



Effects of Elevation, Stand Density, and Inter-Tree Competition on Tree Sizes, Vulnerability, and Health of Planted *Zelkova serrata* and *Quercus glauca* in Reforestation

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Abstract: Taiwan has a long history of reforestation due to land degradation. However, there is a lack of understanding of how tree species grow on reclaimed lands. This study looked at tree sizes, vulnerability, and health of economically important *Zelkova serrata* and *Quercus glauca* trees planted on reclaimed agricultural lands. Thirteen former agricultural sites with trees of six to seven years old were sampled along the elevation from 107 to 2514 m above sea level. Results showed that increasing inter-tree competition reduced tree sizes and health and increased vulnerability to damage, primarily wind, for both tree species. For example, a 1 m² ha⁻¹ increase in inter-tree competition was associated with a 5.68 cm decrease in tree diameter, a 3.21 m decrease in tree height, a 59.31% decrease in tree health for *Z. serrata*. Responses of *Z. serrata* to inter-tree competition were generally stronger than those of *Q. glauca*. Elevation generally reduced tree sizes of both species and reduced health of only *Z. serrata* trees. Stand density has minimal effects on the tree attributes of both species. Our study suggests that *Z. serrata* responds strongly to inter-tree competition leading to stratification of stand structures, which agrees with past studies showing *Z. serrata* developing different growth strategies. *Q. glauca* could resist inter-tree competition so that suppressed trees could compete with its neighbors. This supports past observations that *Q. glauca* could persist under suppression. Our findings of the elevation caution planting both tree species outside their native habitat ranges, which was not shown before.

Keywords: height-to-diameter ratio, land degradation, live crown ratio, reforestation, slenderness.

1. Introduction

Forests are recognized in the Paris Agreement to play an important role in mitigating the impact of climate change (UNFCCC 2015). Among the negative emission technologies (Fuss et al. 2018), afforestation and reforestation are the most relevant to forest management (Nave et al. 2019). Both activities aim to establish tree cover on treeless lands such as abandoned agricultural lands (IPCC 2000). These lands are deserted due to rural depopulation and livelihood change (Stoate et al. 2009; Yirdaw et al. 2019). Abandoned agricultural lands are at risks to the health of forest ecosystems (Stoate et al. 2009). Tree planting with appropriate silviculture practices could accelerate the establishment of tree cover on these lands (Sampaio et al. 2007; Palomeque et al. 2017). However, it requires choosing the right tree species for reforestation effort to be successful.

Taiwan has a long history of national reforestation efforts due to land degradation caused by exploitation and natural disasters. From 1951 to 1975, the government of Taiwan leased about 75,000 ha of heavily degraded national forests to farmers in rural area with financial incentives to reforest them (Lin et al. 2016). However, many farmers chose to illegally convert the leased forest lands to agricultural lands or to entirely abandon them due to the poor market for local timber (Lin et al. 2016). Jen and Lin (1997) found that only 20.7% of leasehold lands were reforested, while 10.9% were abandoned. As a result, the government has reclaimed and reforested these leasehold lands. The choice of reforested tree species is often haphazard even though major tree species selected for plantation include *Michelia compressa*, *Cinnamomum kanehirae*, *Taiwania cryptomerioides*, and *Calocedrus formosana*. For example, Chan (2017) found that broadleaf tree species were planted at an elevation up to 2500 m above sea level (a.s.l.). About 130 tree species have been planted for the past decades without a clear strategy (Lin et al. 2016). Lastly, there is little done to understand

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growth characteristics of major plantation species planted within and outside their native habitat ranges to inform reforestation policy.

Zelkova serrata and *Quercus glauca* are two major tree species for reforestation in Taiwan due to their adaptability to site conditions, high seedling survival rates, and economic importance (Lo and Huang 2005; Yu et al. 2008; Lin et al. 2016). Both are native broadleaf tree species. *Z. serrata* commonly distributes between 300 to 1000 m a.s.l. and is desired for its ability to sequester carbon during early stand development (Chen et al. 2021). *Q. glauca* distributes between 500 and 1500 m a.s.l. and is well adapted to dry and steep sites (Fu et al. 2004; Shen et al. 2004). Chen et al. (2017) found that one to three years old *Z. serrata* and *Q. glauca* seedlings grew better at 400-750 m and 1100-1450 m a.s.l. Both tree species are also widely distributed in China, South Korea, and Japan. *Z. serrata* has been planted for wind break and habitat restoration in southeastern China (Cao and Tao 2021) and on reclaimed lands from sea in South Korea (Kim 2006). Oyama et al. (2018) found that *Z. serrata* enhanced recruitment success on disturbed sites with steep terrain in Japan. In southwestern China, *Q. glauca* thrived on karst seasonal-arid mountainous environments (Huang et al. 2009). These studies highlight why both tree species are preferred tree species for reforestation.

To the best of our knowledge, *Z. serrata* and *Q. glauca* have not been assessed on reclaimed agricultural lands in Taiwan, especially when planted outside their native habitat ranges. Improving our knowledge could help us better plan reforestation using both tree species. The objectives of this study were to understand how elevation, stand density, and inter-tree competition influence tree diameter, height, vulnerability, and health of *Z. serrata* and *Q. glauca* trees planted on reclaimed agricultural lands. This study focused on reclaimed agricultural lands, which are a form of land degradation due to land conversion activities.

2. Materials and Methods

2.1 Data

A total of 13 reclaimed agricultural sites with an area of 0.09 to 1.96 ha were selected for observation. The sites were located at the Taiwan Forestry Bureau Dongshih Forest District, Taiwan Forestry Bureau Nantou Forest District, and National Taiwan University Experimental Forest. Previous land use of the agricultural sites was either a fruit orchard or a bamboo plantation. The sites were selected based on these criteria: (1) over a range of elevation beyond *Z. serrata* and *Q. glauca* native habitat ranges, and (2) similar planting density and establishment year. The sites were reforested between 2010 and 2011 with a planting density of 1500 to 2000 trees ha⁻¹. It was difficult to locate single species plantation of *Z. serrata* and *Q. glauca*. Both were usually mixed with other broadleaf tree species such as *Fraxinus griffithii*, *Liquidambar formosana*, and *Michelia compressa* etc. Eight of the thirteen sites were planted with *Z. serrata* with one site previously a bamboo plantation and the rest as fruit orchards. The eight sites were distributed between 107 to 1964 m a.s.l. (Table 1) with mean annual temperature and annual rainfall of 12 to 23 °C and 1650 to 2931 mm, respectively. Similarly, eight of the thirteen sites were planted with *Q. glauca* with three sites previously bamboo plantations and the rest as fruit orchards. The sites were distributed between 1194 to 2514 m a.s.l. (Table 1) with mean annual temperature and annual rainfall of 12 to 18.5 °C and 2250 to 2931 mm, respectively. Lastly, three of the 13 sites had both *Z. serrata* and *Q. glauca*.

The study was carried out in 2017; thus, the trees in the sites were six to seven years old when measured. A circular plot of 500 m² (0.05 ha) was randomly established within each site. All trees in a plot were tagged and identified to the species-level. The sample trees were measured for diameter at breast height (DBH, cm), total tree height (HT, m), and height to crown base (HCB, m). DBH was measured with a diameter tape. HT and HCB were measured with Höglof Vertex Ultrasonic Hypsometer. As a result, 178 *Z. serrata* trees were measured with mean DBH of 4.92 ± 2.58 cm and mean HT of 4.64 ± 1.78 m (Table 1). A total of 185 *Q. glauca* trees were measured with mean DBH of 4.78 ± 2.36 cm and mean HT of 4.26 ± 1.42 m (Table 1). Lastly, the datasets from this study are available from the corresponding author upon reasonable request.

Table 1. Summary statistics of tree attributes, elevation, and stand- and tree-level competition factors for *Zelkova serrata* and *Quercus glauca*.

Variables	Min	Max	Mean	Median	SD
<i>Zelkova serrata</i>					
Tree Attributes					
DBH (cm)	0.60	14.80	4.92	4.40	2.58
HT (m)	1.50	12.00	4.64	4.30	1.78
HDR	40.00	250.00	105.75	103.41	35.15
LCR	0.1333	0.9459	0.7045	0.7234	0.1372
Predictors					
ELEV (m)	107	1964	958	1044	840
TPH (tree ha ⁻¹)	560	1720	950	840	379
BAL (m ² ha ⁻¹)	0.13	3.76	1.73	1.37	1.11
<i>Quercus glauca</i>					
Tree Attributes					
DBH (cm)	0.80	12.30	4.78	4.70	2.36
HT (m)	1.60	9.10	4.26	4.30	1.42
HDR	45.53	237.50	101.61	95.83	36.07
LCR	0.1875	0.9200	0.6692	0.6744	0.1092
Predictors					
ELEV (m)	1194	2514	1431	1207	370
TPH (tree ha ⁻¹)	280	1720	1021	1080	210
BAL (m ² ha ⁻¹)	0.00	5.02	2.23	2.14	1.26

Eight sites were available to each species group for calculating summary statistics. Min = minimum; max = maximum; SD = standard deviation; DBH = tree diameter at breast height; HT = tree height; HDR = tree height-to-diameter ratio; LCR = tree live crown ratio; ELEV = elevation; TPH = stand density; BAL = basal area in larger trees.

2.2 Statistical analysis

The four response variables were: tree (1) DBH, (2) HT, (3) height-to-diameter ratio (HDR), and (4) live crown ratio (LCR). Tree size was represented by DBH and HT. Both indicated dominance of a tree over its neighbors (Kershaw et al. 2016). A larger and taller tree would be in a more dominant position to intercept light and to compete for underground resources than a smaller and shorter tree. Tree vulnerability was indicated by HDR. HDR was a dimensionless slenderness index calculated as $HT/DBH \times 100$. It implied the vulnerability to damage by factors such as wind or snow (Kershaw et al. 2016). A high HDR implied that a tree was more slender and more susceptible to wind or snow damage (Wonn and O'Hara 2001). Tree health was represented by LCR. LCR was calculated as $(HT-HCB)/HT$. It indicates the amount of live foliage contributing to tree growth (Kershaw et al. 2016). LCR has been used to assess tree vigor and to predict foliage and branch biomass (Keen 1943; Mäkelä and Valentine 2006). A higher LCR implied that a tree was healthier and more vigorous due to a larger crown.

The three predictors were: (1) elevation (ELEV, m), (2) stand density (TPH, trees ha⁻¹), and (3) tree basal area in larger trees (BAL, m² ha⁻¹). Elevation represented environmental effects. It was usually used as a proxy to capture a range of environmental factors such as air temperature, humidity, solar radiation, and water regimes (Malizia et al. 2020). Stand density (TPH) was sometimes used as a proxy for stand-level competition (Lin et al. 2021). TPH, or Trees Per Hectare, described the number of trees in one hectare area. TPH was calculated by expanding the total number of trees in a plot to per hectare unit. BAL was the most common tree-level competition index (Weiskittel et al. 2011). BAL, or Basal Area at Large, was calculated for each tree in a plot by summing basal area per ha of all trees in the plot having larger DBH than the subject tree (Weiskittel et al. 2007). This was done by first identifying all trees in a plot that were larger than the subject tree in terms of DBH, and then summing the basal area per hectare of these larger trees. In short, ELEV and TPH were plot-level predictors, and BAL was a tree-level predictor.

In our data, trees were nested within plots. As such, the nesting effects should be properly

accounted for with random effects. The full mixed-effects model was specified as (Pinheiro and Bates 2000),

$$[1] \quad Y_{ij} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})BAL_{ij} + \beta_2ELEV_i + \beta_3TPH_i + \varepsilon_{ij}$$

where Y_{ij} was one of the four response variables for the j^{th} tree in the i^{th} plot, β_k was k^{th} fixed-effect parameter associated with the intercept and predictors for $k = 0, \dots, 3$, and ε_{ij} was random error for j^{th} tree in the i^{th} plot. The random error was assumed to be Normally distributed, $\varepsilon_{ij} \sim N(0, \sigma_e^2)$. The random effects b_{0i} and b_{1i} associated with the intercept and BAL were assumed to follow a Multivariate Normal distribution (MVN) as,

$$[2] \quad \begin{bmatrix} b_{0i} \\ b_{1i} \end{bmatrix} \sim MVN \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \psi = \begin{bmatrix} \sigma_{b_0}^2 & \sigma_{b_1 b_0} \\ \sigma_{b_1 b_0} & \sigma_{b_1}^2 \end{bmatrix} \right)$$

where ψ was a variance-covariance matrix. A random effect was added to the intercept to account for potential variations between plots that were not modelled. A random effect was added to BAL to account for the nesting structure of trees within plots because the predictor was tree-level. Since ELEV and TPH were plot-level predictors, no random effect was necessary (Pinheiro and Bates 2000).

The response variables DBH, HT, and HDR were assumed to be Normally distributed and were fitted with linear mixed-effects (LME) model. However, LCR was bounded between 0 and 1, which violated the assumption of the Normal distribution. Hence, LCR was fitted with a generalized linear mixed-effects (GLMM) assuming a Beta distribution with a logit link. For LCR under the GLMM framework, Eq.[1] was modified as follows (Yellareddygar et al. 2016),

$$[3] \quad \text{logit}(E(Y_{ij})) = \log \left(\frac{E(Y_{ij})}{1 - E(Y_{ij})} \right) = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})BAL_{ij} + \beta_2ELEV_i + \beta_3TPH_i$$

Statistical analyses were carried out with the R statistical software (R Core Team 2023). The nlme package (Pinheiro and Bates 2000) was used for the LME modeling with GLMMadaptive package (Rizopoulos 2023) for the GLMM modeling. Lastly, likelihood ratio tests using Akaike Information Criterion (AIC) following Pinheiro and Bates (2000) were carried out as a variable selection method to identify significant predictors. The final models were presented in this study.

Preliminary residual analyses showed that the residuals of the fitted LME models of HT and HDR displayed funnel-shaped patterns. To account for heterogeneous variance, weighted LME models for HT and HDR were fitted with the varPower(1) variance function (Pinheiro and Bates 2000, p. 211). The varPower(1) was a variance model as described in Pinheiro and Bates (2000, p. 211) that described the within-group errors of the fitted model to be a power function of fitted values. In short, varPower(1) was the variance function that specified the weights as an inverse function of predicted values $\hat{Y}$, i.e., $g(\hat{Y}_{ij}, p) = \hat{Y}_{ij}^p$, where $g()$ was a variance function that modeled within-group errors as a function of a covariate and a parameter, $\hat{Y}_{ij}$ was either predicted HT or HDR for j^{th} tree in i^{th} plot, and p was the power optimally determined by the nlme package (Pinheiro and Bates 2000, p. 206; Lam et al. 2017). The weighted LME models have successfully resolved the heteroscedasticity in residuals. The residual standard error (RSE) of the weighted LME models was then converted back to the same scale as the response variable for interpretation. The conversion followed the method by Furnival (1961), $RSE = RSE/GM[1/\hat{Y}_{ij}^p]$, where RSE was the output from a weighted LME model, and $GM[]$ was the geometric mean (Lam et al. 2017). was reported in this study for the weighted LME models. For the GLMM model of LCR, pseudo RSE was calculated as the standard deviation of residuals and reported in this study.

3. Results

3.1. Tree size

For *Z. serrata*, the fitted models of DBH and HT produced prediction errors of ± 0.58 cm and ± 1.14 m, respectively (Table 2). The fitted models suggested that BAL was negatively associated

with DBH and HT of *Z. serrata* (Table 2, Fig.1a-b). A $1 \text{ m}^2 \text{ ha}^{-1}$ increase in BAL was associated with about 5.68 cm decrease in DBH and a 3.21 m decrease in HT (Table 2). ELEV was significantly associated with DBH and HT but not TPH (Table 2). ELEV was negatively associated with both tree attributes. A 100 m increase in ELEV was associated with a 0.32 cm decrease in DBH and a 0.18 m decrease in HT (Table 2).

Table 2. Parameter estimates of fitted mixed-effects models of DBH, HT, HDR, and LCR for *Zelkova serrata*.

Predictor	Estimate	SE	p-value	σ_{b_k}	$\rho_{b_0b_1}$
DBH					
Intercept	16.3852	1.8282	<0.0001	3.042	0.381
BAL	-5.6851	0.5176	<0.0001	1.323	
ELEV	-0.0032	0.0012	0.0465		
TPH	ns	ns	ns		
RSE, σ_e			0.581		
HT					
Intercept	10.5165	1.1082	<0.0001	1.198	-0.022
BAL	-3.2057	0.5825	<0.0001	1.311	
ELEV	-0.0018	0.0007	0.0403		
TPH	ns	ns	ns		
RSE, σ_e			1.1422		
p			1.1205		
HDR					
Intercept	52.0544	7.2103	<0.0001	16.3874	0.998
BAL	36.6232	5.1722	<0.0001	11.0635	
ELEV	ns	ns	ns		
TPH	ns	ns	ns		
RSE, σ_e			26.4702		
p			1.1996		
LCR					
Intercept	1.0821	0.3250	0.0008	0.1280	-0.969
BAL	-0.4657	0.2066	0.0241	0.3275	
ELEV	-0.00036	0.00018	0.0451		
TPH	0.00073	0.00029	0.0139		
RSE*			0.1644		

SE = standard error of parameter estimate; σ_{b_k} = standard deviation of random effect b_k for $k = 0, 1$ (Eq.[2]); $\rho_{b_0 b_1}$ = correlation of random effects b_0 and b_1 ; RSE = residual standard error of fitted model; p = power in the variance function of weighted LME model. RSE* = RSE of fitted GLMM model for LCR was pseudo residual standard error. ns = predictors that were insignificant from the likelihood ratio tests as the variable selection method.

Results of *Q. glauca* generally resembled those of *Z. serrata* (Table 3). The fitted models of DBH and HT produced prediction errors of $\pm 0.58 \text{ cm}$ and $\pm 0.71 \text{ m}$, respectively (Table 3). Similarly, the fitted models suggested that BAL was negatively associated with DBH and HT of *Q. glauca* (Table 3, Fig.2a-b). A $1 \text{ m}^2 \text{ ha}^{-1}$ increase in BAL was associated with about 3.76 cm decrease in DBH and 1.69 m decrease in HT. Similar to *Z. serrata*, ELEV was significantly associated with DBH and HT but not TPH (Table 3). ELEV was negatively associated with both tree attributes. A 100 m increase in ELEV was associated with a 0.85 cm decrease in DBH and a 0.40 m decrease in HT (Table 2).

Table 3. Parameter estimates of fitted mixed-effects models of DBH, HT, HDR, and LCR for *Quercus glauca*.

Predictor	Estimate	SE	p-value	σ_{b_k}	$\rho_{b_0 b_1}$
DBH					
Intercept	24.4403	3.5531	<0.0001	2.4772	-0.107
BAL	-3.7623	0.4611	<0.0001	1.0240	
ELEV	-0.0085	0.0020	0.0052		
TPH	ns	ns	ns		
RSE, σ_e			0.5827		
HT					
Intercept	13.5151	2.0847	<0.0001	2.1977	-0.900
BAL	-1.6902	0.4194	0.0001 ??	0.9703	
ELEV	-0.0040	0.0010	0.0089		
TPH	ns	ns	ns		
RSE, σ_e			0.7136		
p			0.7515		
HDR					
Intercept	76.0743	15.7179	<0.0001	42.7005	0.997
BAL	30.8613	6.3453	<0.0001	16.7809	
ELEV	ns	ns	ns		
TPH	ns	ns	ns		
RSE, σ_e			20.2096		
p			1.7950		
LCR					
Intercept	1.1613	0.1208	<0.0001	0.0902	0.7233
BAL	-0.1857	0.0693	0.0073	0.0789	
ELEV	ns	ns	ns		
TPH	ns	ns	ns		
RSE*			0.1045		

SE = standard error of parameter estimate; σ_{b_k} = standard deviation of random effect b_k for $k = 0, 1$ (Eq.[2]); $\rho_{b_0b_1}$ = correlation of random effects b_0 and b_1 ; RSE = residual standard error of fitted model; p = power in the variance function of weighted LME model. RSE* = RSE of fitted GLMM model for LCR was pseudo residual standard error. ns = predictors that were insignificant from the likelihood ratio tests as the variable selection method.

3.2. Tree vulnerability

For *Z. serrata*, the fitted model of HDR produced a prediction error of ± 26.47 unit (Table 2). The fitted model suggested that BAL was the only predictor significantly associated with HDR (Table 2). Results showed that BAL was positively associated with HDR (Table 2, Fig.1c). A $1 \text{ m}^2 \text{ ha}^{-1}$ increase in BAL was associated with a 36.62 unit increase in HDR. For *Q. glauca*, the fitted model of HDR produced a prediction error of ± 20.21 unit (Table 3). Similar to *Z. serrata*, BAL was the only predictor significantly associated with HDR (Table 3). The association was positive (Table 3, Fig.2c). A $1 \text{ m}^2 \text{ ha}^{-1}$ increase in BAL was associated with a 30.86 unit increase in HDR.

3.2. Tree health

For *Z. serrata*, the model prediction error of LCR was ± 0.164 (Table 2). As LCR was modeled with GLMM assuming a Beta distribution with a logit link, the estimated parameters were interpreted as the ratio of LCR to BR (LCR:BR). BR was the bole ratio and was defined as the proportion of tree height without crown, i.e., $\text{BR} = \text{HCB}/\text{HT} = 1 - \text{LCR}$ (Kershaw et al. 2016). A tree with small LCR:BR had a small crown, and vice versa. The fitted model suggested that BAL and ELEV were negatively associated with LCR, but TPH was positively associated with LCR

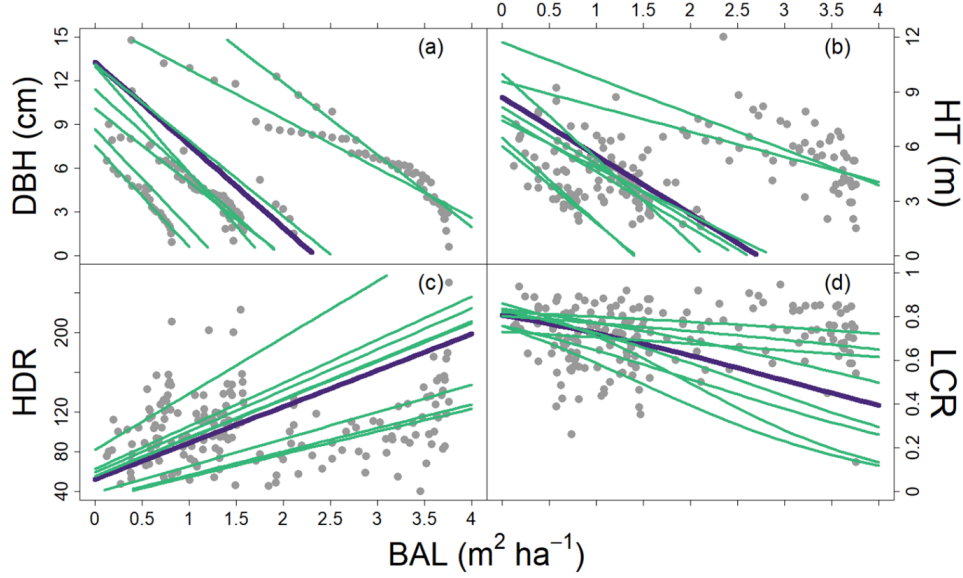


Figure 1. Relationship between tree basal area in larger trees (BAL) and (a) diameter at breast height (DBH), (b) total tree height (HT), (c) height-to-diameter ratio (HDR), and (d) live crown ratio (LCR) for *Zelkova serrata*. Purple thick lines depict predicted global trend while green thin lines depict predicted plot-level trends of the fitted mixed-effects models. Global trend is computed from models with estimated fixed parameters β .

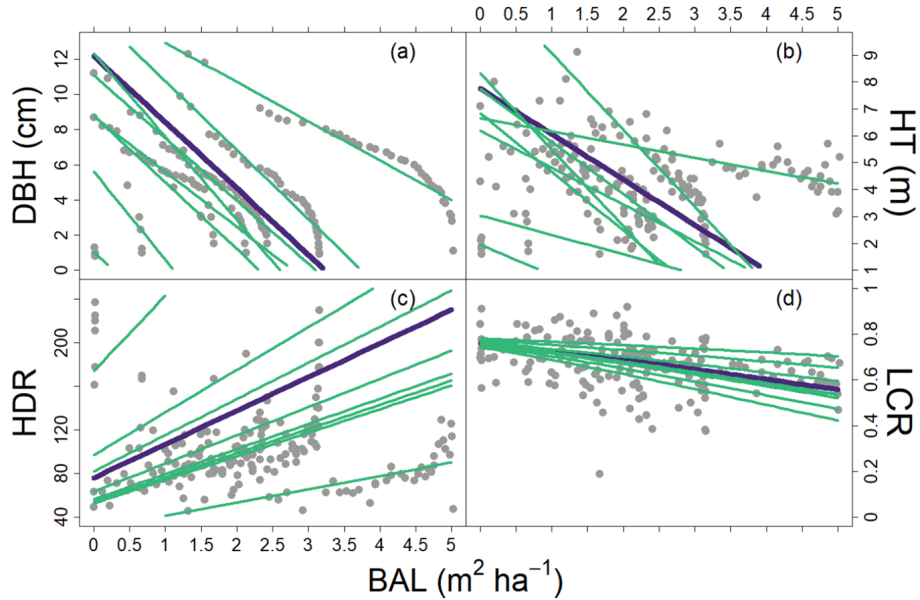


Figure 2. Relationship between tree basal area in larger trees (BAL) and (a) diameter at breast height (DBH), (b) total tree height (HT), (c) height-to-diameter ratio (HDR), and (d) live crown ratio (LCR) for *Quercus glauca*. Purple thick lines depict predicted global trend while green thin lines depict predicted plot-level trends of the fitted mixed-effects models. Global trend is computed from models with estimated fixed parameters β .

(Table 2, Fig.1d). A $1\text{ m}^2\text{ ha}^{-1}$ increase in BAL was associated with a 59.31% [$100\% \times (e^{0.4657}-1)$] decrease in LCR:BR (Table 2). A 100 m increase in ELEV was associated with a 3.67% [$100\% \times (e^{0.036}-1)$] decrease in LCR:BR (Table 2). Lastly, a 100 trees ha^{-1} increase in TPH was associated with a 7.57% [$100\% \times (e^{0.073}-1)$] increase in LCR:BR (Table 2).

Results of *Q. glauca* were different from *Z. serrata*. For *Q. glauca*, the model prediction error was lower than *Z. serrata* with ± 0.104 (Table 3). The fitted model showed that BAL was the only predictor significantly associated with LCR (Table 3). The association was negative (Table 3, Fig.2d). A $1\text{ m}^2\text{ ha}^{-1}$ increase in BAL was associated with a 20.41% [$100\% \times (e^{0.1857}-1)$] decrease in LCR:BR (Table 3).

4. Discussion and Conclusions

Success of a reforestation effort depends on informed silviculture decisions such as choosing the right tree species for a reforestation area. In some instances, tree species suitable for an area may not be immediately available, and as such, it is necessary to reforest with tree species from outside their native habitat ranges. There is currently very little research looking at how *Z. serrata* and *Q. glauca* grow on reclaimed agricultural lands that are within and outside of their native habitat ranges. Because of their economic, carbon sequestration, and reforestation potentials, there is a need to fill this knowledge gap by understanding how environments and competition affect growth of both tree species. Due to their widespread presences in the East Asian regions, findings from this study could inform forest managers on designing reforestation activities on reclaimed lands in these regions.

For inter-tree competition (BAL), our study suggests that *Z. serrata* and *Q. glauca* trees experiencing greater competition tend to be smaller, shorter, more vulnerable to damage, and less healthy. BAL describes local competition experienced by a tree in a stand assuming that it is only affected by trees larger than itself (Weiskittel et al. 2011). Other studies have found results similar to ours. Schütz and Pommerening (2013) showed that diameter growth of *Pseudotsuga menziesii* was lower when inter-tree competition increased. Nunifu (2009) found similar results in height growth of *Pinus contorta*, *Populus tremuloides*, and *Picea glauca*.

Wonn and O'Hara (2001) found that trees in the Northern Rocky Mountain experiencing greater inter-tree competition had higher HDR and risked snow and wind damage, especially when HDR was greater than 80. Holdaway (1986) found that trees tended to have lower LCR when inter-tree competition was high. Jones et al. (2019) found that dominant *Pseudotsuga menziesii* trees have higher LCR due to less inter-tree competition. Thus, our findings generally agree with other tree species in different forest ecosystems.

Despite similar responses to inter-tree competition, *Z. serrata* differs from *Q. glauca* in the strength of the responses. This is consistent with Vospernik (2021) that showed similar general trends but species-specific variations between 22 Austrian tree species. In short, the responses of *Z. serrata* in tree size, vulnerability, and health to inter-tree competition are stronger than *Q. glauca*. This may be due to different growth strategies between the two species. Chen et al. (2021) showed that a nine-year old single species *Z. serrata* plantation displayed significant stratification in stand structures due to strong inter-tree competition. In early stand development, dominant *Z. serrata* trees quickly reach upper strata by investing greater energy in crown development (Chen et al. 2021). As a result, dominant *Z. serrata* trees develop large crowns, which in turn leads to rapid diameter and height growth. On the other hand, *Z. serrata* trees that are suppressed due to inter-tree competition sacrifice crown development in favor of growing main stem (Chen et al. 2021). This strategy perhaps allows suppressed *Z. serrata* trees to persist under greater inter-tree competition. Thus, rapid stratification at early stand development due to inter-tree competition could be a strategy for *Z. serrata* trees to quickly establish on reclaimed lands.

On the contrary, the milder response of *Q. glauca* to inter-tree competition suggests that the tree species could better resist inter-tree competition. There is a lack of study on growth strategy of *Q. glauca* in Taiwan. In Japan, *Q. glauca* is classified as a mid-successional tree species (Itô and Sumida 2017). Sumida et al. (1997) found that diameter growth rate was approximately constant over time suggesting that *Q. glauca* had an intrinsic strategy to persist under suppression. Contrary to *Z. serrata*, Itô et al. (1997) showed that suppressed *Q. glauca* trees still prioritized crown development. These observations suggest that *Q. glauca* has developed an adaptive strategy to persist under canopy and to compete under strong inter-tree competition.

For environmental effects, our study suggests that *Z. serrata* and *Q. glauca* trees at higher

elevation tend to be smaller and shorter. *Z. serrata* trees are also less healthy with smaller crowns at higher elevation. The effects on tree sizes and tree health are expected because trees of both species are growing outside their native habitat ranges. The native ranges are 300 to 1000 m a.s.l. for *Z. serrata* and 500 to 1500 m a.s.l. for *Q. glauca*. In comparison, the eight sites of *Z. serrata* distributed between 107 to 1964 m a.s.l., and the eight sites of *Q. glauca* distributed between 1194 to 2514 m a.s.l. Thus, some of the higher elevation sites are about 1000 m above the tree species native habitat ranges. At higher elevation, we speculate that growing conditions such as colder climate are unfavorable to both broadleaf tree species, which in turn limits annual growth. Chen et al. (2017) found that one to three years old *Z. serrata* and *Q. glauca* seedlings grew better at 400-750 m and 1100-1450 m a.s.l. Our study suggests that the responses of *Q. glauca* were greater than those of *Z. serrata*. This might suggest that *Q. glauca* trees are more susceptible to environments outside its native habitat ranges.

However, it could be that the established sites of *Q. glauca* start at 1194 m a.s.l., which are already close to the upper range of the species native habitat range.

Our study suggests that stand competition as represented by TPH had little effects on tree sizes, vulnerability, and health except the health of *Z. serrata* trees. TPH is often used as a surrogate for trees competing for stand-level resources, e.g., underground nutrients and growth space (Lam and Maguire 2012). As mentioned above, *Z. serrata* trees are more sensitive to competition. This sensitivity may also lead to changes in its crown structures. However, further study is needed to quantify effects of stand-level competition on *Z. serrata* trees. Lastly, our study suggests that stand-level competition might play a minor role in influencing tree attributes compared to the effects from elevation and inter-tree competition.

Our study is limited to trees of six to seven years old with the conventional site treatments of removing competing vegetation during the first three years. Nonetheless, findings from this study have increased our understanding of the responses of *Z. serrata* and *Q. glauca* trees to the environments and competition during early stand development. In summary, our study suggests that caution should be practiced when planting *Z. serrata* and *Q. glauca* trees outside their native habitat ranges. For *Z. serrata*, it is important to control inter-tree competition in early stand development to reduce stratification in stand structures. This can be accomplished by planting *Z. serrata* at an initial density higher than 2000 trees ha⁻¹, which could also avoid tendency of the tree species to branch when stand competition is very low (Chen et al. 2021). For *Q. glauca*, it is recommended to plant it alongside other tree species in mixed species reforestation systems to promote multistoried stand structures. This is to take advantage of the tree species' natural persistence to suppression. For a single species plantation of *Q. glauca*, future study is needed to understand its branching patterns. Early regeneration dynamics strongly determine future stand development and diversity (Lam and Maguire 2011). Thus, success of any reforestation system depends on its capability to promote development of planted seedlings. Lastly, with changing climate and increasing frequency of extreme weather events, maintaining continuous forest cover by reclaiming degraded or abandoned agricultural lands is important to Taiwan.

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Disclosure Statement

The authors declare that there are no competing interest.

Data Availability

The data are available from the corresponding author upon request.

Author Contribution

Conceptualization: TYL, SWL
 Funding acquisition: TYL, SWL
 Investigation: YCL, TYC, TYL, SWL
 Methodology: TYL, SWL
 Project administration: SWL
 Supervision: TYL, SWL
 Writing - original draft: YCL, TYC
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