and stomatal density. However, the reasons why these trait combinations would be under selection remain unclear. Future work should focus on measuring additional traits related to nutrient acquisition to clarify the observed relationships between specific root length and chlorophyll concentration and between specific root length and stomatal density. Specifically, mycorrhizal traits should be investigated because of the significant role of mycorrhiza in the resource uptake strategies of plants.

There are also additional traits that I would have liked to measure for my thesis, which would have been more directly related to water use. I would have liked to measure intrinsic water use efficiency, which can be used to determine stomatal responsiveness (Farquhar & Richards, 1984). This would have provided insights into the water use of each individual, which may have clarified why the angiosperms and gymnosperms differed in their stomatal densities. Intrinsic water use efficiency measurements would have also helped characterize the efficacy of the water exclusion treatments by contrasting the time species in each treatment spent with their stomata closed.

I would also have liked to measure Huber value, which measures the investment of stem tissue per unit leaf area and relates to the rate of evapotranspiration (Tyree & Ewers, 1991). Unfortunately, the timing of these measurements did not coincide with my field season because the needles of the coniferous species mature much later into the year.

Lastly, I would have liked to measure stomatal size in addition to the stomatal density measurements I took. Measuring stomatal size would have been possible using the imprints taken on the leaves of the broadleaf species. But I could not take stomatal density imprints in the same manner for the conifer species. Initially, stomatal density pictures for the conifers were going to be taken on fresh needles using a microscope but an issue with the microscope made this set-up unreliable. Instead, we used high resolution scans to take images of the stomata, which were not magnified enough to measure stomatal size.

Based on the results of my thesis, characterizing multiple aspects of gas exchange, and focusing on traits related to nutrient acquisition or photosynthetic rate would provide an excellent starting point for future studies. However, future studies should not limit their exploration to these specific traits.

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Appendices

Appendix 1. Sampling Locations

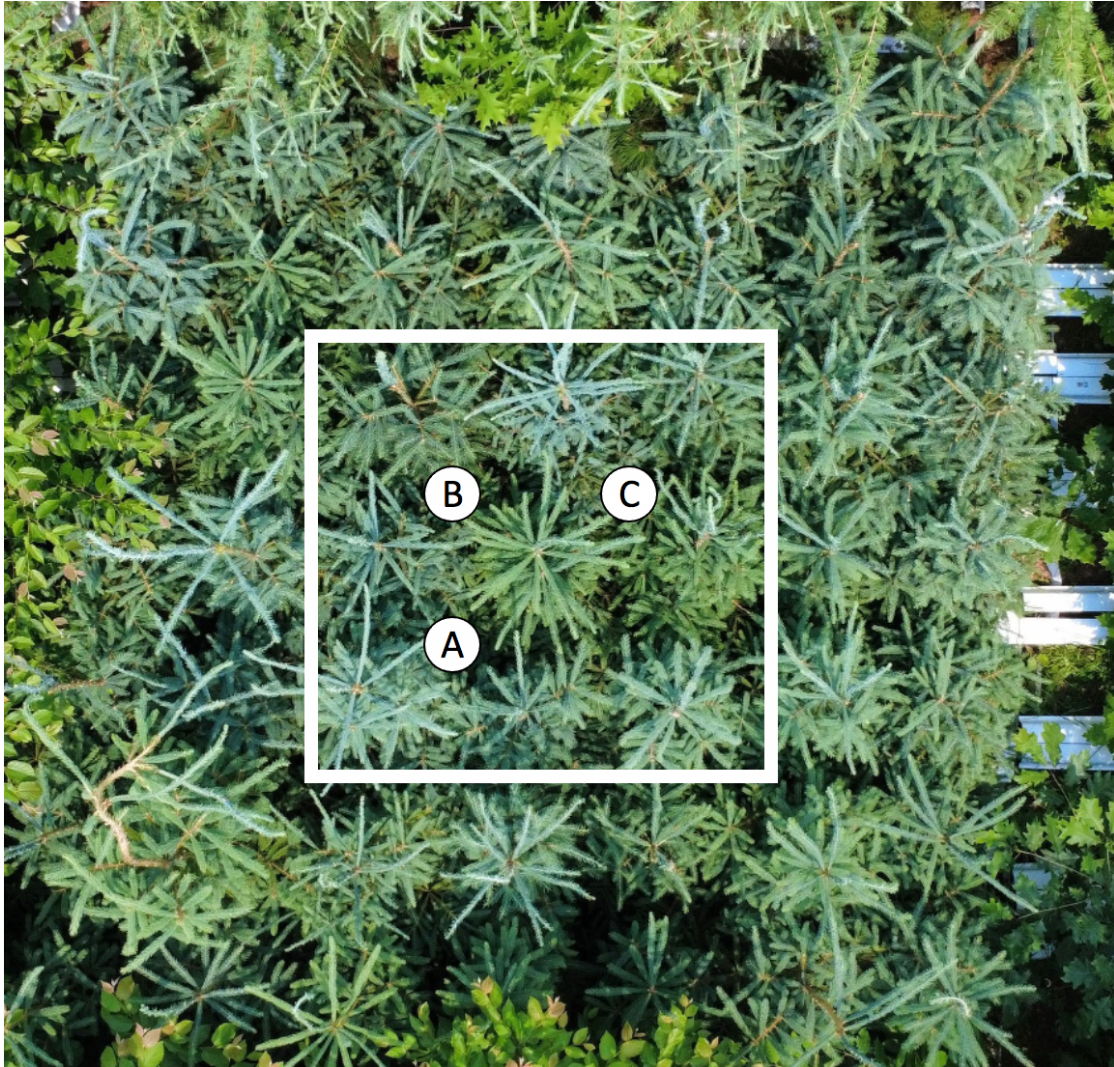


Figure A 1. Sampling locations in each plot. The white square delineates the nine central individuals from which leaf traits and aboveground biomass were measured. The white circles indicate the three locations where soil cores were collected. Trait measurements were not taken for individuals in the outer two rows, as they served as a buffer for edge effects.

Appendix 2. Species Differences in Aboveground Biomass

A two-way ANOVA was conducted to examine the effects of species and treatment on aboveground biomass. There was a significant main effect of species (Two-way ANOVA, $p < 0.001$), but no significant effect of treatment (Two-way ANOVA, $p > 0.05$) and no significant species $\times$ treatment interaction (Two-way ANOVA, $p > 0.05$).

Across broadleaves, post-hoc TukeyHSD tests indicated that *B. alleghaniensis* monocultures had significantly higher aboveground biomass than *A. saccharum* and *Q. rubra* monocultures (Both: $p < 0.001$). Across conifers, *L. laricina* had higher aboveground biomass than *P. glauca* and *P. resinosa* monocultures (Both: $p < 0.001$).

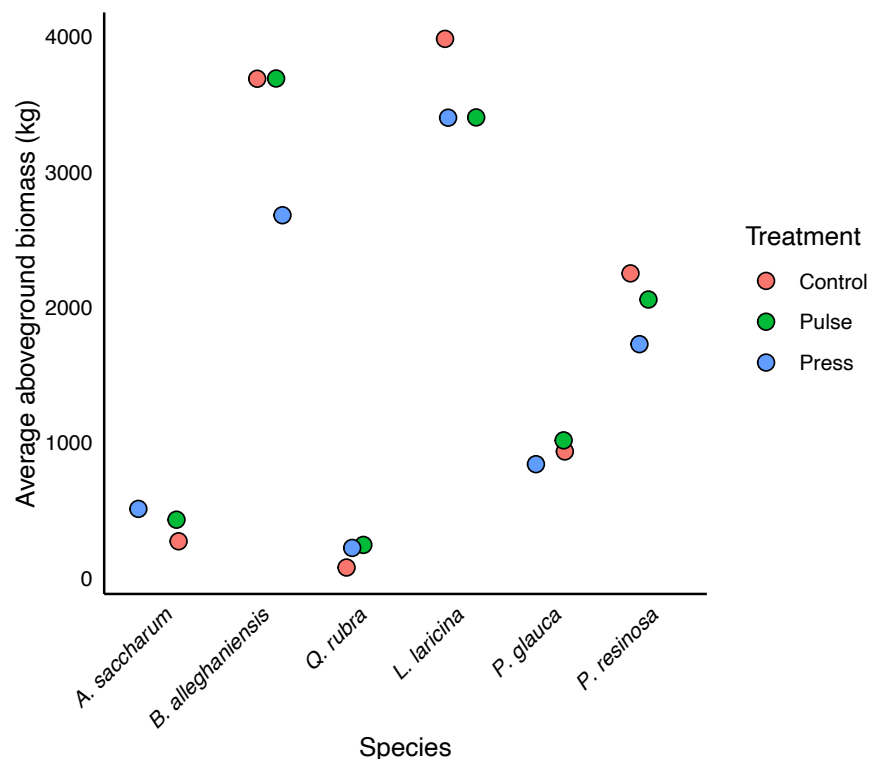


Figure A 2. Differences in average aboveground biomass (kg) across species, in each water exclusion treatment. For *L. laricina*, aboveground biomass was averaged across all individuals

for each treatment. For all other species, aboveground biomass was averaged across individuals growing in monoculture for each treatment. Across all species, aboveground biomass was highest in *L. laricina* and *B. alleghaniensis*.

Appendix 3. Effects of Plot Composition on Trait Values

Table A 1. Comparisons of trait values for each species based on plot composition. T-tests were performed between the trait values of each species in monoculture and their trait values across all mixes, for each trait and each treatment. A false discovery rate correction was applied.

Significant adjusted p-values and the difference in the z-transformed trait values between the monoculture and the mixes are presented below.

Species	Treatment	Trait	Trait difference (Monoculture – Mix)	Adjusted p-value
<i>A. saccharum</i>	Press	Chlorophyll concentration	-70.68 mg/m ²	0.00369
<i>A. saccharum</i>	Control	Chlorophyll concentration	-132.23 mg/m ²	9.3 e ⁻⁰⁵
<i>A. saccharum</i>	Press	Leaf mass per area	0.0021 g/cm ²	6.7 e ⁻⁰⁷
<i>A. saccharum</i>	Pulse	Leaf mass per area	0.0019 g/cm ²	7.8 e ⁻⁰⁸
<i>A. saccharum</i>	Control	Leaf mass per area	0.0016 g/cm ²	0.000096
<i>B. alleghaniensis</i>	Control	Chlorophyll concentration	-94.55 mg/m ²	0.0066
<i>B. alleghaniensis</i>	Press	Leaf mass per area	-0.00083 g/cm ²	0.014
<i>B. alleghaniensis</i>	Pulse	Leaf mass per area	-0.00076 g/cm ²	0.025
<i>B. alleghaniensis</i>	Press	Stomatal density	-7.89 stomata/mm ²	0.036

<i>B. alleghaniensis</i>	Pulse	Specific root length	-29.32 m/g	0.037
<i>P. glauca</i>	Pulse	Chlorophyll concentration	58.00 mg/m ²	0.0016
<i>P. glauca</i>	Press	Leaf area	-0.017 cm ²	0.0096
<i>P. glauca</i>	Press	Leaf mass per area	0.0045 g/cm ²	0.000029
<i>P. glauca</i>	Pulse	Leaf mass per area	0.0060 g/cm ²	5.0 e ⁻⁰⁵
<i>P. glauca</i>	Control	Leaf mass per area	0.0047 g/cm ²	7.1 e ⁻⁰⁸
<i>P. glauca</i>	Press	Root tissue density	0.032 g/cm ³	0.0050
<i>P. glauca</i>	Press	Stomatal density	9.40 stomata/mm ²	0.011
<i>P. glauca</i>	Pulse	Stomatal density	12.74 stomata/mm ²	0.00042
<i>P. glauca</i>	Control	Stomatal density	8.60 stomata/mm ²	0.0038
<i>P. resinosa</i>	Press	Leaf mass per area	0.0030 g/cm ²	0.00066
<i>P. resinosa</i>	Pulse	Leaf mass per area	0.0030 g/cm ²	0.0016
<i>P. resinosa</i>	Control	Leaf mass per area	0.0026 g/cm ²	0.0016
<i>P. resinosa</i>	Press	Root tissue density	-0.035 g/cm ³	0.0063
<i>P. resinosa</i>	Pulse	Stomatal density	5.48 stomata/mm ²	0.036

<i>Q. rubra</i>	Pulse	Leaf mass per area	0.0028 g/cm ²	1.8 e ⁻¹¹
<i>Q. rubra</i>	Press	Leaf mass per area	0.0028 g/cm ²	2.2 e ⁻¹¹
<i>Q. rubra</i>	Control	Leaf mass per area	0.0026 g/cm ²	6.8 e ⁻¹⁰
<i>Q. rubra</i>	Control	Chlorophyll concentration	-141.71 mg/m ²	0.013

Since there were no monocultures of *L. laricina*, an ANOVA comparing all three-species mixes in which it was present was conducted for this species in each treatment. For *L. laricina*, there was no differences in trait values across plot compositions ($p > 0.05$).

Appendix 4. Exploration into the Effects of the Water Exclusion Treatments

Table A 2. Summary statistics of the percent volumetric water content (VWC%) across plots in the press, pulse, and control water exclusion treatments. These summary statistics were calculated using the mean VWC% for each plot and represent the mean, minimum, maximum, and the variance in VWC% across plots over the whole summer.

Treatment	Variance	Mean	Min	Max
Press	34.03	18.16	8.64	33.00
Pulse	26.31	14.86	6.01	28.91
Control	18.50	18.16	11.06	26.74

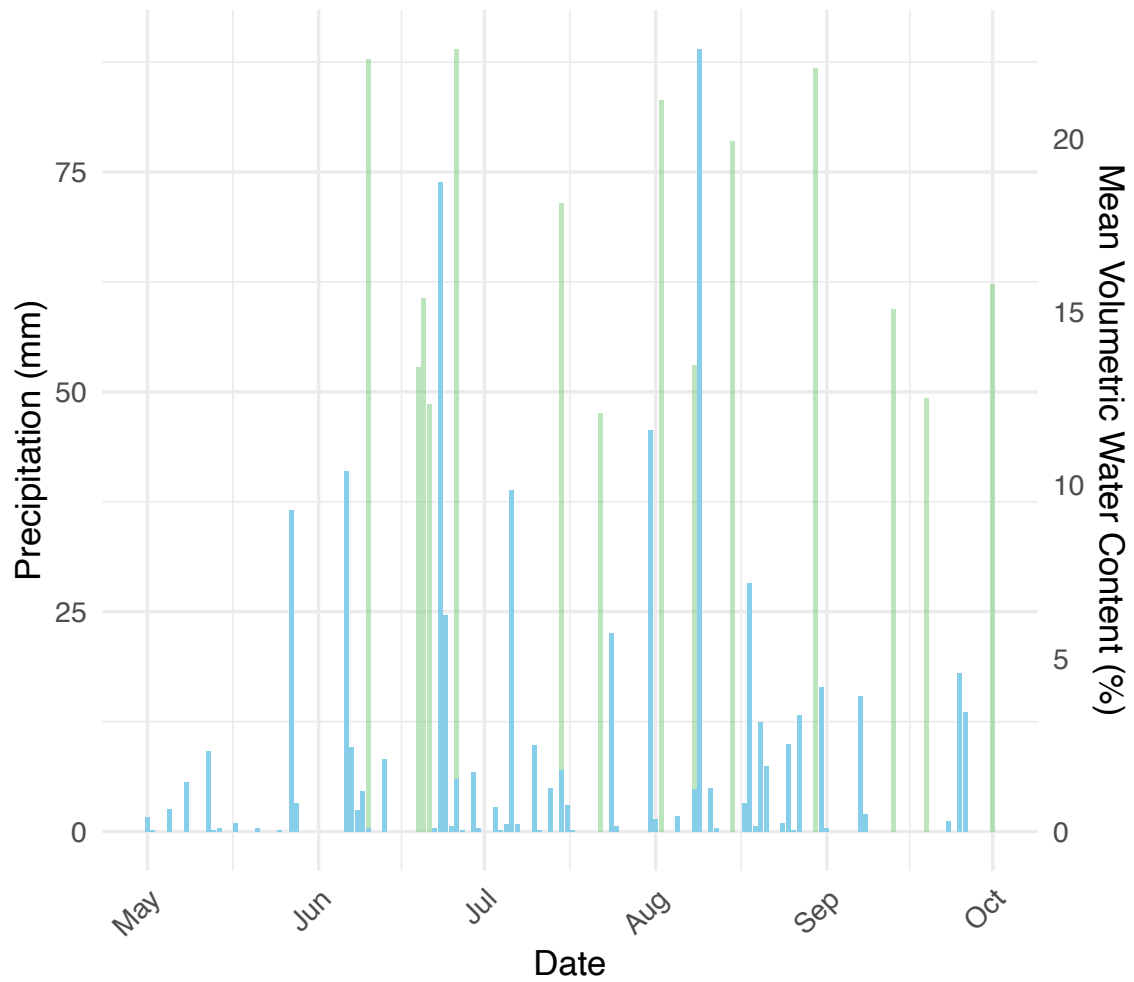


Figure A 3. Plot of daily precipitation and mean volumetric water content (VWC%) from May to October 2024. Green bars represent mean VWC% across all treatments and blue bars represent daily precipitation (mm).

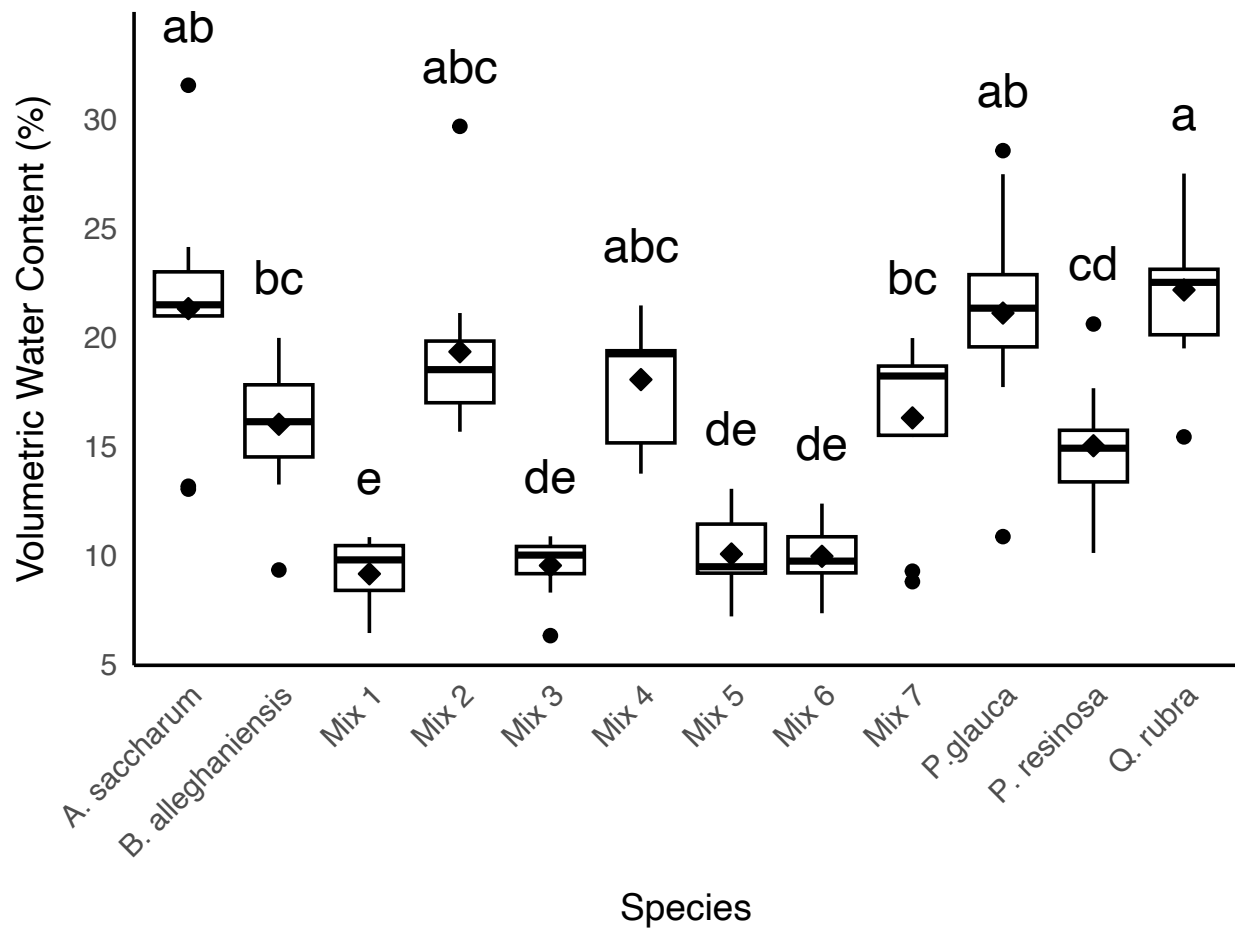


Figure A 4. Differences in the percent volumetric water content (VWC%) based on community composition. VWC% was first averaged within a plot, then VWC% based on community composition was compared across all treatments. Mix compositions are as follows: Mix 1, *L. laricina*, *Q. rubra*, *A. saccharum*; Mix 2, *B. alleghaniensis*, *Q. rubra*, *A. saccharum*; Mix 3, *P. glauca*, *P. resinosa*, *L. laricina*; Mix 4, *B. alleghaniensis*, *P. glauca*, *A. saccharum*; Mix 5, *Q. rubra*, *P. resinosa*, *L. laricina*; Mix 6, *P. glauca*, *A. saccharum*, *L. laricina*; Mix 7, *B. alleghaniensis*, *Q. rubra*, *P. resinosa*. Mixes 1, 3, 5, and 6, which had the lowest VWC% values are plots which contained *L. laricina*.

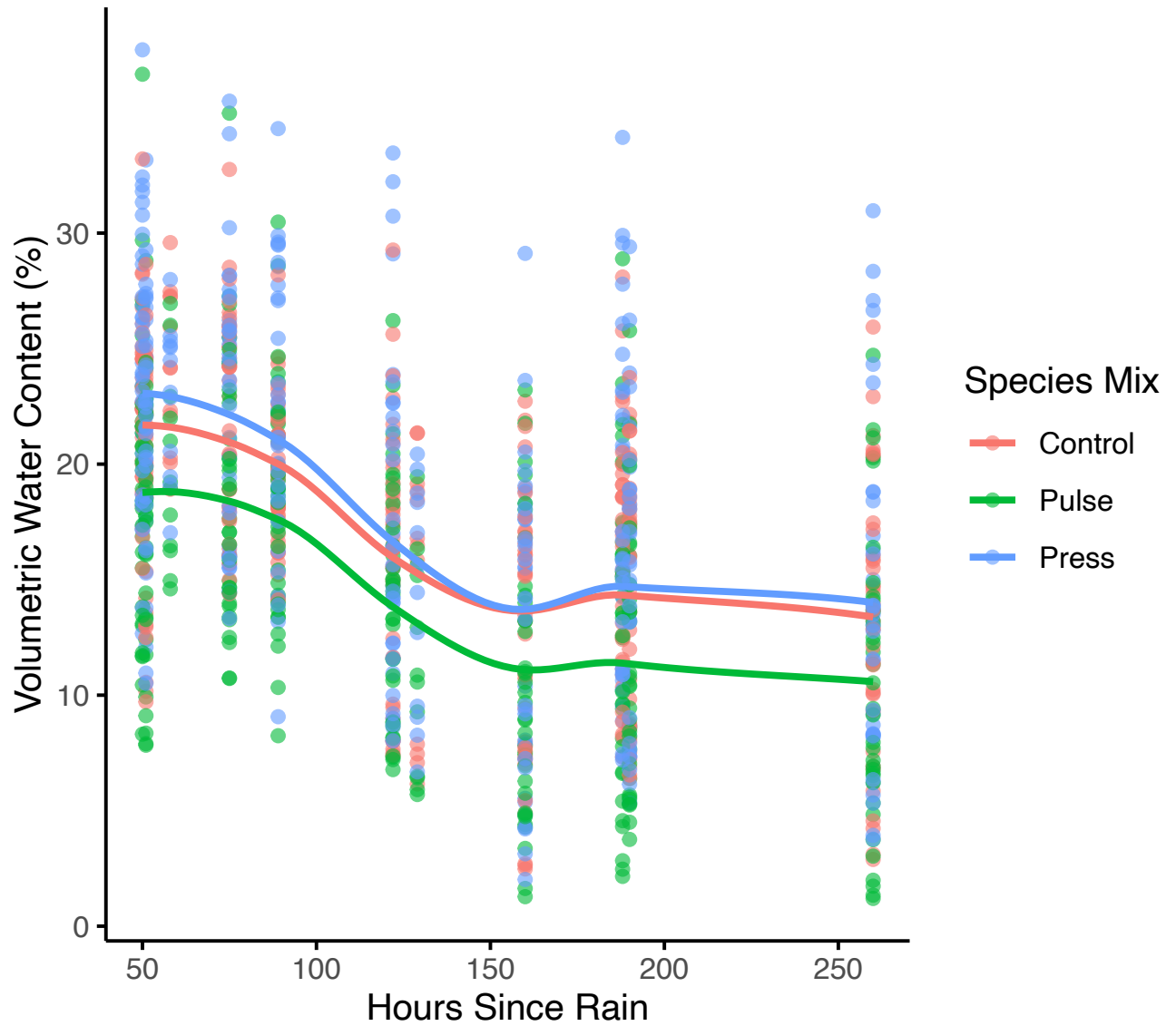


Figure A 5. Change in percent volumetric water content (VWC%) with hours since the last rain event greater than 5 mm. Each datapoint represents the mean VWC% of a single plot at a given time.

To quantify drought intensity in each treatment, I calculated relative extractable soil water using the percent volumetric water content measurements. To calculate relative extractable soil content for each plot, I used the following equation from Garnier et al., (2007):

$$\mathbf{REW} = \frac{\mathbf{EW}_t}{\mathbf{EW}} \quad \mathbf{Eqn. 6}$$

where $\mathbf{EW}_t$ is the extractable soil water on a given day t , and $\mathbf{EW}$ is the maximum extractable soil water. To use percent volumetric soil water content to calculate relative extractable water, equation 6 can be written as:

$$\mathbf{EW} = \frac{\mathbf{SWC}_t - \mathbf{SWC}_{\min}}{\mathbf{SWC}_{\max} - \mathbf{SWC}_{\min}} \quad \mathbf{Eqn. 7}$$

where $\mathbf{SWC}_t$ is the soil water content on a given day t , $\mathbf{SWC}_{\min}$ is the minimum soil water content for the entire rooting zone during the period of interest, and $\mathbf{SWC}_{\max}$ is the maximum soil water content for the entire rooting zone during the period of interest (Vilhar, 2015). In this case, the period of interest spanned from June to October 2024. To identify periods of drought, a relative extractable water threshold of 0.4 was used (Garnier et al., 1999).

Table A 3. Characterization of the water stress in each treatment based on relative extractable water. Start date represents the first date on which relative extractable water dropped below 0.4 in each treatment. Days below 0.4 represents the number of days where the relative extractable water stayed below 0.4 for at least one plot. Days majority below 0.4 represents the number of days where the relative extractable water stayed below 0.4 for more than half the plots in a treatment.

Treatment	Start date	Days below 0.4	Days majority below 0.4
Press	2024-06-19	9	6
Pulse	2024-06-19	11	6
Control	2024-06-19	10	5

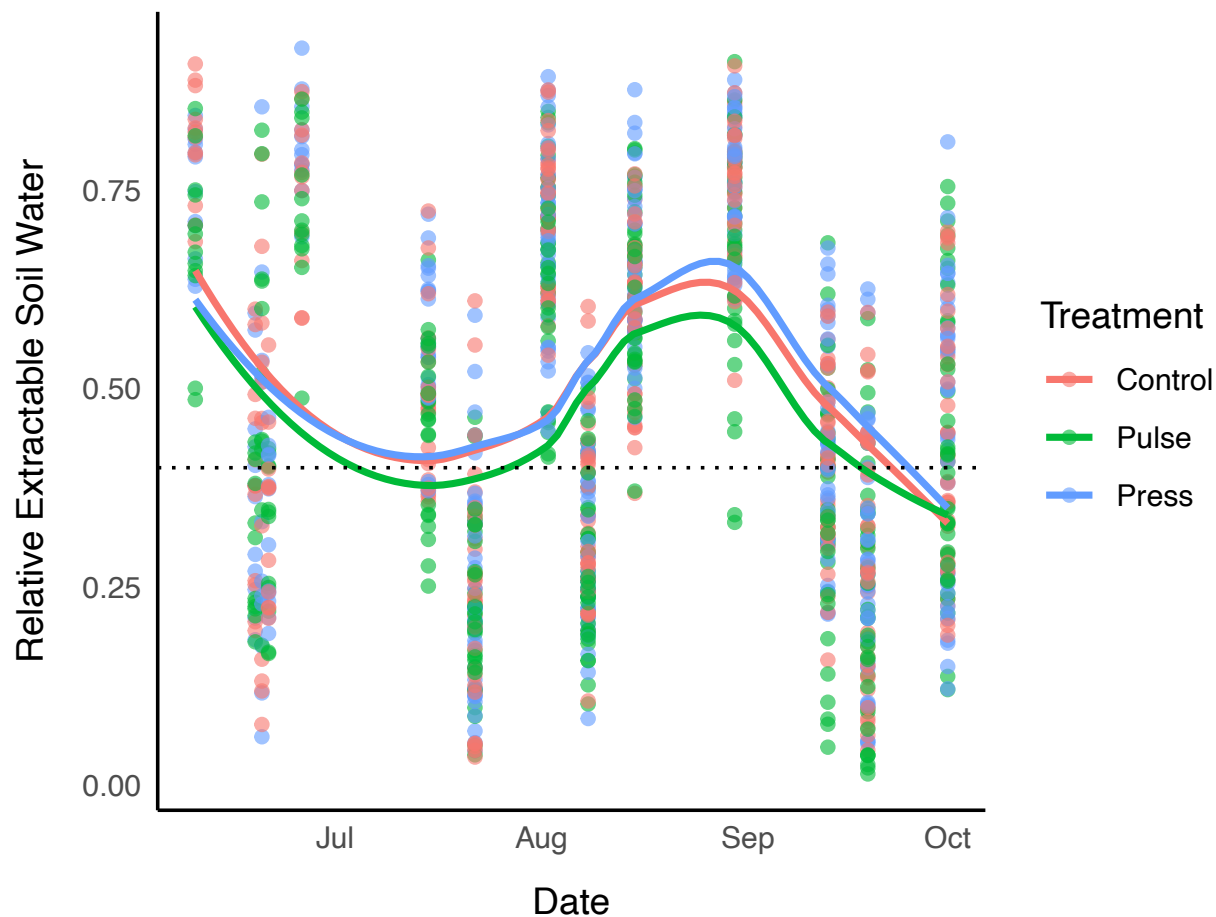


Figure A 6. Change in relative extractable soil water during the growing season, based on treatment. Each datapoint represents the relative extractable water of a single plot on a given day. A threshold level of 0.4 was used to determine periods of water stress, indicated by the black dotted line. All treatments followed the same pattern over time, with drops in REW in July and September. The pulse treatment was the only treatment in which the REW trendline drops below threshold level of 0.4 in July. The average REW in the pulse treatment was consistently lower than in the control and press treatments.

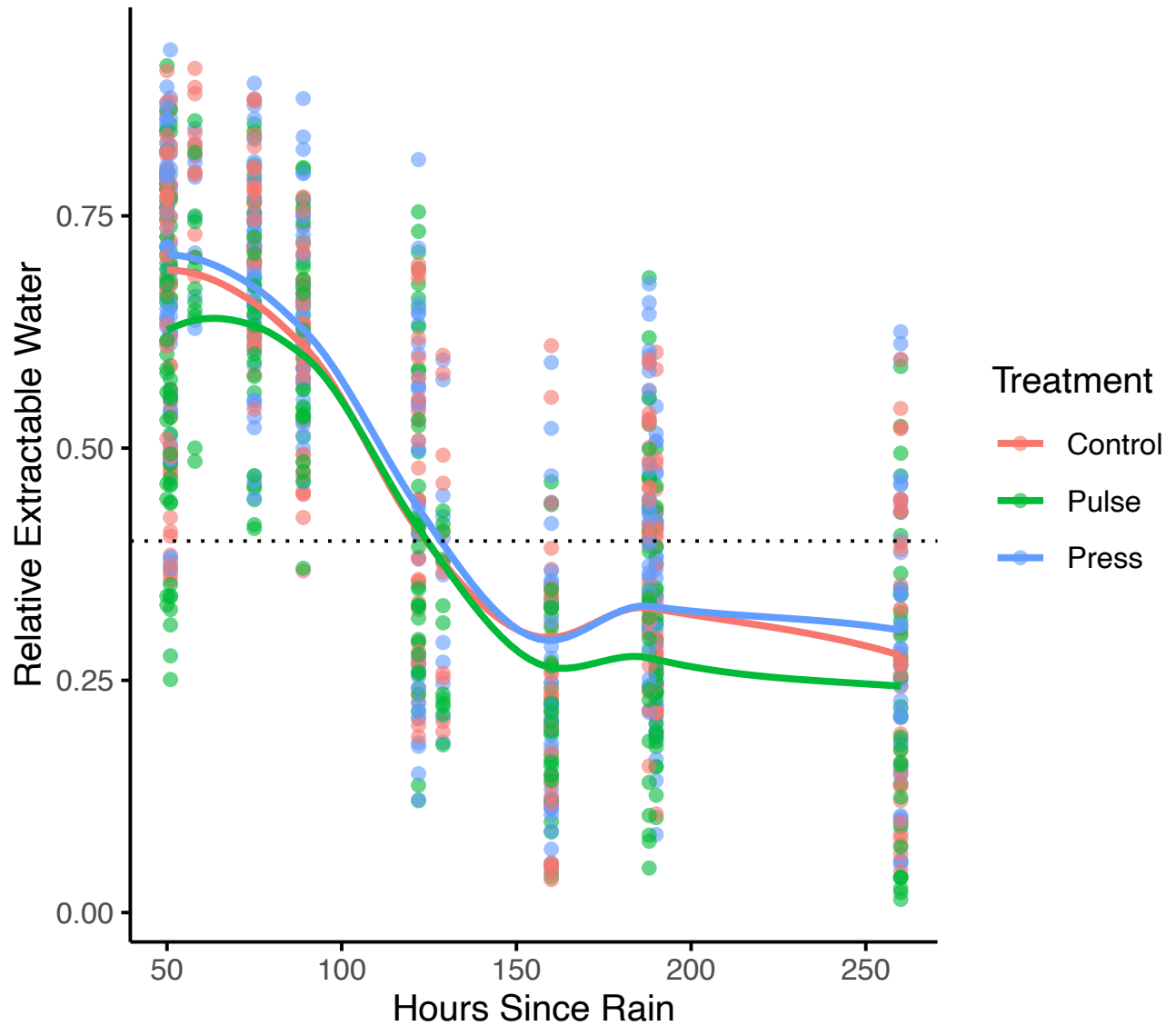


Figure A 7. Change in relative extractable water with hours since the last rain event greater than 5 mm. Each datapoint represents the relative extractable water of a single plot at a given time. A threshold level of 0.4 was used to determine periods of water stress indicated by the black dotted line. In each treatment, the threshold of 0.4 was reached ~125 hours after a rain event.

Appendix 5. Significant Regressions That Did Not Provide Evidence of Complementarity or Selection Effects

Table A 4. List of regressions that were significant or marginally significant (*italics*) but did not provide evidence of either complementarity or selection effects. In cases in black, biomass decreased with functional dispersion (FDis), the metric used to calculate multivariate trait complementarity. This indicates that productivity was lower in communities that had a high trait diversity of a given group of traits. In cases in red, biomass increased with the community weighted distance to best (CWD). This indicates that productivity was higher in communities that had trait values that diverged from the traits of the most productive species.

Treatment	Trait	Biomass metric	R ²	Adjusted p-value
Control	Log(FDis Leaf area & Specific root length)	Aboveground biomass	0.62	0.027
Control	Log(FDis Leaf area & Stomatal density)	Belowground biomass	0.37	0.049
Control	Log(FDis Leaf mass per area & Stomatal density)	Belowground biomass	0.37	0.049
<i>Control</i>	<i>Log(FDis Leaf area & Root diameter)</i>	<i>Aboveground biomass</i>	<i>0.50</i>	<i>0.055</i>
<i>Control</i>	<i>CWD Leaf mass per area</i>	<i>Aboveground biomass</i>	<i>0.33</i>	<i>0.068</i>
<i>Control</i>	<i>Log(FDis Leaf area & Root tissue density)</i>	<i>Aboveground biomass</i>	<i>0.42</i>	<i>0.098</i>
Press	Log(FDis Leaf area & Root tissue density)	Aboveground biomass	0.76	0.010

Press	FDis Leaf area & Stomatal density	Aboveground biomass	0.51	0.019
Press	Log(FDis Leaf area & Root diameter)	Aboveground biomass	0.68	0.026
Press	Log(FDis Root tissue density & Specific root length)	Aboveground biomass	0.62	0.035
Press	Log(FDis Root tissue density & Root diameter)	Aboveground biomass	0.57	0.049
Press	Log(FDis Specific root length & Root diameter)	Aboveground biomass	0.57	0.049
Press	Log(FDis Leaf area & Specific root length)	Aboveground biomass	0.61	0.039
Press	<i>FDis All traits</i>	<i>Aboveground biomass</i>	<i>0.35</i>	<i>0.055</i>
Press	<i>FDis Leaf mass per area & Root diameter</i>	<i>Aboveground biomass</i>	<i>0.49</i>	<i>0.075</i>
Press	<i>Sqrt(FDis Leaf area & Chlorophyll concentration)</i>	<i>Aboveground biomass</i>	<i>0.19</i>	<i>0.098</i>
Pulse	Log(CWD Leaf mass per area)	Aboveground biomass	0.63	0.0042

Appendix 6. Principal Component Analysis for Gymnosperm and Angiosperm Traits

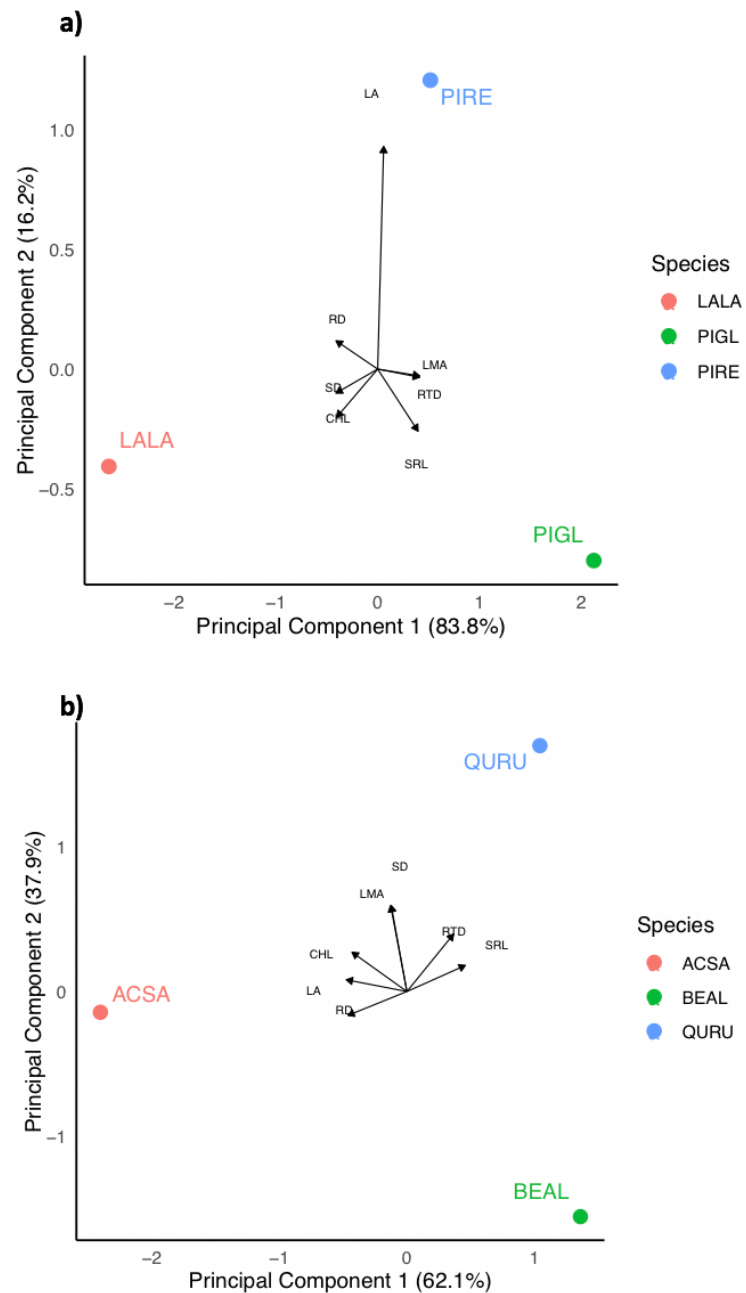


Figure A 8. Principal Component Analysis for traits of a) gymnosperms and b) angiosperms. In panel a), principal component 1 explains 83.8% of the variation in traits and principal

component 2 explains 16.2% of the variation in traits. In panel b), principal component 1 explains 62.1% of the variation in traits and principal component 2 explains 37.9% of the variation in traits. These Principal Component Analyses were done using the trait values measured at the IDENT-Outaouais plantation in 2024.