# Do hardwood species benefit from mixing with hybrid poplar? Evidence from a 10-year temperate tree-based intercropping system

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# Abstract

Temperate tree-based intercropping (TBI) systems, which integrate tree rows into crop fields, offer opportunities to diversify farm income and enhance ecosystem services. Yet, adoption remains limited, given uncertainties regarding species performance, especially in mixtures of fast- and slow-growing trees intended for timber and carbon benefits. This study assessed the 10-year performance of five temperate hardwood species (*Alnus glutinosa*, *Juglans nigra*, *Quercus macrocarpa*, *Q. rubra*, *Tilia americana*) that are planted in monoculture or interplanted with hybrid poplar (*Populus deltoides × P. nigra*) within tree rows of a TBI system (50 trees $ha^{-1}$) in southern Québec, Canada. Tree growth (height and diameter), carbon accumulation, and external defects were evaluated. Most mixtures performed as expected based on monoculture productivity, with net biodiversity effects not significantly differing from zero, except in *Q. rubra*-poplar mixtures, which showed positive net effects. Selection effects, driven by hybrid poplar dominance, were occasionally significant, while complementary effects were weak or negative. Tree carbon sequestration rates averaged 1.2 Mg C $ha^{-1}$ $yr^{-1}$ in hardwood monocultures, 4.4 Mg C $ha^{-1}$ $yr^{-1}$ in mixtures, and 7.1 Mg C $ha^{-1}$ $yr^{-1}$ in poplar monocultures. While hardwoods showed reduced diameter growth in mixtures, similar tree heights led to higher height-to-diameter ratios, suggesting improved stem form. Physical injuries and morphological defects tended to be less frequent in mixtures, although not significantly so. These findings underscore the importance of species selection in TBI design. Functional contrasts may not ensure positive interactions, especially under fertile conditions or when competition dominates. Species-specific vulnerabilities, e.g., *A. glutinosa* necrosis, warrant further attention. Long-term monitoring is needed to evaluate the persistence of diversity effects.


# 1. Introduction

Temperate tree-based intercropping (TBI) systems, which are also known as alley cropping or silvoarable systems, have been recognized for their ability to deliver a broad spectrum of ecosystem services, often surpassing those that are provided by conventional agricultural practices. These services include enhancing the stability of crop yields in the face of climate change, promoting soil and water conservation, increasing carbon (C) sequestration, and supporting greater biodiversity (Reyes et al. 2021; Jacobs et al. 2022; Kletty et al. 2023; Rolo et al. 2023). TBI systems also offer opportunities for producing high-quality timber, encompassing both short-rotation species such as poplars (*Populus* spp.) and long-rotation hardwoods like walnut (*Juglans* spp.) and oak (*Quercus* spp.), while simultaneously generating annual returns from agricultural crops. Despite these potential benefits, TBI systems have seen limited adoption in several temperate regions, especially when compared to other agroforestry systems like windbreaks and hedgerows (Thevathasan et al. 2012; Santiago-Frejanes et al. 2018). One of the key barriers to their adoption is the lack of accessible information regarding their productivity and feasibility for farmers (Borremans et al. 2016; Hotelier-Rous et al. 2020). Addressing these knowledge gaps is essential to encouraging wider implementation and unlocking the full potential of TBI systems.

In TBI systems designed to simultaneously produce high-quality timber and annual cash crops, initial tree planting densities are typically kept low (e.g., 50 trees $ha^{-1}$) to facilitate machinery operations and minimize competition between trees and crops (Graves et al. 2007; Carrier et al., 2019). The successful establishment and early growth of each tree, which is free from wood defects, are crucial for maximizing both economic returns and the environmental benefits that are provided by the trees. However, research on the establishment success of tree species with contrasting growth strategies in temperate TBI systems remains limited. Existing studies highlight that tree survival and vigorous early growth are strongly influenced by species selection (Balandier and Dupraz 1999; Delate et al. 2013; Rivest and Cogliastro 2019; Udawatta et al. 2024). Among commonly used genera, poplar is prominent in temperate TBI systems due to its adaptability and rapid growth (Wolz et al. 2018; Piotto et al. 2024). Poplars are particularly valued in TBI systems for their ability to provide a range of ecosystem services rapidly, including C sequestration, soil health improvement, and wind speed reduction (Gagné et al. 2022; Veldkamp et al. 2023). Yet, as poplars mature, they may increasingly compete with adjacent agricultural crops, potentially leading to reduced crop yields (Burgess et al. 2005; Reynolds et al. 2007; Bouttier et al. 2014). Most previous studies on TBI systems have predominantly examined single-species plantations rather than multi-species combinations (Wolz and DeLucia 2018). Furthermore, growing evidence suggests that greater tree species diversity enhances ecological niche availability, strengthens resistance and resilience to pests, pathogens and weather extremes, and supports increased biodiversity (Liu et al. 2018; Messier et al. 2022).

This study investigates an innovative TBI system that combines fast-growing poplars with a variety of moderately growing hardwood species within tree rows. The underlying rationale is that integrating fast- and moderate-growing species, rather than relying solely on monocultures, can help distribute wood income more evenly over time, while simultaneously balancing trade-offs in the delivery of ecosystem services within TBI systems. By incorporating poplar as a “shelter tree,” this approach can create favourable environmental conditions (e.g., wind protection, moderate shading) that would enhance the timber quality of associated hardwood species (Paquette and Messier 2010f et al. 2014). These improvements include achieving a higher height-to-diameter ratio, which is associated with reduced stem taper, and minimizing morphological defects such as forks, large branches, and stem sweeps. Furthermore, evidence from various agroforestry and forest plantation systems suggests that even simple mixtures of two species can outperform monocultures in terms of biomass production and C storage (Ma et al. 2020; Feng et al. 2022; Warner et al. 2023). This over-yielding process may result from complementary relationships between structural and functional traits (e.g., shade tolerance, growth rate, root depth and crown architecture) of different tree species, leading to more efficient use of resources. Mixing tree species with different functional traits can also improve the reliability of establishment compared to mosaics of monocultures, where some species may perform poorly (Tuck et al. 2016). Integrating species with specific traits, such as nitrogen ($N_2$) fixation, also can enhance the productivity of mixed stands. For example, $N_2$-fixing species can increase N availability for neighbouring non-fixing species, thereby promoting their growth and C sequestration potential (Piotto 2008; Richards et al. 2010). Yet, increasing species diversity is not without challenges. Under some conditions, tree species

mixtures may reduce soil nutrients and water, and productivity due to intense interspecific competition (Liu et al. 2018). These responses highlight the need to carefully select and combine tree species in mixtures that are based on complementary traits to maximize positive interactions and minimize negative ones, ultimately enhancing the benefits of TBI systems.

The objective of this study was to evaluate the performance of five hardwood species (*Alnus glutinosa*, *Juglans nigra, Quercus macrocarpa, Q. rubra*, *Tilia americana*) that are either grown in monoculture or interplanted with hybrid poplar (*Populus deltoides* x *P. nigra*) within the tree rows of a 10-year-old temperate TBI system (50 trees $ha^{-1}$) that had been established in southern Québec, Canada. Tree performance was assessed through size (height and diameter), C stocks, and the presence of external defects. This study tested three hypotheses: 1) biomass C accumulation would be greater in the hardwood-poplar mixtures than in the respective monocultures; 2) *Alnus glutinosa* would facilitate poplar growth due to its $N_2$-fixing ability; and 3) hardwood species grown in mixtures with poplars are expected to exhibit higher height-to-diameter ratios and fewer external defects compared to those grown in monoculture.

## 2. Materials and methods

# 2.1 Study site and experimental design

The study was conducted near St-Télesphore, Québec, Canada (45°17'N, 74°26'W; about 67 m above sea level), in the southwestern region of the province. According to 30-year climate normals (1981–2010) that were recorded from the Dalhousie Mills, ON, station (45°19'N, 74°28'W), the area experiences an average annual temperature of 5.8°C and total precipitation of 1077 mm. The terrain is gently sloping and free of stones. The soil, originating from marine deposits, is classified as a Humic Gleysol (Dalhousie soil series; Soil Classification Working Group 1998) with a clay loam texture (24% sand, 38% silt, 38% clay) and a pH of 6.3 in the uppermost 20 cm.

The experimental site encompassed a 10-ha field with subsurface drainage, where a TBI system had been established in May 2014. The system included eight single rows of trees, each measuring 170 m in length and aligned northwest-southeast (Fig. 1). Trees were spaced 5 m apart within rows and 40 m between rows, resulting in a density of 50 trees $ha^{-1}$. The experimental design was structured into three replicated blocks, each containing two adjacent tree rows and 11 TBI plots (sequences of five to ten trees). The first and last rows of trees were designated as guard rows and were excluded from all analyses.

Within the TBI system, six randomly distributed plots in each tree row were planted with either high-value hardwood species (European black alder, *Alnus glutinosa* [L.] Gaertner; red oak, *Quercus rubra* L.; black walnut, *Juglans nigra* L.; bur oak, *Quercus macrocarpa* Michauux; basswood, *Tilia americana* L.) or fast-growing hybrid poplar (*Populus deltoides* W. Bartram ex Marshall × *Populus nigra* L., clone 3570) in monoculture. Additionally, five plots that were randomly distributed in other rows, consisted of

alternating high-value hardwoods and hybrid poplars (Fig. 1). Each plot included single buffer trees at both ends, which were excluded from the statistical analyses. The hardwood species were planted using 2-year-old pot transplants, which were about 75 cm in height, while hybrid poplar was established with 1-year-old bare-root transplants, averaging 150 cm in height at the time of planting. Since their establishment in 2014, both poplars and hardwoods have undergone annual pruning to maintain a single straight stem and to remove branches up to one-third of the tree height. Along each tree row, a 1.5 m-wide uncultivated strip was maintained, with herbaceous vegetation that was managed using continuous black polyethylene-film mulch.

In the cultivated alleys, the crop rotation alternated between perennial forages and annual crops. The rotation sequence included a perennial forage mixture (*Medicago sativa* L.; *Phleum pratense* L.; *Festuca arundinacea* [Schreb.] Dumort.), which was harvested twice per growing season (2014–2015 and 2019–2021), maize (*Zea mays* L., 2016 and 2023), wheat (*Triticum aestivum* L., 2017 and 2022), and soybean (*Glycine max* [L.] Merrill, 2018). Annual crops that were grown for their grain were cultivated using conventional tillage practices: a mouldboard plough set to a depth of 20 cm in the autumn after harvest, followed by disking and harrowing to 10 cm depth before seeding. Management practices, including herbicide applications, cultivar/hybrid selection, and fertilization, adhered to local agronomic guidelines (CRAAQ 2010; RGCQ 2016). Nitrogen fertilizer was applied at standard rates: approximately 150 kg $ha^{-1}$ for maize, 100 kg $ha^{-1}$ for wheat, 25 kg $ha^{-1}$ for soybean, and 60–80 kg $ha^{-1}$ for perennial forages.

## 2.2 Tree measurements

Survival, tree heights and diameters at breast height (DBH, measured at 130 cm above ground) of all individuals were recorded in April 2024, marking the completion of 10 growing seasons. Heights were measured using an 11 m graduated pole (hardwood species; Sokkia, Tokyo, Japan) or with a hypsometer (hybrid poplars; Vertex III, Haglöf, Sweden). DBH was determined with standard calipers. The height-to-DBH (H/D) ratio, which is a measure of tree shape, was calculated for each tree and used as an indicator of competition intensity (Thomas et al. 2021). We also assessed the occurrence (presence or absence) of different external tree defects, including suckers, sprouts, forks (occurring at ≥ 2.75 m height), strong branches (diameter ≥ 5 cm), checks (surface wood cracks), sweeps (stem curvatures), frost cracks (longitudinal wood separations), trunk inclination (≥ 10 degrees off vertical), necrosis, physical injuries at the tree base, and crown breakage.

Above-ground biomass (including branches, wood, and bark) of bur oak (*Q. alba* was used as the closest species phylogenetically), red oak, basswood, and black alder was estimated using allometric equations that were developed for forest conditions (Lambert et al. 2005; Liepiņš et al. 2021), with a correction factor of 1.2 applied to account for enhanced crown development that is typical of trees growing on agricultural land (Zhou et al. 2015). For hybrid poplar and black walnut, above-ground biomass was estimated using allometric equations that were specifically designed for agroforestry contexts (Fortier et al. 2013; Bazrgar et al. 2024). Below-ground biomass for all species was estimated using Eq. 5 from Li et al. (2003). Tree C stocks were then calculated based on species-specific C concentrations for stems,

which were obtained from the global database that was compiled by Doraisami et al. (2022). These stocks were then divided by the area that was occupied by each tree (10 $m^2$) on the uncultivated strip to express values in Mg C per hectare. Tree C stocks of the four dead individuals were estimated at zero. For the four suckers that survived the death of their main stems and lacked which DBH measurements, C stocks were estimated as the half-value of the smallest recorded tree stock.

# 2.3 Statistical analysis

Net effects on tree C stocks were calculated for each mixture plot as the difference between the observed and the expected values based on the performance of corresponding monocultures within the same block:

$$Net\ effect = Observed - Expected = \sum p_i \times Mixture_i - \sum p_i \times Monoculture_i$$

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where $p_i$ is the proportion of each species *I* in the mixture (always 0.5), and $Mixture_i$ and $Monoculture_i$ are the average C stocks (Mg C $ha^{-1}$) for each species in mixture and monoculture, respectively. We used the method of Loreau and Hector (2001) to partition the net effect into complementarity effects (positive species interactions) and selection effects (dominance of productive species).

Mixture effects (net, complementary and selection) were compared among the five mixture compositions using the following model:

*Mixture effect (Mg C* $ha^{-1}$*) ~ Composition + random(1 | Block)* (2)

where *Composition* is a categorical variable (five mixture compositions) and *Block* is included as a random effect to account for spatial correlation. One-way ANOVA was used to test the effect of Composition. To assess whether mixture effects differed significantly from zero overall, we used the same model without *Composition* and tested the intercept. Mixture effects were also compared to zero within each composition using one-sample *t*-tests.

Transgressive over-yielding (i.e., when tree productivity in mixture exceeds that of the best monocultures) was tested with the following model:

*Tree C stocks (Mg C* $ha^{-1}$*) ~ Composition + random(1 | Block)* (3)

where *Composition* includes all mixtures and monocultures. If the overall effect was significant, Tukey's HSD was used for post hoc comparisons.

Relative yields (RY = mixture value / average monoculture value within the same block) in terms of tree C stocks were calculated for each individual tree in mixtures. Differences in relative yield from the null hypothesis of one were tested for each species within each mixture composition, as well as for all hardwood species combined, using the following model:

*(RY − 1) ~ Composition × Tree type + random(1 | Block/Plot)* (4)

where *Composition* (five mixture compositions) and *Tree type* (hardwood species vs. hybrid poplar) are treated as categorical variables; and the nested random effects account for spatial correlation within each mixture plot and within each block. Confidence intervals of the means for hardwood species and hybrid poplar within each composition were used to assess the difference from the null hypothesis. ANOVA with type III sums-of-squares were used to test the significance of fixed effects, and multiple comparisons were performed using Tukey tests when *Composition* or its interaction was significant.

For DBH, height and H/D ratio, dead trees and suckers (from dead main stems) were excluded. The effect of mixing was tested for each variable using the following model:

*Size ~ Treatment × Species + random(1 | Block/Plot)* (5)

where *Size* is DBH, height or H/D ratio; *Treatment* (mixture vs. monoculture) and *Species* are categorical variables; and the nested random effects are the same as Eq. 4. Type-III ANOVAs were conducted, after which Tukey tests were used for post hoc comparisons when interaction or *Species* effects were significant.

Tree survival analysis was not conducted, given that mortality occurred in only one species (4 of 26 black alders). Yet, mixed-effect logistic regressions were used to test the difference between mixtures and monocultures in terms of the proportion of individual trees that were affected by four categories of defects: 1) physical injuries (crown breakage, checks and frost cracks, tree base injuries, and trunk inclination); 2) morphological defects (forks, strong branches and sweeps); 3) pruning-related defects (suckers and sprouts); and 4) necrosis. One model was run for each defect category:

*Presence of defect ~ Treatment × Species + random(1 | Block/Plot)* (6)

where *Presence of defect* is a binary variable and the fixed and random effects are the same as in Eq. 5. The significance of fixed effects was evaluated using likelihood ratio tests. A sub-model excluding hybrid poplar was also fitted to test the third hypothesis directly.

Natural logarithm or square-root transformations were applied when necessary to meet assumptions of normality and homoscedasticity. All analyses were conducted in R version 4.2.3 (R Core Team 2023) using the packages “glmmTMB” for mixed models (Brooks et al. 2017), “car” for ANOVA (Fox and Weisberg 2019) and “emmeans” for multiple comparisons (Lenth 2023).

# 3. Results

# 3.1 Tree C stocks

On average, mixtures performed as expected based on their corresponding monocultures, with net effects not significantly differing than zero (Fig. 2). The only exception was red oak mixed with hybrid

poplar, which exhibited a positive net effect ($P < 0.05$, 3.4 ± 0.6 Mg C $ha^{-1}$). Mixtures involving black walnut or bur oak with hybrid poplar showed significant selection effects, driven by the dominance of the most productive species (i.e., the hybrid poplar) over the less productive hardwood species within the mixtures (Fig. 2). However, negative trends in complementary effects (i.e., species yielding less on average within the mixtures) resulted in overall net effects that were not different from zero for these mixtures. Net, complementary and selection effects did not differ among mixture compositions (Eq. 2 model, $P > 0.05$).

On average, hardwood species accumulated less C in mixtures with hybrid poplar compared to their monocultures (RY < 1), with black walnut and bur oak showing significant growth reductions (Fig. 3). Although 75% of hybrid poplars in mixtures had greater C stocks than individuals in monoculture (RY > 1), this trend was not statistically significant (Fig. 3). According to the model comparing RY (Eq. 4), RY were, on average, lower for hardwoods species than for hybrid poplars (*Tree type*: $P < 0.001$). Mixture composition was not significant ($P > 0.05$), but its interaction with *Tree type* was significant ($P < 0.05$). Yet, multiple comparisons did not reveal significant differences in RY across mixture compositions for either tree type (Fig. 3).

No transgressive over-yielding was observed, i.e., no mixture outperformed both of its corresponding monocultures (Table 1). Tree C sequestration rates 10 years after plantation was lowest in hardwood monocultures (1.2 Mg C $ha^{-1}$ $y^{-1}$), intermediate in hardwood-poplar mixtures (4.4 Mg C $ha^{-1}$ $y^{-1}$) and highest in hybrid poplar monoculture (7.1 Mg C $ha^{-1}$ $y^{-1}$). Note that the C stock estimates in Table 1 are based on one hectare of uncultivated tree strip. For estimates based on one hectare of the full TBI system, including the cultivated alley, see Supp. Table 1.

Table 1
Average tree C stocks per hectare of uncultivated strip (± SE) within each monoculture and each mixture with hybrid poplars, 10 years after planting. Different letters indicate significant differences based on multiple comparisons (Tukey tests, $P < 0.01$).

| | Tree C stocks (Mg C $ha^{-1}$) | |
|---|---|---|
| Species | Monoculture | Mixture |
| Basswood | 12.3 ± 0.6 c | 40.0 ± 6.9 b |
| Black alder | 17.9 ± 4.0 c | 49.0 ± 2.5 b |
| Black walnut | 12.0 ± 1.3 c | 46.7 ± 5.4 b |
| Bur oak | 8.8 ± 0.9 c | 41.1 ± 3.2 b |
| Red oak | 10.0 ± 1.5 c | 44.0 ± 2.8 b |
| Hybrid poplar | 71.3 ± 5.9 a | N/A |

## 3.2 Tree diameter and height

Tree height, DBH and H/D ratio differed significantly among species (ANOVA on models from Eq. 5, $P < 0.001$). The average treatment effect (mixture vs. monoculture) was significant for height ($P < 0.05$), DBH and H/D ratio (both $P < 0.001$). This treatment effect varied significantly among species for DBH and the ratio ($P < 0.01$ and $P < 0.001$, respectively, for Eq. 5 interactions). Hardwood species averaged smaller DBH values in mixtures with hybrid poplars than in monocultures, while heights remained comparable (Fig. 4A and 4B). Significant DBH reductions in mixture were observed for black walnut and bur oak, with bur oak also showing reduced height. These changes led to significantly increased H/D ratios in mixtures for most hardwoods (all species except black alder and red oak; Fig. 4C). For hybrid poplar, the H/D ratio was slightly reduced in mixtures compared to monocultures ($P < 0.1$; Fig. 4C).

## 3.3 Tree external defects

There was a trend toward reduced physical injuries (Fig. 5A, all species except black alder) and morphological defects (Fig. 5B) in mixtures compared to monocultures. However, this difference was not significant for physical injuries and only marginally significant ($P < 0.1$) for morphological defects (*Treatment* effect from the Eq. 6 models). Although the categorical variable *Species* was highly significant ($P < 0.001$, see Eq. 6) in explaining morphological defects, post hoc comparisons did not reveal significant differences among species. Interactions between *Treatment* and *Species* were not significant in the models for physical injuries and morphological defects, but were marginally significant ($P < 0.1$) for the proportion of suckers or sprouts. On average, this proportion did not increase in mixtures relative to monocultures (*Treatment* at $P > 0.05$), but marginally significant increases were observed generally for hardwood species and specifically for black alder (Fig. 5C). The proportion of suckers or sprouts also differed significantly among species ($P < 0.001$), with basswood, black alder and hybrid poplar exhibiting higher proportions than black walnut and bur oak (Fig. 5C). Black alder was the only species that was affected by necrosis, with no significant difference between mixtures (44% of individual trees) and monocultures (47%).

# 4. Discussion

## 4.1 Biodiversity effects in hardwood-poplar mixtures

Several authors have emphasized the importance of increasing species diversity in tree plantations, including agroforestry systems, as a strategy for promoting complementary resource use, improving structural complexity, reducing vulnerability to pests and climatic extremes, and potentially increasing C sequestration through over-yielding effects (Lovell et al. 2018; Schwarz et al. 2021; Messier et al. 2022). To our knowledge, this is one of the first studies to explicitly evaluate net biodiversity, selection, and complementarity effects in mixtures of multiple hardwood species that were interplanted with fast-growing hybrid poplar within the tree rows of a TBI system. These mixed-species systems, which were

established a decade ago, offer a unique opportunity to examine early-stage interactions among species with contrasting growth rates and functional traits.

Our first hypothesis, predicting greater biomass C accumulation in mixtures, was not supported. Overall, the net biodiversity effects on aboveground tree C stocks were generally neutral (Fig. 2). One possible explanation lies in the stress-gradient hypothesis (Maestre et al. 2009), which posits that positive interactions such as facilitation are more likely to occur under high environmental stress (e.g., low nutrient availability), while competition tends to dominate in more favourable conditions. In our case, the experimental site was characterized by high baseline N availability (with bioavailable $NO_3^-$-N often exceeding 1 μg $cm^{-2}$ $d^{-1}$ during the growing season; Rivest et al. 2025) and received regular fertilization targeted to the alley crops. Previous work has shown that alley cropping can help alleviate nutrient limitations for trees in similar TBI systems, partly by allowing trees to benefit from residual fertilizer inputs that are not taken up by the crops (Rivest et al. 2009). These favourable conditions likely reduced the potential for belowground complementarity in nutrient uptake between species. Moreover, under high-fertility conditions, different tree species may compete for the same resources rather than partition them, further weakening biodiversity effects. Similar findings have been reported in mixed-species plantations that were established on fertile lands (Richards et al. 2010; Pretzch et al. 2013).

The only exception to the generally neutral net biodiversity effects was the red oak-poplar mixture, which exhibited a significant positive net effect (Fig. 2). This response was primarily driven by a strong selection effect that was attributed to the dominance of hybrid poplar, rather than true species complementarity. This highlights that biodiversity effects in TBI systems can be species-specific and largely influenced by the performance of the most productive species. Indeed, the selection effect tended to be significant when considering all hardwood species that were combined with poplar (Fig. 2), indicating that the presence of a highly productive species like hybrid poplar often governs mixture productivity. This pattern aligns with findings from other young experimental tree communities, where acquisitive, shade-intolerant species tend to over-yield, likely due to reduced competition from neighbouring species (Tobner et al. 2016; Dietrich et al. 2023). Hybrid poplar, with its rapid height growth and shade intolerance, appears to suppress slower-growing, shade-tolerant hardwoods, reinforcing its dominant role in early productivity.

On average, hardwood species accumulated less C when grown in mixture with hybrid poplar compared to in monoculture (RY < 1), especially for black walnut and bur oak (Fig. 3). These reductions may be partly attributed to interspecific competition for light, given that the rapid height growth of hybrid poplar, which on average was about 3.4 times greater than the hardwood species (Fig. 4B), likely led to canopy dominance. Shade tolerance appears to be a key trait influencing performance in these mixtures. Black walnut and bur oak are both considered light-demanding and relatively shade-intolerant species (Niinemets and Valladares 2006), making them less competitive under the partial shading that is created by poplar canopies. In contrast, species such as basswood and red oak, which exhibit greater shade tolerance, maintained more stable growth in mixtures. These findings underscore the importance of

considering functional compatibility, especially shade tolerance, when selecting species with contrasting growth strategies in temperate TBI systems.

Our results suggest that while early-stage TBI mixtures may not consistently enhance C accumulation relative to monocultures, species-specific interactions, functional traits, and stand development dynamics remain key drivers. Despite some growth reductions in individual hardwoods, hardwood-poplar mixtures appear more promising for biomass C sequestration than TBI systems that are composed solely of moderate- or slow-growing hardwood species (Table 1). These mixed-species systems can also deliver other ecosystem services more rapidly, including crop yield stabilization under climate change, improved water infiltration, reduced soil erosion, increased soil C inputs, and windbreak functions (Gagné et al. 2022; Rivest et al. 2025). Moreover, they are more likely to sustain these ecosystem services over the long-term compared to hybrid poplar monocultures, which are typically harvested about 15 years after planting. Longer-term studies are needed to assess whether the balance between competition and complementarity shifts over time, potentially enhancing the net benefits of mixtures, as has been observed in other tree diversity experiments (Urgoiti et al. 2022; Zheng et al. 2024). Furthermore, new experimental designs are required to assess how management practices, such as tree spacing, species combinations, and harvesting schedules, can be optimized to balance growth, C sequestration, and ecosystem services delivery in TBI systems with species of contrasting growth rates.

## 4.2 Limited evidence for facilitation by black alder

Our second hypothesis posited that black alder, through its capacity for biological $N_2$-fixation, would facilitate hybrid poplar growth in mixture. However, we found no evidence of such a facilitative effect, i.e., equivalent relative yields for hybrid poplars among mixture compositions (Fig. 3). A likely explanation is that the expected positive effect of $N_2$-fixing trees may be substantially diminished on fertile sites where soil N availability is already high. This was likely the case at our study site, which had elevated baseline N levels and received regular fertilization. Moreover, N fertilization or other nutrient additions often suppress fixation rates, given that free-living $N_2$-fixing bacteria are typically facultative and tend to reduce fixation when N is abundant (Reed et al. 2011). This suggests that the potential growth benefits that are conferred by $N_2$-fixing species may be highly context-dependent. Other factors may also exert limited facilitation, including possible belowground competition between black alder and poplar for water or other nutrients, or a lack of temporal complementarity in N uptake. Overall, these results challenge the assumption that $N_2$-fixing species consistently enhance the productivity of non-fixers neighbours in temperate TBI systems.

## 4.3 Influence of species mixtures on hardwood height-to-diameter ratios and defect occurrence

Our third hypothesis had posited that hardwoods that were grown in mixtures with hybrid poplars would exhibit higher height-to-diameter (H/D) ratios and fewer external defects than their monoculture counterparts. Our results partially supported this hypothesis. While H/D ratios were indeed higher in mixtures for most hardwood species, particularly basswood, black walnut, and bur oak, this response

was primarily driven by significant diameter reductions rather than by increases in height (Fig. 4). This morphological pattern likely reflects asymmetric light competition, whereby fast-growing poplars cast substantial shade on neighbouring hardwoods, given the greater stature and rapid early growth of the former. This can limit diameter growth in the understory trees, a dynamic that is commonly observed in mixed-species plantations where so-called "nurse trees" dominate early resource capture (Kelty 2006; Pretzsch et al. 2013). Interestingly, a moderate increase in H/D ratio can have positive implications for stem quality. It may be associated with reduced stem taper, increased stem stiffness and fewer lower branches; these are traits that are desirable for high-quality timber production (Kijidani et al. 2010; Huuskonen et al. 2014). These findings suggest that beyond potential growth trade-offs, hardwood-poplar mixtures may offer structural benefits that enhance the value of hardwood timber in temperate TBI systems.

Contrary to expectation, the incidence of morphological and physical defects, including forks, strong branches, checks, sweeps, frost cracks, trunk inclination, and physical injuries at the tree base, was only marginally lower in mixtures compared to monocultures (Fig. 5). Several factors may explain this limited improvement in stem quality. First, although shading from fast-growing poplars might suppress lateral branching in some understory trees, light conditions in the lower canopy were likely to be too heterogeneous or weak to consistently promote self-pruning and strong apical dominance. This inconsistent light may allow large or codominant branches to persist, particularly in shade-tolerant species. Second, physical injuries such as trunk base wounds or frost cracks often result from microclimatic or mechanical factors (e.g., from mowing or frost-thaw cycles) that mixing tree species cannot mitigate without sufficient canopy cover to buffer thermal fluctuations or reduce maintenance damage, such defects persist. Third, species-specific architecture and growth habits may override mixture effects; for example, black walnut is inherently prone to forking or strong lateral branching regardless of light availability (Nicolescu et al. 2020). Additionally, annual formative pruning to correct structural defects (e.g., forks or large branches) may have contributed to reducing variability in stem quality among treatments, thereby masking potential effects of species mixtures. Overall, while mixtures can sometimes improve stem form by encouraging vertical growth, our results suggest that species identity, planting design, and early management practices have a stronger influence than species diversity alone in controlling external defects in hardwoods grown in TBI systems.

High necrosis rates were observed in black alder in both monoculture and mixture treatments, often occurring at the root collar or lower stem (Fig. 5). Similar symptoms have been widely reported in Europe and North America, and are frequently associated with infections by oomycete fungi of the *Phytophthora alni* complex (root and collar rots) or other opportunistic pathogens such as *Diaporthe alnea* (= *Phomopsis alnea*; Ascomycota; bark canker), particularly under conditions of drought stress, mechanical injury, or poor drainage (Brasier et al. 1995; Moricca et al. 2002). In our study, this recurrent necrosis likely induced significant physiological stress, which in turn triggered a strong sprouting response from the base of the stem. The proliferation of suckers or basal shoots is a known adaptive mechanism in alder species following injury or disturbance, but it compromises stem form and wood quality, and may reflect poor adaptation to the site conditions. In light of these observations, black alder appears to be an

unsuitable species for TBI systems in eastern Canada, where freeze–thaw cycles, soil saturation, or pathogen pressure may exacerbate susceptibility to stem damage and undermine tree performance.

## 5. Conclusion

This study evaluated C stocks in tree biomass, tree size (height and diameter), and external stem defects in five temperate hardwood species grown in monoculture and in combination with hybrid poplar in a 10-year-old TBI system. Overall, species diversity conferred limited benefits for C accumulation during the first decade. Rather than complementarity effects, we observed a selection effect, with fast-growing hybrid poplar driving productivity in mixtures. This suggests that early biomass outcomes were shaped more by species-specific growth dominance than niche differentiation. The limited complementarity likely reflects the site's high fertility, which may have reduced opportunities for facilitation, consistent with the stress-gradient hypothesis, and diminished $N_2$-fixation by black alder. Most hardwood species showed reduced diameter growth in mixtures, resulting in slightly higher H/D ratios, a trait potentially favourable for timber quality. Yet, improvements in stem defects were modest and species-specific, with black alder performing poorly due to high levels of necrosis and sprouting. Despite some growth reductions in individual hardwoods, mixtures with hybrid poplar sequestered substantially more biomass C than hardwood monocultures and may better sustain ecosystem services over the long term, particularly in TBI systems where productivity is a key objective. Our study underscores the importance of considering species traits, site fertility, and early interspecific competition when designing TBI systems. Continued monitoring will be essential to assessing whether complementarity effects emerge as agroforestry stands mature.

## Declarations

# Author Contribution

David Rivest: Conceptualization, Writing—original draft preparation, Supervision. Marc-Olivier Martin-Guay: Data analysis, Writing—Review & Editing. Alain Cogliastro: Conceptualization, Data collection, Writing—Review & Editing.

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# Data Availability

Data is provided within the manuscript.

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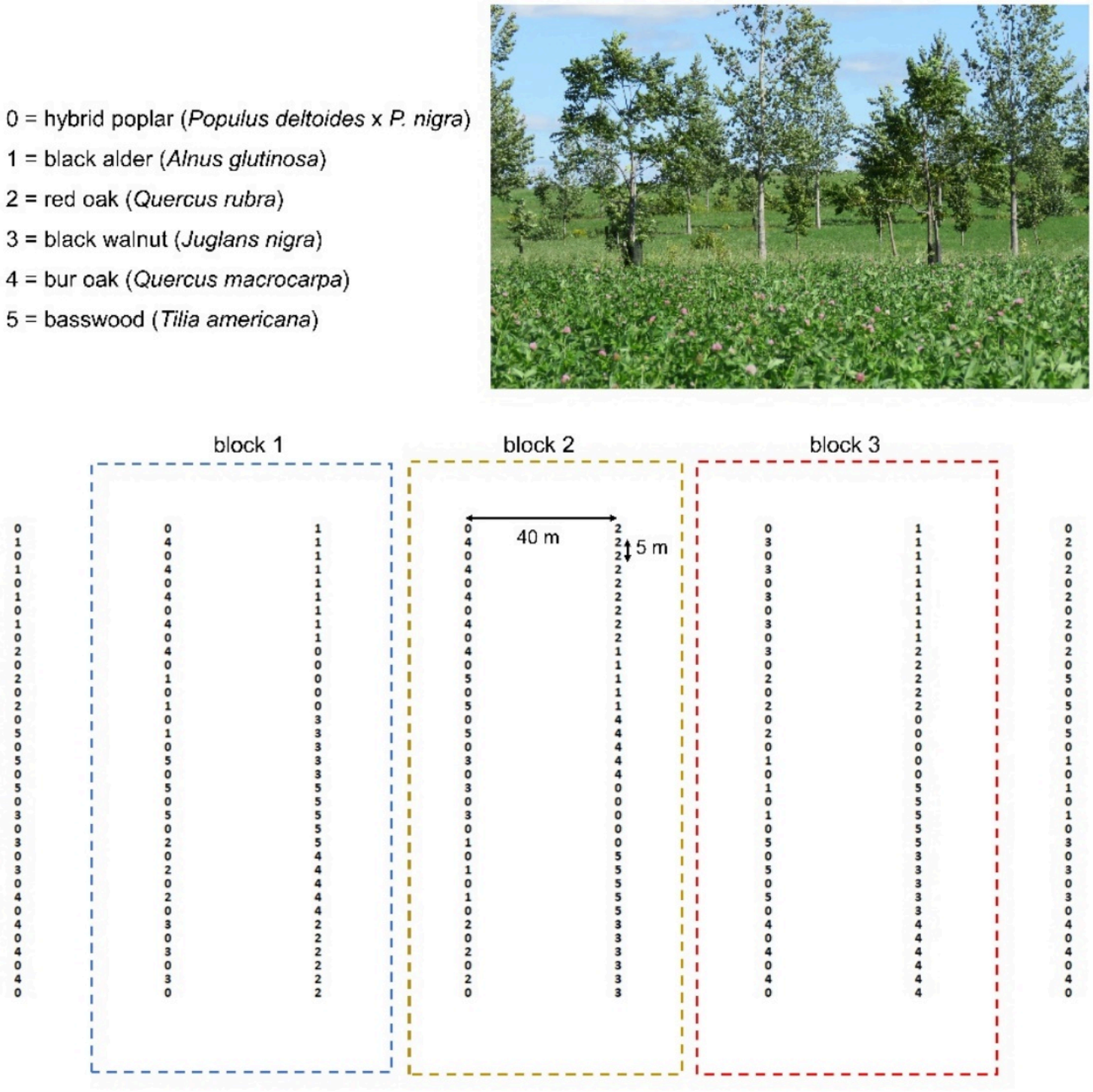
# Figures




## Figure 1

Experimental layout (not to scale) of the tree-based intercropping system. The first and last rows of trees form guard rows. The photo showing black walnut alternating with poplar within a tree row was taken when the system was 6-years-old.

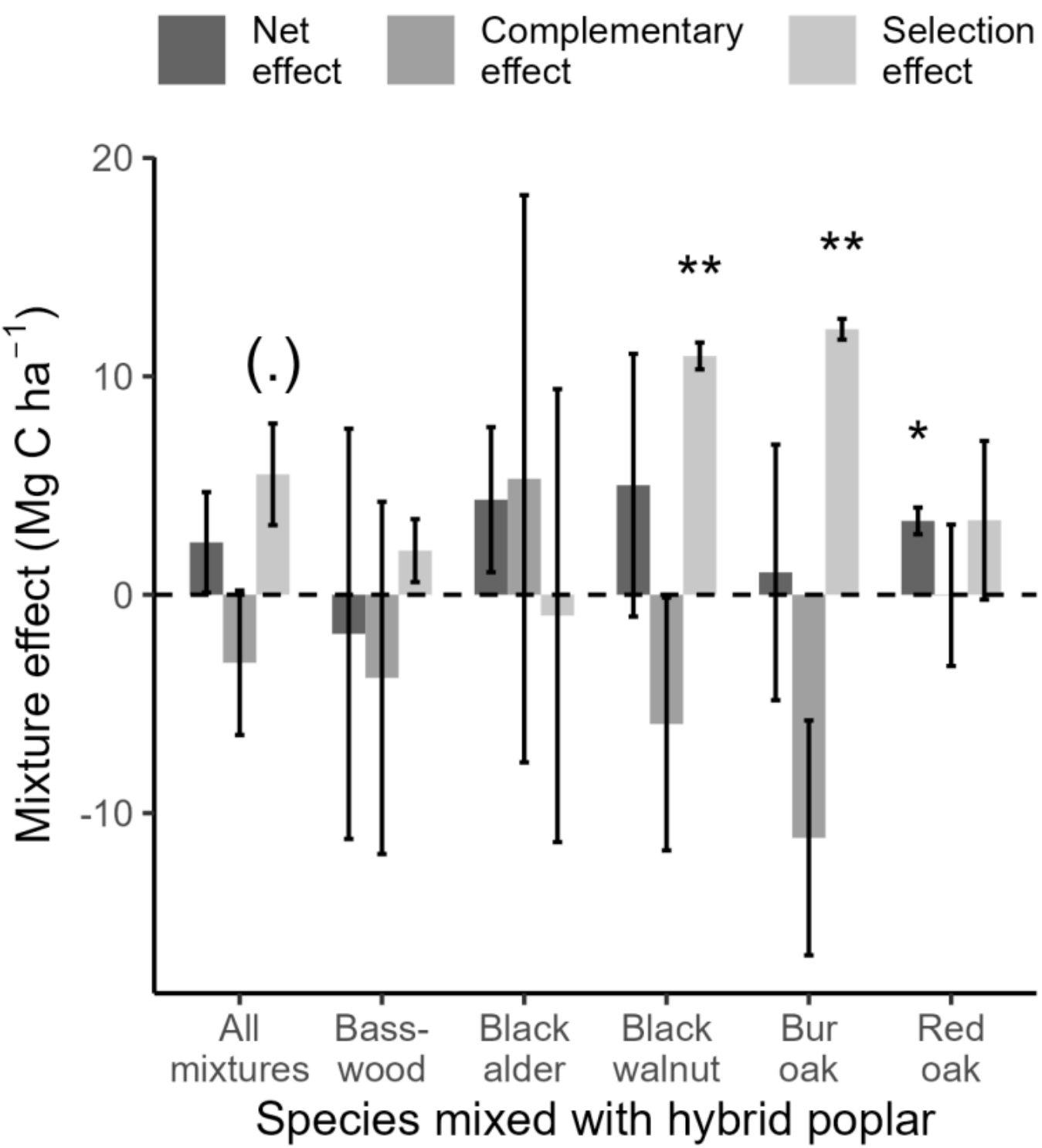



**Figure 2**

Net, complementarity and selection effects (from darker to lighter grey) on tree C stocks for all mixtures combined ($N$ = 15) and for each mixture composition separately ($N$ = 3). Means and standard errors are shown. Significance levels for differences from zero (dashed line): (.) $P$< 0.1, * $P$< 0.05 and ** $P$< 0.01.

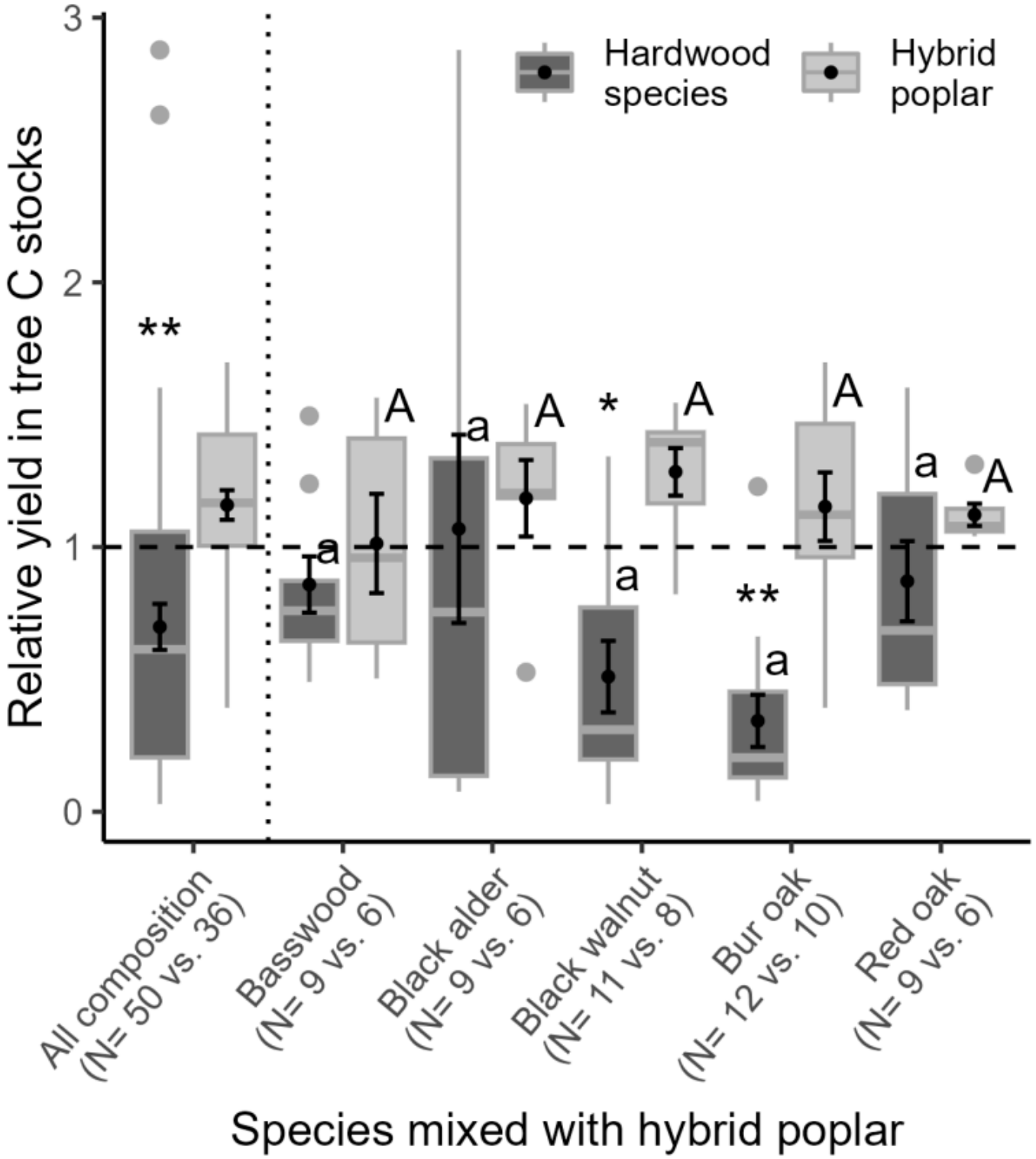
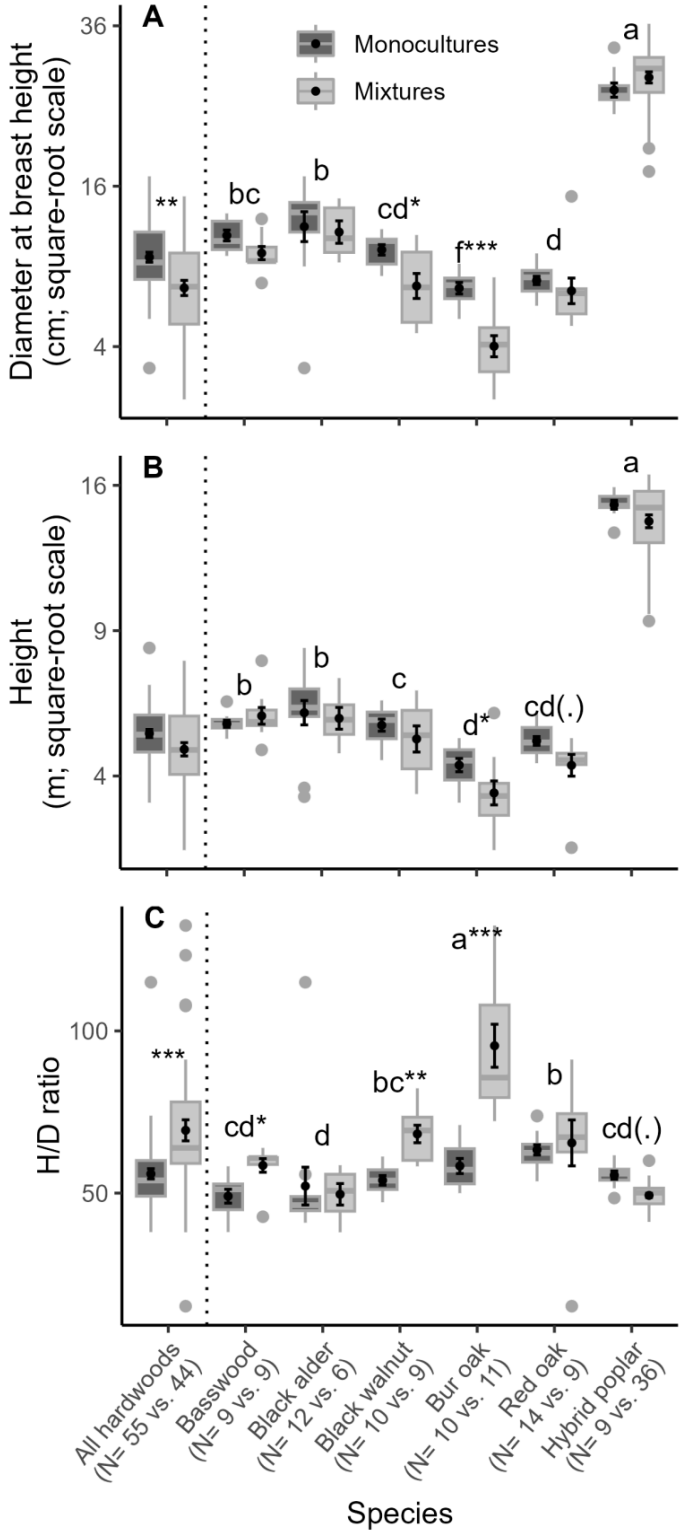



**Figure 3**

Relative yield in terms of tree C stocks for each species within each mixture composition and for all compositions combined. Means and standard errors are shown. Box-and-whisker plots display medians and interquartile ranges (IQR), with whiskers extending to the farthest value within 1.5 × IQR; points beyond whiskers represent outliers. Sample sizes (*N*) indicate the number of individual trees within mixtures (hardwood species vs. hybrid poplars). Significance levels for differences from the null

hypothesis (dashed line) are indicated as * $P < 0.05$, and ** $P < 0.01$. Multiple comparisons among hardwood species (lowercase letter) and among hybrid poplars (uppercase letter) revealed no significant differences (Tukey tests, $P > 0.05$).




## Figure 4

Differences between mixtures and monocultures in diameter at breast height (**A**), height (**B**) and height-to-diameter (H/D) ratio (**C**) for all hardwoods combined and for each species separately. Means and

standard errors are shown. Different letters indicate significant differences among species (averages of mixture and monoculture values; Tukey tests, $P < 0.05$). Significance levels for difference between mixtures and monocultures within each species are indicated as (.) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

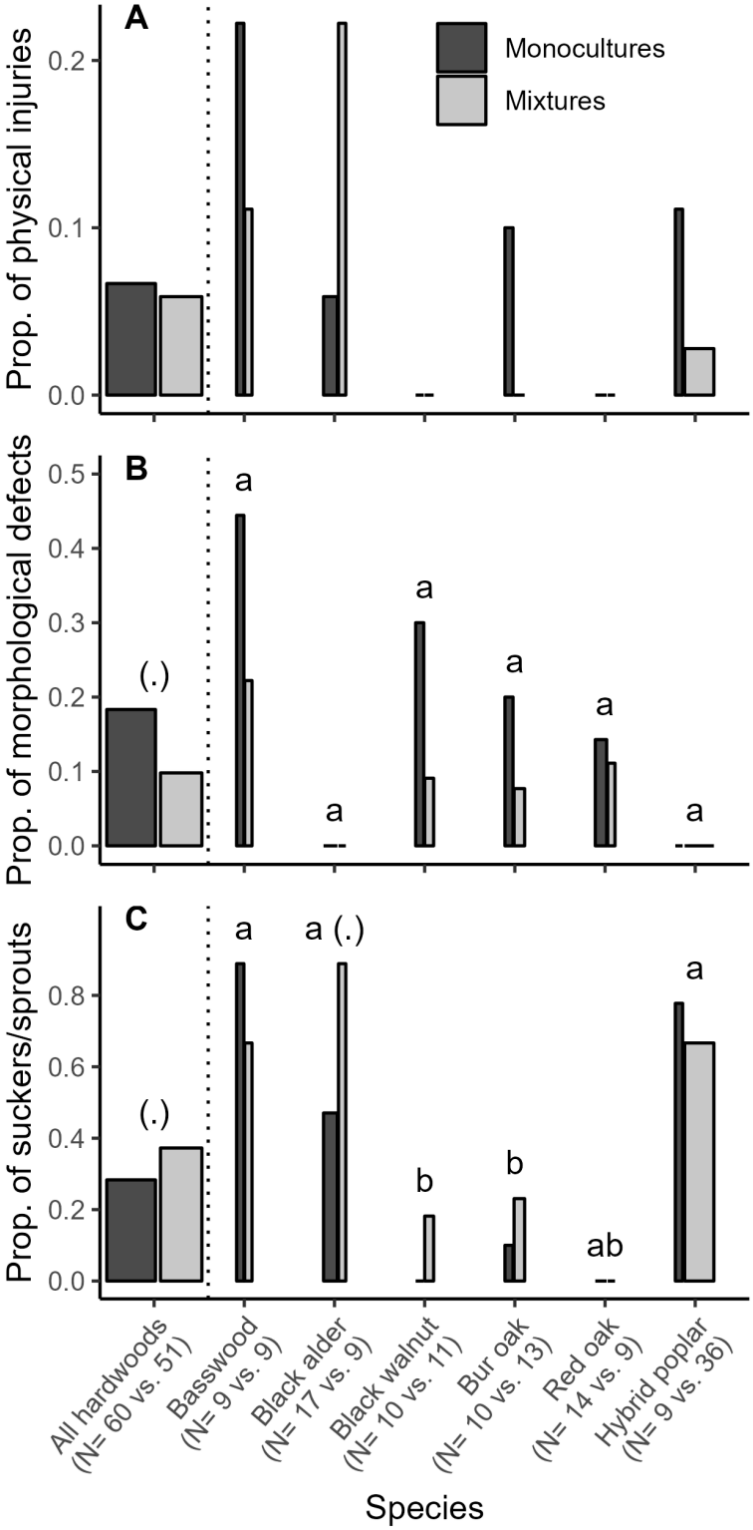



Figure 5

Differences between mixtures and monocultures for the proportion of individual trees with physical injuries (A), morphological defects (B) and suckers of water sprouts (C), for all hardwoods combined and for each species separately. Average proportions are shown; bar widths represent the number of compared trees (N = number in monoculture vs. number in mixture). Significance levels for the difference between mixtures and monocultures: (.) $P < 0.1$. Different letters indicate a significant difference among species in (B) and (C) (Tukey tests, $P < 0.05$).

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryTable1.docx