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Trait plasticity and trade-offs shape intra-specific variation in competitive response in a foundation tree species

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Summary

- The ability to tolerate neighboring plants (i.e. degree of competitive response) is a key determinant of plant success in high-competition environments. Plant genotypes adjust their functional trait expression under high levels of competition, which may help explain intra-specific variation in competitive response. However, the relationships between traits and competitive response are not well understood, especially in trees. In this study, we investigated among-genotype associations between tree trait plasticity and competitive response.
- We manipulated competition intensity in experimental stands of trembling aspen (*Populus tremuloides*) to address the covariance between competition-induced changes in functional trait expression and aspects of competitive ability at the genotype level.
- Genotypic variation in the direction and magnitude of functional trait responses, especially those of crown foliar mass, phytochemistry, and leaf physiology, was associated with genotypic variation in competitive response. Traits exhibited distinct plastic responses to competition, with varying degrees of genotypic variation and covariance with other trait responses.
- The combination of genotypic diversity and covariance among functional traits led to tree responses to competition that were coordinated among traits yet variable among genotypes. Such relationships between tree traits and competitive success have the potential to shape stand-level trait distributions over space and time.

Introduction

Competition for resources is a defining feature of plant populations and communities. Much attention has been given to the prospect of predicting competitive ability from plant functional traits. Nonetheless, the role of functional traits in competitive interactions – especially intra-specific competitive interactions – among large, long-lived plants such as trees is poorly understood (Goldberg, 1996; Kunstler *et al.*, 2016).

Competitive ability comprises two attributes: competitive effect (the ability of plants to suppress neighbors) and competitive response (the degree to which plants tolerate competition by neighbors) (Goldberg, 1996). Competitive effect is commonly measured as a short-term growth rate, and extensive research has identified the key functional traits predicting intra- and inter-specific variation in plant growth rates. In particular, functional traits on the resource-acquisitive end of the leaf economic spectrum, e.g. high photosynthetic capacity and high specific leaf area, are generally associated with greater competitive effect (Wright *et al.*, 2004; Franklin *et al.*, 2014; Kunstler *et al.*, 2016). Competitive response is harder to measure than competitive effect because it necessitates comparing plant growth between high- and low-competition environments rather than quantifying a single growth rate. It may, however, be the more important attribute of the two for long-term competitive outcomes (Goldberg, 1996; Golivets & Wallin, 2018). The functional traits driving variation in competitive response are less well established than those driving competitive effect, especially in the context of intra-specific competition (Kunstler *et al.*, 2016).

Intra-specific competition is a key driver of population dynamics in plant communities (Adler *et al.*, 2018). Research with the model for *Arabidopsis thaliana* has shown that plant genotypes can vary both in competitive response and in the plasticity of various functional traits in response to competition (Filiault & Maloof, 2012; Baron *et al.*, 2015). In that species, genotypic variation in competitive response is largely independent of genotypic variation in competitive effect (Baron *et al.*, 2015). Little is known about whether similar genotypic variation in competitive response and trait plasticity exists in trees, nor about which traits may be predictive of genotype-level competitive response. Any genotypic variation in competitive response that does exist has the potential to drive evolutionary trajectories of tree populations based on their competitive environment.

Covariance between aspects of competitive ability and functional trait expression may lead to trade-offs between performance under high competition and performance in other contexts. For example, tree genotypes with a high competitive effect are potentially more vulnerable to future disturbance, due to covariance between a fast growth rate and high-risk functional traits such as low wood density and low herbivore resistance that increase tree vulnerability to structural injury and tissue loss (Fine *et al.*, 2006; Wright *et al.*, 2010). Trade-offs stemming from trait covariance may indeed help explain negative correlations between juvenile growth rate and lifespan in trees (Büntgen *et al.*, 2019). Because the traits and trait trade-offs associated with genotype-level competitive response are poorly understood in trees, it is unclear how intra-specific variation in competitive response might impact variation in tree resistance to biotic threats beyond competition.

Trembling aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America and exhibits high within-population genetic diversity, especially in the northern part of the continent where it is a ubiquitous forest species (Callahan *et al.*, 2013). Aspen is likewise phenotypically diverse and plays an important role in maintaining biodiversity and ecosystem functioning across its range (Lindroth & St Clair, 2013; Rogers *et al.*, 2020). After a seeding event, aspen stands regenerate at a high population density (Romme *et al.*, 2005). As stand development proceeds, the outcomes of intra-specific competitive interactions determine the genotypic composition of the population, particularly when competitive effect differs among genotypes (Moran & Kubiske, 2013). Beyond intra-specific competition, aspen stands are increasingly vulnerable to both abiotic and biotic stressors including drought, wood-boring insects, and pathogens (Hogg *et al.*, 2002, 2008; Singer *et al.*, 2019).

This study aimed to improve understanding of how functional traits shape competitive ability within a tree species. To that end, we tested the hypotheses that genotypes vary in competitive response and that such variation is linked to variation in competitive effect as well as a suite of competition-induced functional trait responses. This work was conducted in replicated, 14-genotype stands of trembling aspen that had been manipulated to create two contrasting levels of competition intensity. We measured tree growth and a suite of functional traits related to both resource acquisition (leaf quantity and quality) and biotic stress resistance (phytochemical concentrations) and compared those metrics between trees of the same genotype growing in high- vs low-competition stands.

Materials and Methods

Study site and experimental design

The 18 experimental aspen stands used in this study were located in a common garden at the Arlington Agricultural Research Station (College of Agricultural and Life Sciences, University of Wisconsin-Madison) near Arlington, Wisconsin, USA (43°18′9.47″ N, 89°20′43.32″ W). The 0.2-ha site is underlain by a silt loam soil (Huntsville series, mesic Cumulic Hapludoll) and was plowed prior to planting. The 14 aspen genotypes used for this study were originally collected (in the 1990s) throughout south-central Wisconsin (Supporting Information Table S1), propagated from root stock, and maintained in common gardens. Genotype identity was confirmed using microsatellite analysis (C. Cole, K. Mock & R. Lindroth, unpublished data). The 14 genotypes displayed low relatedness ($Ajk < 0.06$) and no meaningful population structure (J. Riehl, unpublished data). Trees for this experiment were derived from those genotypes and propagated via commercial tissue culture in spring 2010 (Knight Hollow Nursery, Middleton, WI, USA). In late August 2010, trees were transplanted from the propagation trays into Cone-tainers™ (D40H Deepots, Stueve & Sons, Tangent, OR, USA) with a 50–50 mix of torpedo sand and MetroMix 366-PSC (Sun Gro Horticulture, Agawam, MA, USA), then moved outside and allowed to transition to dormancy naturally. The dormant seedlings were planted at the study site in late October through early November 2010.

The experimental design was a split plot, with genotype nested within competition treatment. Each stand comprised individuals from each of the 14 genotypes. Trees were initially planted at a density of 40 000 ha^{-1} (0.5 m × 0.5 m spacing) with a border of nonexperimental aspen trees at the same spacing. Total area of each stand, including border trees, was 20.25 m^2 and stands were assigned to treatments in a randomized grid with 2 m mowed aisles. Stands were divided into four quadrants, each with one replicate individual per genotype, for a total of four replicate individuals per genotype per stand and 56 total experimental trees. Genotype locations were randomized within quadrants. In the years between planting and thinning, cumulative natural mortality was 6.5% throughout all stands (approximately one tree per quadrant).

In early spring 2014, when trees were four years old and an average of 3.7 m tall, half of the stands were randomly selected for manual thinning treatment and reduced to 10 000 ha^{-1} (one randomly-chosen replicate individual per genotype in each stand; border trees were reduced similarly). Hereafter, these nine stands will be referred to as 'low-competition' stands and the nine remaining 40 000 ha^{-1} stands will be referred to as 'high-competition' stands (Fig. S1). The partial mortality created here represents an experimental disturbance of intermediate intensity, which reduces competition by removing some but not all trees. Such disturbances are a common driver of forest structure (Frelich & Lorimer, 1991), and in aspen stands are caused by multiple mechanisms, including drought and natural enemies (Hogg *et al.*, 2002, 2008; Singer *et al.*, 2019). All traits were measured in 2015, one year after the treatment was imposed.

Trait measurements

Light-saturated photosynthetic rate and stomatal conductance were measured in mid-summer 2015 using a LI-6400 Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NE, USA). Canopy leaves were collected for photosynthesis measurements using telescoping pole pruners. During measurements, photosynthetic photon flux density, CO_2 partial pressure in the reference chamber, and block temperature were maintained at 2000 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$, 40 Pa, and 25°C, respectively. We scanned the leaves used for photosynthesis measurements on a LI-3100

Area Meter, vacuum-dried, then weighed them in order to calculate photosynthetic performance (A_{mass}) and stomatal conductance (g_s) on a leaf mass basis. Photosynthesis and conductance were measured at four time points during the season (one morning and one afternoon measurement each in both June and August) and then averaged by tree. Due to time restrictions, replication for these measurements consisted of one tree per genotype in each of five high-competition and five low-competition stands.

Leaves were collected for phytochemical analysis from each experimental tree in mid-summer 2015. Approximately 15–20 leaves were collected from each third of the tree crown using telescoping pole pruners. Once collected, leaves were vacuum-dried and ground to a fine powder using a ball mill. Foliar phenolic glycosides (also known as 'salicinoids'), including salicin, salicortin, tremuloidin and tremulacin, were quantified using ultra-high performance liquid chromatography (UHPLC) (Rubert-Nason *et al.*, 2018). Salicortin, tremulacin and tremuloidin analytical standards were purified from *P. tremuloides* foliage (Rubert-Nason *et al.*, 2018) and salicin analytical standard was purchased from Sigma-Aldrich (St Louis, MO, USA). Foliar condensed tannins were quantified using an acid–butanol method (Porter *et al.*, 1985), with analytical standards purified from *P. tremuloides* foliage (Hagerman & Butler, 1989). Total foliar nitrogen concentration was quantified using near-infrared reflectance spectroscopy (NIRS) referenced to laboratory-assayed values from a subset of samples (Rubert-Nason *et al.*, 2013). Laboratory assays for foliar nitrogen reference samples were performed with an elemental analyzer (Thermo Fisher Scientific, Waltham, MA, USA). All foliar trait values were averaged across the three crown collection levels for each tree.

The height (H) and diameter at breast height (D, 1.4 m) of each experimental tree were measured in the fall of 2014 and 2015. Growth was calculated as the 2014–2015 annual increment in an index of tree volume (D^2H), which is an effective proxy for aboveground woody biomass in *Populus* species (Causton, 1985; Stevens *et al.*, 2008; Kruger *et al.*, 2020). Total crown foliar mass was calculated by estimating the total number of leaves on each tree, then multiplying that number by the average mass per leaf for that tree. The total number of leaves was nondestructively estimated in the crown of one randomly selected tree per genotype in six stands per treatment. Crowns were surveyed from temporary scaffolding. Each sampled crown was divided into 0.5-m height increments, and, within each increment, the total number of leaves was tallied on five to six representative short (proleptic) shoots. For a given increment, the average number of leaves per short shoot was then multiplied by the observed number of short shoots. To this product we added the total number of leaves on all long (sylleptic) shoots in the increment. From each increment of every surveyed crown, two leaves were scanned for leaf area, dried at 70°C to a constant mass and weighed. These data were used to scale leaf counts to total crown mass, and to estimate increment-weighted crown averages for specific leaf area (SLA). Genotype-specific and competition treatment-specific regression models were used to normalize crown foliar mass to concurrent measures of tree basal area ($\pi D^2/4$).

Statistical analyses

The independent and interactive effects of genotype and competition level on individual tree trait values were evaluated using linear mixed models with the 'lmer' function (v.1.1-21; Bates *et al.*, 2015) in R (v.3.6.0; R Core Team, 2020). Stand identification (ID) number was included as a random effect and type III ANOVA was used for significance tests. Competitive response and the direction and magnitude of trait responses to competition were quantified for each genotype as the ratio of the mean growth increment or trait value, respectively, in high-competition stands to that in low-competition stands (sometimes called the 'response coefficient'; Valladares *et al.*, 2006). Salicin responses were calculated and analyzed separately from the other three phenolic glycosides because of the potential for higher metabolic turnover of salicin in leaf tissue (Kruger *et al.*, 2020). Hereafter, we will refer to pooled concentrations of salicortin, tremulacin and tremuloidin as 'complex phenolic glycosides' because the structure of each of these compounds consists of salicin plus one or more additional functional groups. Competitive effect was calculated for each genotype as the mean volumetric growth rate in 2013, the year prior to thinning treatments (based on data in Kruger *et al.*, 2020). The bivariate relationships between genotype-level trait responses and competitive response were evaluated using simple linear regression, with competitive effect natural log-transformed to decrease heteroscedasticity.

Variation in genotype competitive response was modeled based on the entire suite of measured leaf and crown functional trait responses using multiple linear regression. Trait responses were transformed as needed to decrease heteroscedasticity and/or improve model fit. First, all possible regression models were generated, and then models that contained excessively collinear predictors (i.e. models containing at least one predictor with a variance inflation factor greater than 2) were removed. The five remaining models with the lowest values of Akaike information criterion (AIC) were then selected for presentation.

Results

Across the 14 aspen genotypes, stem volume growth (D^2H increment) decreased by 13–80% in response to high competition (Fig. 1; Table S2). Correspondingly, competitive response, the ratio of D^2H increment in high- vs low-competition stands, varied more than four-fold among genotypes (Table 1). Genotypes also differed with respect to the direction and magnitude of functional trait responses to high competition (significant Genotype × Competition effects, Fig. 1; Table S2) for all traits except foliar nitrogen, salicin, and conductance (g_s). For the most part, concentrations of foliar chemical defenses declined under high competition across genotypes (response ratios < 1; Table 1), although salicin levels rose by 5–62%. Crown foliar mass, normalized for tree basal area, decreased by 16–60%. Overall, responses of foliar nitrogen, photosynthesis (A_{mass}), and g_s were comparatively modest (response ratios close to 1), while SLA increased by 12–43%.

Genotypic variation in competitive response was positively related to that in competitive effect ($F_{1,12} = 16.64$, $P = 0.002$; Fig. 2). Significant bivariate relationships were also observed between competitive response and the responses of functional traits to high competition (Fig. 3). Among genotypes, competitive response was negatively associated with both g_s response ($F_{1,12} = 14.56$, $P = 0.002$) and SLA response ($F_{1,12} = 5.94$, $P = 0.031$), as well as positively associated with condensed tannins response ($F_{1,12} = 9.60$, $P = 0.009$). When the explanatory roles of trait responses were analyzed together using multiple linear regression, competitive response was negatively associated with g_s response in three of the top five regression models, based on AICc (Table 2). Competitive response was also associated with plasticity in foliar chemistry in the top models: decreases in salicin, decreases in foliar nitrogen, and increases in condensed tannins were associated with higher competitive response in one, two, and three of the five best-fitting models, respectively. Additionally, competitive response was positively associated with competition-induced increases in crown foliar mass in the top regression model and negatively associated with increases in SLA in two of the five best models.

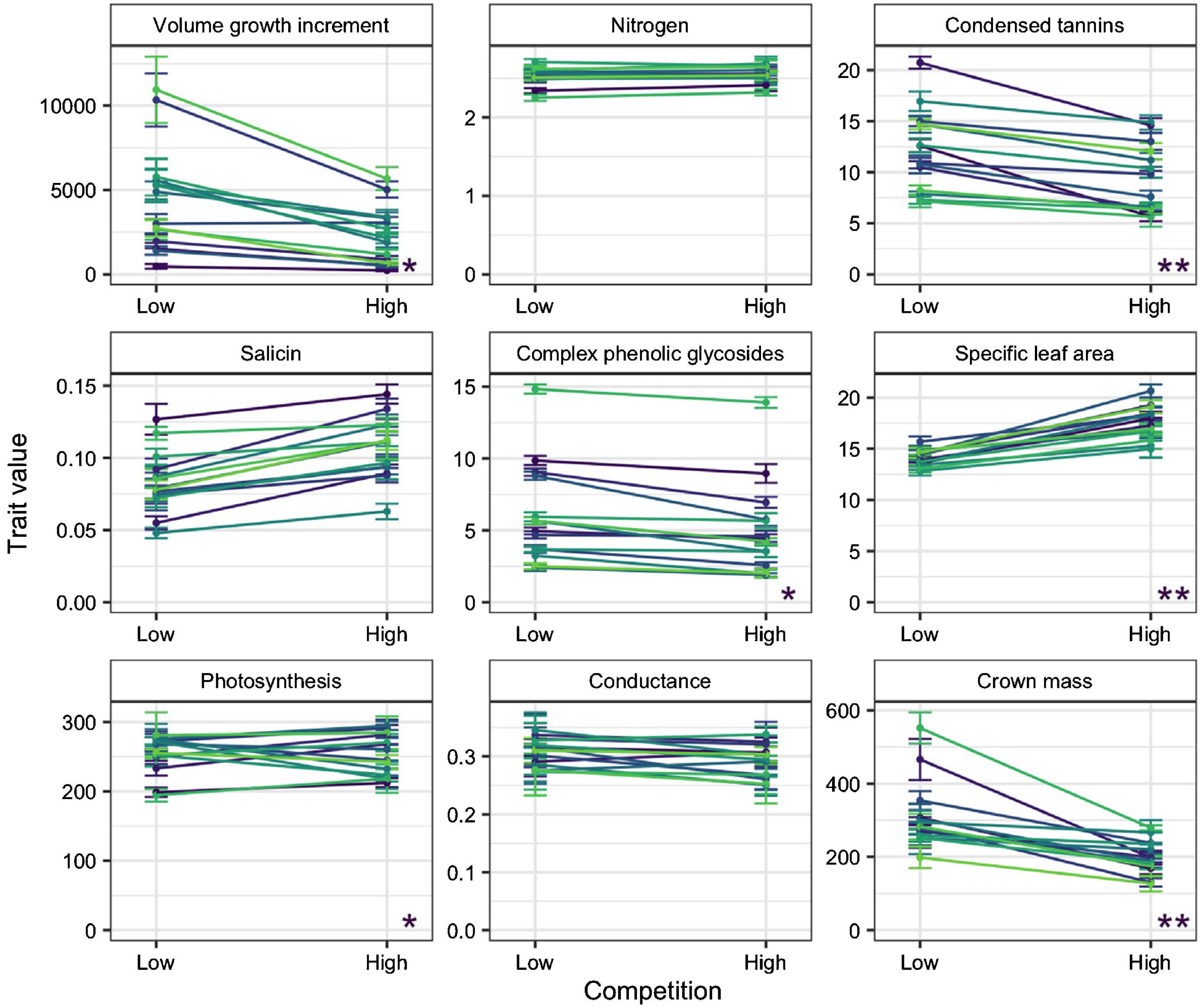

Fig. 1 Genotype-level norms of reaction for *Populus tremuloides* traits in low-competition vs high-competition stands. Points are genotype means and error bars are ± 1 SE. Foliar chemistry trait values are in units of percent dry mass, photosynthesis and conductance are light-saturated and on a mass basis, and crown mass is normalized for tree basal area. Genotypic variation is significant for all traits at $\alpha = 0.05$. Genotype × Competition interactions are significant for traits marked with a single asterisk. Both Genotype × Competition and Competition main effects are significant for traits marked with two asterisks. Statistical results were derived from ANOVA of linear mixed models containing Genotype × Competition treatment fixed effects and stand as a random effect.

Table 1 Summary of genotype-level competitive response and functional trait responses to competition in *Populus tremuloides*.

	Mean[c]	Minimum	Maximum	SE
Competitive response[a]	0.55	0.20	0.87	0.06
Trait responses[b]				
Nitrogen	1.00	0.96	1.04	0.01
Condensed tannins	0.77	0.45	0.90	0.03
Salicin	1.30	1.05	1.62	0.04
Complex phenolicglycosides	0.82	0.61	1.02	0.04
Specific leaf area (SLA)	1.24	1.12	1.43	0.02
Photosynthesis (A_{mass})	1.00	0.80	1.15	0.03
Conductance (g_s)	1.18	1.00	1.31	0.03
Crown mass	0.61	0.40	0.84	0.03

[a] Ratio of growth in high-competition stands to growth in low-competition stands, calculated for each genotype based on volumetric growth increments.

[b] Ratios of the mean trait value in high-competition stands to the mean trait value in low-competition stands.

[c] Summary statistics are calculated among genotypes.

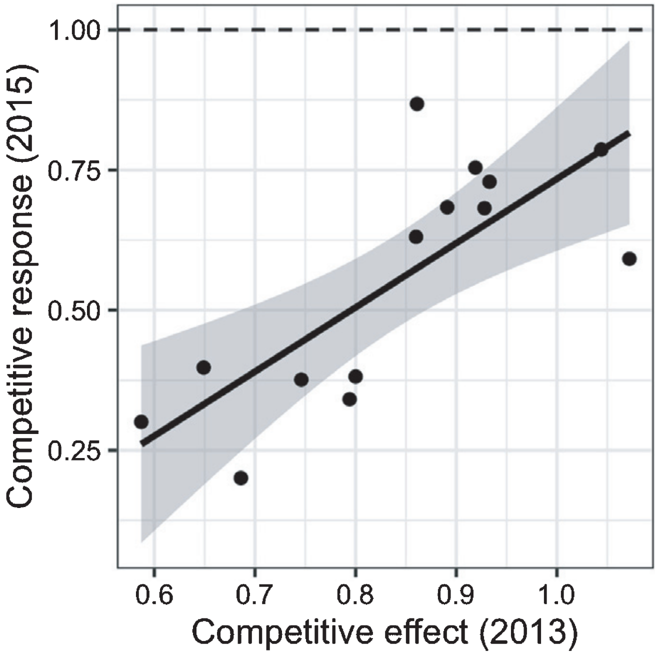

Fig. 2 Relationship between competitive effect and competitive response among *Populus tremuloides* genotypes. Competitive effect represents the ability of genotypes to outgrow neighbors and is measured as pre-thinning relative growth rate in terms of stem volume (D^2H). Competitive response, the tolerance of genotypes to competition by neighbors, is measured as the ratio of annual volume increment of trees in high-competition stands to that of in trees in thinned, low-competition stands. Each point represents a genotype and the shaded area is a 95% confidence interval for the linear regression line.

Functional trait responses to high competition covaried among traits in several cases (Fig. 4). Genotypes with increased A_{mass} in response to competition also had positive responses of complex phenolic glycosides (r = 0.61, P = 0.021) and g_s (r = 0.69, P = 0.002), but negative responses of crown foliar mass (r = −0.74, P = 0.002). In addition, competition responses of g_s were positively associated with those of SLA (r = 0.58, P = 0.031).

Discussion

This study evaluated the role of functional trait plasticity in shaping tree competitive response at the genotype level. We found that tree genotypes with a large competitive effect, that is, those more able to suppress their neighbors, also had high competitive response, meaning they were also more tolerant of competition by conspecifics. Tree functional traits exhibited plastic responses to intra-specific competition that were coordinated among traits yet variable among genotypes. The functional trait responses that were most positively associated with genotypic variation in competitive response were those of crown foliar mass and foliar condensed tannins, while the trait responses most negatively associated with competitive response were those of foliar salicin, nitrogen, stomatal conductance, and SLA.

The majority of aspen secondary metabolites measured, including condensed tannins and complex phenolic glycosides, occurred at lower concentrations under intense competition (Fig. 1). Typically, complex phenolic glycosides exhibit weaker phenotypic plasticity than do condensed tannins (Lindroth & St Clair, 2013), but in this case the two classes had similar responses to competition. Our results are consistent with the general expectation that production of carbon-rich secondary metabolites decreases with reduced light availability (Herms & Mattson, 1992). Notably, however, root competition alone has been shown to increase concentrations of both types of metabolites in aspen saplings (Donaldson *et al.*, 2006). The observed decrease in aspen defense compounds under high competition suggests, therefore, that light limitation is more important than nutrient limitation in the closed-canopy stands described here.

Changes in leaf chemistry due to competition for light could have numerous consequences for ecosystem functioning. Lower condensed tannin concentrations in high-competition stands have the potential to alter soil microbial communities and nutrient cycling (Hättenschwiler & Vitousek, 2000). Low condensed tannins in leaf litter are associated with faster litter decomposition, and have been linked to poorer retention of forest floor carbon stocks (Henneron *et al.*, 2018) and lower nitrogen reuptake following major defoliation (Madritch & Lindroth, 2015). These functions could help explain our observation that genotypes with large competition-induced decreases in foliar condensed tannins had poor competitive response at the genotype level (Fig. 3), but the mechanistic basis underlying this association is still unclear. Complex phenolic glycosides are the most important herbivore defense compounds in aspen (Lindroth & St Clair, 2013); reduced concentrations of these compounds under high competition would likely render stands less resistant to subsequent herbivore pressure.

In contrast to every other compound measured, foliar salicin increased in concentration under high competition across

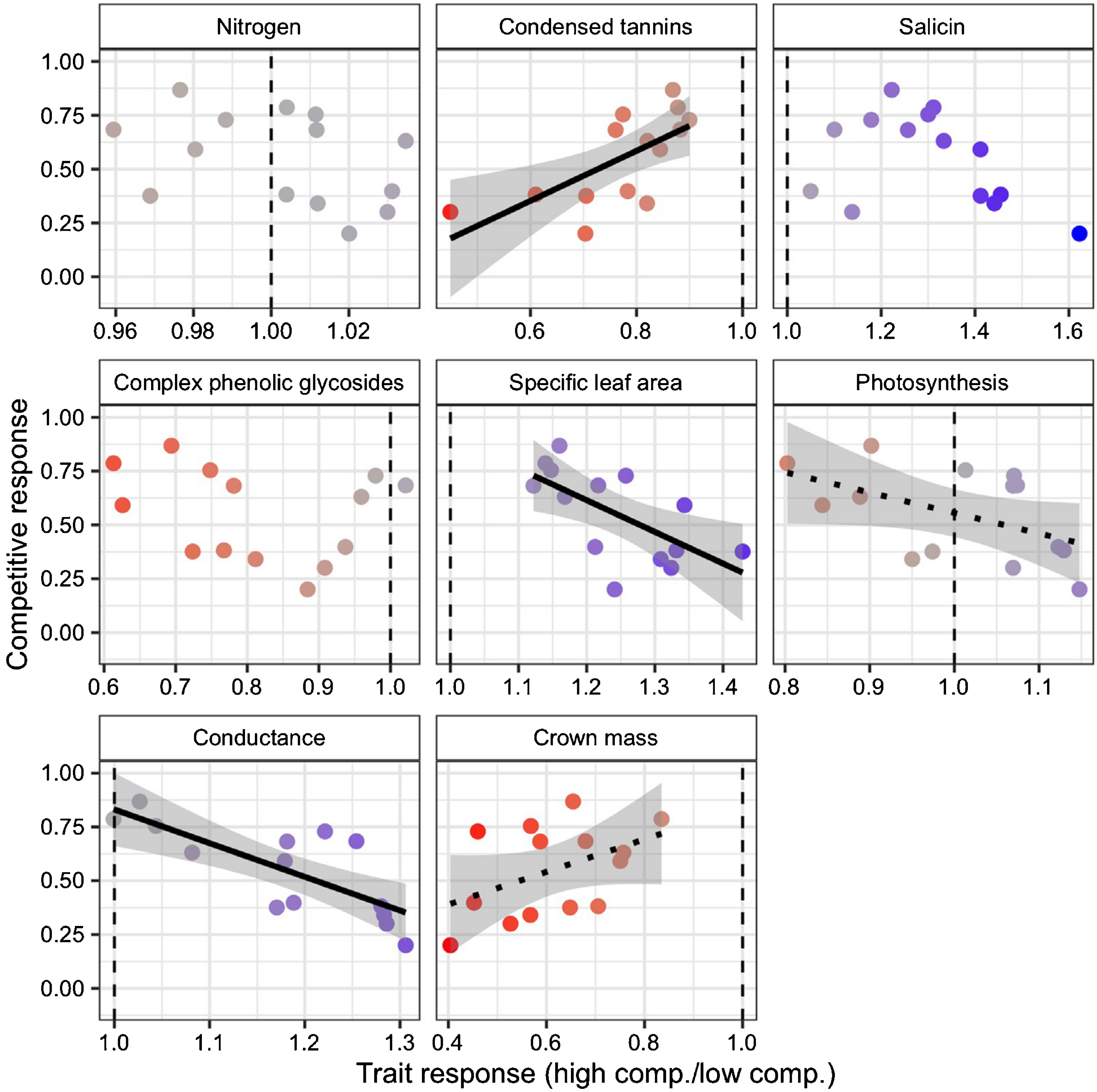

Fig. 3 Relationships between genotype-mean trait responses and genotype-mean competitive response in *Populus tremuloides*. Trait responses are ratios of the mean trait value in high-competition stands to the mean trait value in low-competition stands; a response of 1 (dashed vertical lines) indicates no effect of competitive environment on trait expression. Competitive response is the ratio of volume growth in high- vs low-competition stands. Dotted regression lines are significant associations at $\alpha = 0.10$, solid lines are significant associations at $\alpha = 0.05$. Each point represents a genotype and shaded areas are 95% confidence intervals for the linear regression lines. Color scale matches *x* axis and proceeds from red (trait responses << 1) to blue (trait responses >> 1).

genotypes (Fig. 1). Salicin increases, in particular, were associated with lower competitive response among genotypes, while competition-induced changes in other phenolic glycosides were not significantly associated with competitive response (Table 2). The negative covariance between competitive response and foliar salicin production is consistent with a genotypic growth-defense trade-off. Aspen defense compounds are known to covary negatively with growth rate among genotypes, although the magnitude of that trade-off varies with nutrient availability, sex, and developmental stage (Osier & Lindroth, 2006; Cope *et al*., 2019;

Table 2 Selected regression models explaining genotypic variation in competitive response in *Populus tremuloides*.

	Explanatory variable coefficients								
Intercept	Crown mass	Salicin	Condensed tannins	N	g_s	SLA	R^2	RMSE	AICc
−0.27	0.844*	−0.481*	1.392**				0.79	0.23	11.7
1.26			1.146*		−2.238*		0.69	0.27	11.8
11.65**				−8.708*	−1.957*	−0.832*	0.77	0.24	12.7
3.04**					−3.157**		0.55	0.31	13.1
12.29**				−10.8**		−1.375**	0.52	0.33	14.0

Competitive response is quantified as the ratio of volume growth in high-competition stands to growth in low-competition stands. Explanatory variables are drawn from a set of coincident trait responses (shown in Table 1). In all models, growth response is $\log_e$-transformed to decrease heteroscedasticity and improve model fit. For the same purposes, the explanatory variables salicin, condensed tannins, and SLA (specific leaf area) are squared and crown mass is $\log_e$-transformed. N, percent foliar nitrogen; g_s, conductance.
*, $P \leq 0.05$; **, $P \leq 0.01$.

Cole *et al*., 2020; Kruger *et al*., 2020). Growth and defense traits may trade-off because of metabolic costs, or because they are transcriptionally or genetically linked (Züst & Agrawal, 2017). While phenolic glycosides can benefit genotype-level fitness during periods of high herbivory (Bailey *et al*., 2007), non-outbreak conditions like those in the present study tend to magnify the costs, rather than the benefits, of defense. As a result, negative effects of salicin production on genotype competitive ability may be diminished or even reversed in environments with higher herbivore loads.

Several factors may explain the difference between the effects of salicin on genotype competitive ability and those of the other, more complex, phenolic glycosides. First, recent work suggests that salicin undergoes higher turnover in leaf tissue than the other phenolic glycosides, resulting in a greater allocation cost per unit dry mass (Kruger *et al*., 2020). Second, although the biosynthetic pathways for production of phenolic glycosides remain unresolved, salicin appears to be synthesized via a downstream pathway different from that of other phenolic glycosides (Babst *et al*., 2010; Fellenberg *et al*., 2020). Thus, differences between salicin and the more complex phenolic glycosides in terms of their influence on genotype competitive ability may derive from differences in metabolic turnover rates, or differences in costs associated with its biosynthetic pathway. Although salicin comprises a small portion of aspen's overall defense profile, trade-offs between competitive response and salicin plasticity may influence the evolutionary trajectories of aspen populations and ultimately contribute to the long-term vulnerability of stands to subsequent stressors.

Biomass allocation to foliage (crown mass, normalized for variation in individual tree basal area) was among the most important trait responses in this study for predicting competitive response (Table 2). When relativized to basal or sapwood cross-sectional area, the amount of leaf mass (and area) produced by an individual tree often declines in response to increased competition (e.g. McDowell *et al*., 2006; Simonin *et al*., 2006; Benomar *et al*., 2012; Forrester *et al*., 2012). Indeed, we observed a convergence in crown mass around a low and relatively narrow range of values in high-competition stands (Fig. 1). Notably, those genotypes that responded to higher competition by allocating substantially less mass to foliage exhibited the poorest competitive response (Fig. 3). This result for crown mass response corroborates the importance of light competition in our system. Though comparable genotype-level data are scarce, a synthesis of findings from an experiment conducted by Benomar *et al*. (2011, 2012) reveals a similar positive link between competitive and crown mass responses in a comparison of two hybrid poplar clones grown at different densities. In both studies, genotypes that were most tolerant of competition also possessed crowns that responded the least to competitive pressures imposed by neighbors.

Further analysis of data in Benomar *et al*. (2011, 2012) yields negative trends between poplar competitive response and foliar trait responses, including those of SLA and mass-based photosynthesis, that were consistent with the relationships observed in our study. Increases in SLA at higher levels of competition, reported in a number of studies (e.g. Larocque, 1999; Medhurst & Beadle, 2005; Forrester *et al*., 2012), have been attributed in part to a reduction in light availability by neighboring crowns. Although altered light environment was a plausible driver of leaf morphological responses in our study, we measured SLA on sunlit foliage sampled in the upper portion of the crown. Thus, we suspect that other factors, such as treatment differences in foliar exposure to turbulence (Wu *et al*., 2016), might have contributed to observed SLA variation. Moreover, we cannot identify a compelling, mechanistic rationale for the correlation between competitive response and SLA response.

Our negative, albeit marginally significant, relationship between competitive and photosynthetic responses also lacks a readily identifiable explanation. Published responses of area- and mass-based photosynthesis to competition vary considerably in direction and magnitude across studies (Kolb *et al*., 1998; Medhurst & Beadle, 2005; McDowell *et al*., 2006; Benomar *et al*., 2011; Forrester *et al*., 2012), and the causes underlying this variation remain elusive. In general, positive responses of mass-based photosynthesis have been accompanied by increases in SLA (Medhurst & Beadle, 2005; Benomar *et al*., 2011; Forrester *et al*., 2012), but the two responses were not significantly related in our study (Fig. 4). An alternative explanation for the variation in responses we observed is the possible existence of a trade-off between crown structural and functional responses to competition. This hypothetical trade-off is evinced by a negative relationship between the responses of crown mass and photosynthesis to

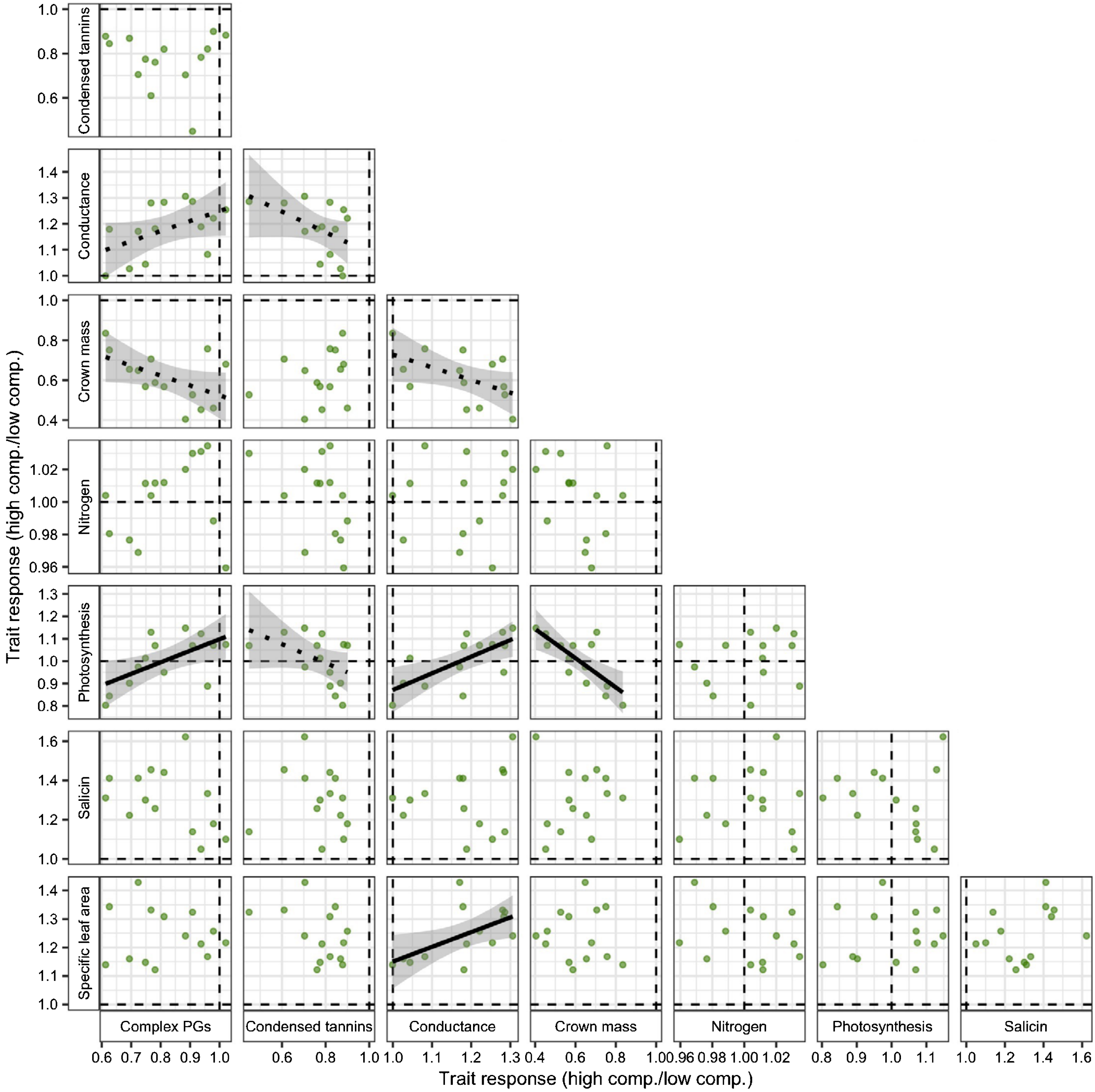

Fig. 4 Scatterplot matrix of genotype-level trait responses to competition in *Populus tremuloides*. Trait responses are calculated as the ratio of the mean trait value in high-competition stands to the mean trait value in low-competition stands. Dotted regression lines are significant associations at $\alpha = 0.10$, solid lines are significant associations at $\alpha = 0.05$. Each point represents a genotype and shaded areas are 95% confidence intervals for the linear regression lines. PGs, phenolic glycosides.

competition, along with a positive relationship between photosynthesis and stomatal conductance responses (Fig. 4). This coupling of crown mass and physiology is consistent with the inference drawn by Simonin *et al.* (2006) that stomatal conductance, a key determinant of photosynthetic performance, is negatively related to the ratio of leaf area to sapwood (or, by extension, basal) area, reflecting the balance between water demand and hydraulic capacity. Thus, this hydraulically mediated trade-off between crown mass and acquisitive leaf physiological traits may, accordingly, help explain the surprising negative correlation between competitive and stomatal responses in our study. Although not measured in this study, the responses of stem hydraulic traits and root traits to competition may elucidate the importance of hydraulic limitation for competitive ability.

Our study presents a snapshot of a single year of intra-specific competitive interactions among juvenile trees. Differences in competitive response among genotypes at this early stage may compound over time, due to the exponential nature of plant growth. Alternatively, genotypic variation in competitive response may attenuate over time, especially if alternative stressors such as herbivore outbreaks come into play. Production of secondary metabolites changes throughout development in aspen; such changes are nonlinear and show significant variation among genotypes (Cope *et al*., 2019). Therefore, differential competitive ability among genotypes based on their defense trait expression as juveniles may shape the phenotypic composition of populations at future developmental stages in unexpected ways. Future studies should follow competitive outcomes over time to determine the consequences of variation in early competitive response for trait distributions as plants develop.

Our results show that genotypic variation in plastic trait responses, especially those of phytochemistry, crown foliar mass, and leaf physiology, can shape the ability of trees to tolerate intra-specific competition. We also found that different phytochemical and physiological traits exhibit different degrees of plasticity in response to competitive environment, as well as different degrees of genotypic variation and genotype by environment interactive effects. These findings underscore the need to move beyond species-mean functional trait values in predicting plant responses to biotic environments. We show here that intra-specific genotypic diversity can combine with covariance among functional traits to drive not only static trait values but trait responses to biotic pressures like competition. Coordinated functional trait responses associated with different competitive outcomes have the potential to shape both the structure and function of forests over time, as well as their resilience to future stressors.

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Author contributions

RLL, ELK and KK-R obtained funding, and, along with AH, designed the experiment. AH and KK-R collected the data. OLC and ELK analyzed the data. OLC led the writing of the article, with input and approval from all authors.

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Data availability

The data that support the findings of this study are available in the Dryad data repository at https://doi.org/10.5061/dryad.m0cfxpp2m (Cope *et al*., 2021).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Layout of aspen stands in common garden.

Table S1 Source locations for aspen genotypes used in common garden.

Table S2 Genotype-level summary of trait values.

New
Phytologist

New Phytologist Supporting Information

Article title: Trait plasticity and tradeoffs shape intraspecific variation in competitive response in a foundation tree species
Authors: Olivia L. Cope, Richard L. Lindroth, Andrew Helm, Ken Keefover-Ring, and Eric L. Kruger
Article acceptance date: 15 December 2020

The following Supporting Information is available for this article:

Fig. S1 Layout of aspen stands in common garden

Table S1 Source locations for aspen genotypes used in common garden

Table S2 Genotype-level summary of trait values

Fig. S1 Layout of aspen stands in common garden. Numbers are stand identifiers and shading denotes stand-level competition treatment. Scaling is approximate.

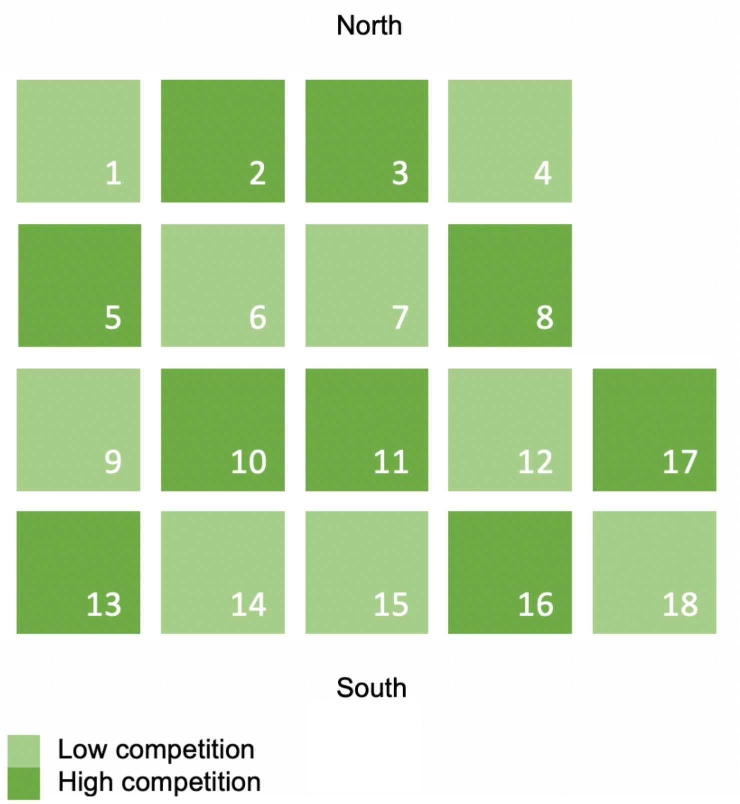

Table S1 Source locations for aspen genotypes used in common garden

Genotype	Latitude	Longitude
1	43.040114	-89.42756
2	43.4110366	-89.635728
3	43.4112127	-89.63567
4	43.540778	-89.572166
5	43.5348736	-89.542794
6	43.5338644	-89.542826
7	43.5280203	-89.541652
8	43.5277489	-89.542111
9	43.5278921	-89.551014
10	43.3970484	-89.806901
11	43.3970484	-89.806901
12	43.3970484	-89.806901
13	44.144085	-89.171283
14	44.1440942	-89.171271

Table S2 Genotype-level summary of trait values in high- and low-competition environments, including mean and standard error (SE). Foliar chemistry trait values are in units of percent dry mass, photosynthesis and conductance are light-saturated and on a mass basis, and crown mass is normalized for tree size.

Genotype	Competition	Volume growth increment		Nitrogen		Condensed tannins		Salicin		Complex phenolic glycosides		Specific leaf area		Photo-synthesis		Conductance		Crown mass	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	High	236.18	55.75	2.41	0.08	5.65	0.46	0.14	0.01	8.96	0.66	17.98	0.65	212.30	6.45	0.31	0.02	169.06	16.18
1	Low	470.85	139.16	2.34	0.03	12.59	0.63	0.13	0.01	9.86	0.32	13.58	0.31	198.54	6.72	0.32	0.01	306.67	19.95
2	High	527.22	105.89	2.54	0.06	14.59	0.72	0.09	0.01	4.38	0.35	17.28	0.74	267.71	9.86	0.31	0.02	198.05	18.88
2	Low	1514.44	346.70	2.49	0.04	20.74	0.59	0.06	0.00	4.96	0.23	13.92	0.26	233.23	10.72	0.29	0.03	465.91	56.44
3	High	880.70	214.03	2.56	0.09	6.40	0.44	0.13	0.01	6.95	0.38	19.24	0.77	281.85	13.80	0.33	0.02	198.91	14.10
3	Low	1959.93	420.76	2.55	0.04	10.49	0.60	0.09	0.01	9.05	0.25	14.45	0.45	249.58	10.58	0.34	0.02	270.49	38.20
4	High	5024.62	480.51	2.54	0.07	9.80	0.33	0.09	0.01	4.59	0.39	18.42	0.61	291.05	12.48	0.32	0.04	130.39	11.39
4	Low	10340.4	1578.7	2.57	0.02	10.90	0.52	0.07	0.01	4.69	0.25	14.65	0.24	271.89	14.21	0.33	0.04	284.50	59.50
5	High	3075.66	317.12	2.50	0.06	13.02	0.82	0.09	0.01	2.57	0.21	18.21	0.87	244.77	22.00	0.27	0.02	237.84	28.92
5	Low	2998.30	574.78	2.56	0.06	14.99	0.47	0.08	0.01	3.70	0.27	15.70	0.50	271.41	11.27	0.30	0.02	354.01	25.67
6	High	527.00	85.53	2.53	0.07	7.60	0.60	0.11	0.01	5.76	0.43	20.66	0.62	260.65	16.07	0.26	0.02	182.55	12.09
6	Low	1411.47	259.00	2.57	0.03	10.78	0.87	0.08	0.01	8.80	0.29	14.46	0.40	267.58	10.58	0.32	0.03	277.50	14.90
7	High	3335.07	338.84	2.60	0.07	11.19	0.68	0.09	0.01	1.90	0.13	16.65	0.61	294.38	5.97	0.29	0.03	187.59	18.84
7	Low	4892.82	609.59	2.57	0.04	14.72	0.84	0.07	0.00	2.43	0.25	14.84	0.46	275.28	14.21	0.28	0.02	303.04	42.67
8	High	1903.05	315.56	2.51	0.07	6.65	0.31	0.12	0.01	3.55	0.41	18.36	0.77	232.29	10.49	0.25	0.02	220.39	18.01
8	Low	5559.78	1273.3	2.56	0.05	7.87	0.26	0.09	0.01	5.67	0.26	13.67	0.39	275.18	21.88	0.29	0.03	251.65	44.45
9	High	3303.04	425.35	2.50	0.09	14.88	0.70	0.06	0.01	1.99	0.26	15.29	1.17	217.91	14.08	0.30	0.03	266.94	33.27
9	Low	5315.98	875.40	2.49	0.03	16.95	0.94	0.05	0.00	3.24	0.63	13.42	0.47	271.49	6.51	0.35	0.03	294.36	31.84
10	High	2165.83	325.66	2.69	0.09	10.36	0.91	0.10	0.01	3.54	0.40	14.97	0.81	223.67	9.45	0.29	0.03	235.65	30.61
10	Low	5286.57	978.46	2.60	0.03	12.63	0.68	0.07	0.01	3.69	0.19	12.82	0.43	251.74	15.47	0.32	0.05	259.09	17.85
11	High	2610.18	302.80	2.66	0.09	6.43	0.60	0.11	0.01	5.67	0.52	16.72	0.50	270.24	12.37	0.34	0.01	183.96	17.87
11	Low	5776.47	1107.1	2.71	0.04	7.28	0.37	0.10	0.01	5.95	0.31	13.74	0.39	251.63	16.00	0.33	0.03	251.97	22.24
12	High	1139.37	272.55	2.32	0.04	5.63	0.96	0.12	0.00	13.90	0.38	15.82	0.85	218.20	20.63	0.27	0.03	279.21	6.98
12	Low	2667.49	612.23	2.25	0.04	7.19	0.62	0.12	0.00	14.83	0.32	13.05	0.36	194.32	9.25	0.27	0.03	551.72	42.43
13	High	5673.12	680.91	2.65	0.08	6.37	0.43	0.11	0.01	4.24	0.22	16.94	0.51	284.34	23.49	0.25	0.03	174.47	27.05
13	Low	10945.9	1967.8	2.62	0.03	8.23	0.48	0.09	0.01	5.67	0.26	14.76	0.31	280.67	32.92	0.28	0.04	282.43	34.98
14	High	652.52	76.30	2.54	0.06	12.05	0.81	0.11	0.01	2.03	0.29	19.11	0.63	242.54	9.86	0.30	0.01	127.39	21.69
14	Low	2739.27	486.66	2.51	0.03	14.70	0.48	0.08	0.01	2.50	0.21	14.61	0.51	255.25	5.16	0.31	0.02	198.38	29.20