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Article

Effect of Planting Density on Knot Attributes and Branch Occlusion of *Betula alnoides* under Natural Pruning in Southern China

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Abstract: Knot-related defects are the major cause of timber quality degradation, and diminishing this kind of defects is an important issue in forest management. For the purpose of clear-wood production, knot attributes and branch occlusion of *Betula alnoides* under natural pruning were investigated in a 14-year-old experimental plantation with five planting densities ranging from 500 to 3333 stems per hectare in southern China, and a total of 1325 occluded branches from 30 trees were sampled and dissected. The mean occluded branch diameter (OBD), radius of knots and branch insertion angle (IA) decreased significantly with increasing planting density. Planting with high stocking density significantly reduced the frequency of thick occluded branches (diameter ≥ 20 mm) while increasing the frequency of small ones (diameter < 10 mm). Branch occlusion time (OT) also tended to increase with decreasing planting density. The results of generalized linear mixed models showed that OBD was the major factor influencing OT, radius of dead portion of knot (RDP), total radius of knot (TRK) and IA. In addition, OT was positively correlated with RDP but negatively correlated with stem diameter growth rate during branch occlusion (SDGR). Silvicultural strategies with appropriate planting density for large-diameter clear-wood production of *B. alnoides* were discussed.

Keywords: *Betula alnoides*; spacing; self-pruning; branch occlusion; knottiness; mixed models; wood quality

1. Introduction

The demand for high-quality timber has recently been increasing, which leads to a remarkable variation of timber prices depending on the quality [1]. Consequently, growing large-sized and high-quality timber has become an important target in plantation forestry. It is well known that knot-related defects in the stems greatly affect the manufacturing and joinery industries, and the amount and size of knot-related defects are crucial factors for log grading and timber quality [2–4].

In general, occluded knots include two parts: live knot (tight portion) and dead knot (loose portion). The dead knot has no physical connection to the surrounding wood and interrupts the wood grain. Knot-related defects are mostly caused by the dead knot, which can lower the mechanical strength of timber, decrease the performance of veneered wood, and even make the logs unusable. Contrary to dead knot, live knot is attached physically to surrounding wood and distorts the wood grain, which has less influence on the mechanical strength of timber. The distorted rings in the live knot sometimes can even increase the ornamental value of wood texture. Branch occlusion is the process of trees forming callus and clear wood over the dead branch stubs, which would become dead knots after occlusion [5]. It determines the amount of time that branch stubs are exposed to the external environment. The earlier the branches occlude the earlier the production of clear wood can start, which could also lower the risk of timber coloration and stem rot caused by microorganisms such as fungi during occlusion. Hence, shortening the occlusion time and making the dead knot small through forest management are essential to produce high-quality timber.

Planting density, as a major tool of forest management, has been studied and proven to markedly influence branch attributes. For example, low planting densities may result in thick branches in the most valuable section of the log [6–9], while planting with high stocking density can effectively reduce the maximum and average branch size [10–13]. Some studies have also demonstrated that the angle of live branches became steeper with increasing planting densities [14,15], and a more acute branch angle might have the potential to cause larger dead knots and higher knot-related defects [14]. Additionally, planting density also affects crown dynamics, which is closely related to branch development and occlusion [16,17]. Nonetheless, the effects of planting density on branch occlusion and knot attributes have been rarely assessed. Most studies have mainly focused on predicting or comparing the branch occlusion and knot attributes under natural or artificial pruning [18–22], and the relationship between planting density and knot size was only studied for some species, such as *Pseudotsuga menziesii*, *Picea abies* and *Pinus* *sylvestris* in temperate zones [23–25]. There have been no published reports on the effect of planting density on branch occlusion and knot attributes for valuable tropical and subtropical tree species. For the purpose of valuable timber production in these regions, target-adapted management tools, such as planting density, are warranted.

Betula alnoides Buchanan-Hamilton ex D. Don is a well-known, fast-growing and valuable timber species indigenous to Southeast Asia and southern China [26]. Its wood is of moderate density, less likely to crack and warp and easily manufactured. It is extensively used for making floorboards, panels and high-grade furniture, and is also an ideal material for high-class interior decoration and overlaid veneer [27]. *B. alnoides* has a wide adaptability to soil type, altitude and climate condition [28]. It has been widely planted in the tropical and warm subtropical areas of southern China. The main planting densities used in afforestation for this species are 1667 and 1111 stems per hectare (sph), and the rotation length is about 20 years. However, most logs of *B. alnoides* suffer from knotty defects, which seriously degrade the timber quality and lower the economic value.

The objectives of the present study were to examine the effect of planting density on the branch occlusion and knot attributes of *B. alnoides* and to test the hypothesis that higher planting densities would lead to (1) shorter occlusion time; (2) smaller knot size; (3) more acute branch angles; and (4) smaller occluded branch diameters than lower planting densities. Models were also built based on a dataset of routine branch measurements to explore the relationships between branch occlusion and knot attributes, and thus to predict branch occlusion and knot size of *B. alnoides*. The findings could improve the understanding of the effect of planting density on knot attributes and branch occlusion, and provide evidence for making practical guidelines for foresters in large-sized clear-wood productions of *B. alnoides*. This study could also contribute to a better understanding of branch occlusion processes and their relationship with planting density under natural pruning for other valuable timber tree species in these regions.

2. Materials and Methods

The study material was sampled in a 14-year-old planting density experiment of *B. alnoides* established in 1999 at the Experimental Center of Tropical Forestry (ECTF), Chinese Academy of Forestry in Pingxiang City, Guangxi Zhuang Autonomous Region, China (22°02′ N, 106°52′ E). The site belongs to the northern tropical monsoon climate zone, with a mean annual temperature of 22 °C. The mean annual precipitation is 1550 mm, with 75% of rainfall being concentrated in May to September. The plantation is on a south-facing slope, with a mean altitude of 420 m above sea level. The soil is red earth soil derived from siliceous rock.

The experimental plantation consisted of five planting densities made up of 3333, 1667, 1111, 833 and 500 sph. The design was a randomized complete block with three replicates, two of which were located on the lower slope and one on the upper slope. Each plot (30 m × 40 m) was surrounded by two buffer rows. No thinning and fertilization had been applied in this plantation. In March 2013, tree height, diameter at breast height, height to the crown base and crown diameter were measured for all trees in each plot (see Table 1 for abbreviations and Table 2 for data description). One dominant and one co-dominant tree in each plot were selected and felled for stem analysis and knot dissection. Discs with completely occluded branches were then cut with a chainsaw along the stem where the branch scars could be detected from the bark surface.

In case of branch whorls, only the largest branch in each whorl was chosen for further analyses. The insertion height of each sampled knot from 0.26 m to 19.72 m on the stem bole was recorded. The number of discs sampled on each tree ranged from 25 to 79, and a total of 1325 discs from 30 trees were collected. For each disc, a longitudinal dissection was performed at the middle of occluded branch with an electric saw, and a dissected half segment with the integrated knot was selected and sanded using an electric sander with 120-grit sandpaper to make the annual rings clearly visible. The years of branch birth (YB), branch death (YD) and complete occlusion (YO), radius of living (RLP) and dead (RDP) portion of knot, insertion angle of the occluded branch (IA), diameter of the occluded branch (OBD) and stem diameter growth rate during the branch occlusion (SDGR) were measured (Figure 1 and Table 1).

As the process of die-off is long for some branches of *B. alnoides*, which has diffuse-porous wood, we determined the year of death for naturally pruned branches according to a method described by Hein [19]. The year of death was calculated as the mean value of the last year (YD1) when the branch was still alive and the first year (YD2) when tree rings clearly took part in the branch occlusion process. The last year that a branch was alive was defined as the year when tree rings in the stem still clearly joined the rings in the branch. The branch occlusion time was the time from the year of death to the year of complete occlusion. The branch diameter was measured at the broadest position of the occluded branch. The insertion angle of the occluded branch was the angle of intersection between the stem pith and branch pith. The radius of live portions of knot was the distance from stem pith to the end of live portion of knot in radial direction ($\overline{BC}$ in Figure 1). The radius of dead portion of knot was the distance from the end of live portion of knot to the end of dead portion of knot in radial direction ($\overline{AB}$ in Figure 1). The stem diameter growth rate was the average diameter growth rate at the position of knot during branch occlusion; it was calculated as two times the average value of the distance from the year of branch death to the year of complete occlusion in radial direction divided by branch occlusion time. The frequencies of branch occurrence in diameter classes (0–9.99, 10–19.99, 20–29.99, 30–39.99 and ≥40 mm) and branch angle levels (30–39, 40–49, … and 80–89°) were expressed as a percentage of the total number on an individual tree basis.

Table 1. Explanation of the symbols.

Symbols	Attributes represent	Precision
	Tree attributes	
DBH	Stem diameter at breast height	0.1 cm
HCB	Height of the crown base	0.1 m
CD	Crown diameter	0.1 m
	Branch attributes	
OT	Time of branch occlusion	1 year
OBD	Diameter of occluded branch	0.01 mm
IA	Insertion angle of the occluded branch	1°
IH	Insertion height of the occluded branch on stem	0.01 m
SDGR	Stem diameter growth rate during the branch occlusion	mm year^{-1}
RLP	Radius of the living portion of knot (live knot)	0.01 mm
RDP	Radius of the dead portion of knot (dead knot)	0.01 mm
TRK	Total radius of knot (RLP + RDP)	0.01 mm

Table 1. *Cont.*

Symbols	Attributes represent	Precision
YB	Year of birth of the branch	1 year
YD	Year of death of the branch	1 year
YO	Year of the complete occlusion of the dead branch	1 year
	Model descriptors	
a, b, c, d	Coefficients of fixed effect	
p, pt, ptb	Subscripts for plot, tree and branch	
α, β, γ, δ	Variance components (random effects)	
ln()	Symbol for link function in GLMM; here: Log-link	
E, $\|E\|$, E^2	Mean error, mean absolute error, mean squared error	
Φ	Dispersion parameter	
	Units	
sph	Stems per hectare	

GLMM: generalized linear mixed models.

Table 2. Plot and tree characteristics of *Betula alnoides* plantations.

Planting Density (sph)	Spacing (Row × Tree) (m)	Tree Height $\bar{x}$ (m)	DBH $\bar{x}$ (cm)	HCB $\bar{x}$ (m)	CD $\bar{x}$ (m)	Basal Area ($m^2\ ha^{-1}$)
3333	1.5 × 2	13.76 (0.69) ^{a}	14.11 (0.39) ^{c}	8.63 (0.43) ^{a}	2.84 (0.07) ^{b}	20.52 (0.61) ^{a}
1667	2 × 3	14.04 (1.51) ^{a}	14.81 (0.51) ^{b,c}	8.46 (1.26) ^{a}	3.03 (0.19) ^{b}	15.76 (1.46) ^{b}
1111	3 × 3	13.10 (0.60) ^{a}	14.71 (0.33) ^{b,c}	7.27 (0.40) ^{a}	3.47 (0.10) ^{b}	13.02 (0.72) ^{b,c}
833	3 × 4	13.71 (0.60) ^{a}	16.38 (0.45) ^{a,b}	7.40 (1.00) ^{a}	3.35 (0.33) ^{b}	11.09 (1.05) ^{c}
500	4 × 5	13.99 (1.35) ^{a}	17.45 (0.62) ^{a}	6.00 (1.00) ^{a}	4.62 (0.20) ^{a}	7.59 (0.32) ^{d}

Note: The number in parentheses is the standard error of mean value; Different superscript letters indicate significant differences between planting density treatments at the 0.05 level; sph: Stems per hectare; DBH: Stem diameter at breast height; HCB: Height of the crown base; CD: Crown diameter.

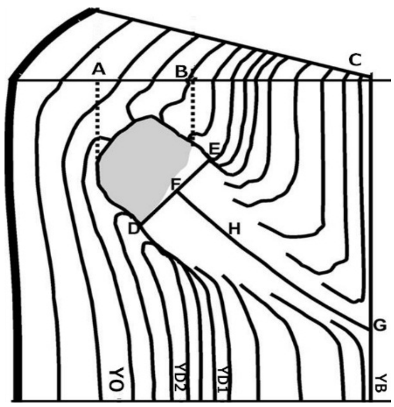

Figure 1. Measured occluded branch attributes at the longitudinal dissection (modified from Hein [19]). The shaded portion of occluded branch is the dead knot; the remaining portion of occluded branch is the live knot. $\overline{AB}$: Radius of dead portion of knot; $\overline{BC}$: Radius of live portion of knot; $\overline{AC}$: Total radius of knot; $\overline{DE}$: Diameter of occluded branch; ∠FGC: Insertion angle of occluded branch, FG: The branch pith; GC: The stem pith. YB, YD and YO are the year of branch birth, death and occlusion, YD = (YD1 + YD2)/2.

As the dataset had a hierarchical structure with branches nested within trees which were clustered within plots, the statistical significance between treatments was analyzed using mixed models including random plot (subscript p), tree (subscript pt) and branch effects (subscript ptb). The model used to test the treatment effects was: $y_{pt} = \mu + \beta_D + \mu_p + \mu_{pt} + \eta$, where y is a dependent variable, μ is the overall mean, β_D is the fixed effect of planting density, μ_p and μ_{pt} are the random effects for plot and tree and η is the residual error at the lowest level (random effect for branch). Multiple comparisons of the planting density effects were performed by computing least-square means of each treatment and testing with a Bonferroni adjustment for branch occlusion time, occluded branch diameter, insertion angle, radius of live and dead portions of knot and total radius of knot. Restricted maximum likelihood (REML) estimation was used in the mixed models. Analysis of variance (ANOVA) and Duncan's multiple comparison tests were used to examine the differences between planting density treatments for growth performance of the stand, the mean frequency of occluded branch occurrence in diameter size classes or insertion angle levels.

As to model building, generalized linear mixed models (GLMM) were used to explore the potential relationships among the knot attributes since the dataset had a hierarchical structure (plot, tree and branch) and contained discrete and continuous variables. Models were built with the dataset of routine branch measurements, and variables and random effects were included in the models at the 0.05 significant level. Final models were selected according to corrected Akaike's Information Criteria (AIC), Bayesian's Information Criteria (BIC), biological explanation and simplicity. Since under-dispersion was encountered when modeling the branch occlusion time (a count variable) with negative binomial distribution, an under-dispersion parameter Φ was added to the variance function to prevent misinterpretation for inflated or deflated test statistics [29]. In order to examine the performance of the models, error statistics (E, $|E|$ and E^2) were calculated using only the fixed part of the models. To examine the model fit, the empirical "best linear unbiased predictors" (BLUPs) were calculated, and the residual graphs were displayed over independent variables and corresponding predicted values. The predictive powers of the models were calculated as the squared correlation between the measured observation and the predicted value [19]. All values were used in their original data scale. Data analyses were conducted in SPSS 21.0 (IBM-SPSS Inc, Chicago, IL, USA).

3. Results

3.1. Effect of Planting Density on the Time of Branch Occlusion

A decreasing trend was found for the time of branch occlusion with increasing planting density (Table 3), and it varied from 2.3 years for 500 stem per hectare (sph) to 1.8 years for 3333 sph. The occlusion time of 3333 sph was significantly shorter than that of all other planting density treatments except for 833 sph.

Table 3. Characteristics of knot and branch occlusion of *Betula alnoides*.

	Planting Density (sph)									
	3333		**1667**		**1111**		**833**		**500**	
	Min–Max	**Mean**	**Min–Max**	**Mean**	**Min–Max**	**Mean**	**Min–Max**	**Mean**	**Min–Max**	**Mean**
IH	0.33–14.78	6.00 (0.21) [a]	0.48–19.72	7.23 (0.78) [a]	0.26–15.79	5.89 (0.24) [a]	0.31–16.74	6.59 (0.26) [a]	0.32–17.92	6.10 (0.30) [a]
SDGR	4.81–40.98	13.95 (0.34) [a]	4.32–34.75	13.12 (0.33) [a]	4.85–40.74	15.35 (0.44) [a]	6.8–38.04	15.10 (0.36) [a]	5.45–42.94	14.28 (0.40) [a]
OT	1–7	1.8 (0.1) [b]	1–10	2.1 (0.1) [a]	1–9	2.2 (0.1) [a]	1–8	2.1 (0.1) [a,b]	1–9	2.3 (0.1) [a]
OBD	3.49–29.95	10.60 (0.25) [c]	3.73–29.63	11.77 (0.24) [b,c]	2.93–31.91	12.4 (0.35) [b]	4.74–39.81	14.21 (0.43) [a]	4.67–55.1	14.98 (0.51) [a]
IA	33–81	55.5 (0.5) [b]	40–82	56.0 (0.4) [b]	30–82	56.0 (0.5) [b]	30–88	58.6 (0.6) [a]	31–88	59.6 (0.9) [a]
RLP	6.11–64.22	25.26 (0.61) [c]	4.14–70.97	28.47 (0.69) [c]	4.58–86.6	27.75 (0.99) [c]	8.45–96.06	33.48 (1.02) [b]	4.14–102.29	38.8 (1.29) [a]
RDP	3.23–38.45	11.79 (0.33) [c]	2.6–51.53	13.09 (0.41) [b,c]	2.93–70.06	16.82 (0.62) [a]	1.7–53.22	15.05 (0.52) [a,b]	3.76–71.05	16.75 (0.86) [a]
TRK	13.37–78.47	37.05 (0.72) [d]	11.92–102.22	41.56 (0.81) [c]	14.43–109.57	44.57 (1.14) [b,c]	17.00–135.18	48.53 (1.29) [b]	16.01–127.89	55.45 (1.55) [a]

Note: The numbers in the parentheses refer to the standard error of mean value; Different superscript letters indicate a significant difference between planting density treatments at the 0.05 level; sph: Stems per hectare; IH: Insertion height of the occluded branch; SDGR: Stem diameter growth rate during the branch occlusion; OT: Time of branch occlusion; OBD: Diameter of occluded branch; IA: Insertion angle of the occluded branch; RLP: Radius of the living portion of knot; RDP: Radius of the dead portion of knot; and TRK: Total radius of knot.

3.2. Effect of Planting Density on the Radius of Knot

The mean radius of dead portion of knot (RDP), live portion of knot (RLP) and mean total radius of knot (TRK) showed a significant downward trend with increasing planting density from 500 sph to 3333 sph (Table 3). No significant differences were found among the three low planting density treatments (500, 833 and 1111 sph) for RDP, and among the three high planting density treatments (3333, 1667 and 1111 sph) for RLP. As for TRK, it decreased more sharply with increasing planting density, from 37.05 mm in 3333 sph to 55.45 mm in 500 sph.

3.3. Effect of Planting Density on the Insertion Angle of Occluded Branch

The mean insertion angle of occluded branches increased significantly from 55.5° to 59.6° with the decrease of planting density (Table 3). The insertion angle of 500 and 833 sph was significantly larger than that of 1111, 1667 and 3333 sph. The occluded branch insertion angles mostly ranged from 50° to 70°, and no branch insertion angle below 30° was seen. Although lower planting densities had a higher percentage of large branch insertion angles, there were no significant differences in any insertion angle levels among all the planting density treatments (Table 4).

Table 4. Frequency distribution of insertion angle of occluded branches for *Betula alnoides.*

Planting Density (sph)	**Frequency of Branch Insertion Angle Level (%)**					
	30–39 (°)	**40–49 (°)**	**50–59 (°)**	**60–69 (°)**	**70–79 (°)**	**80–89 (°)**
3333	1.2 (0.4)	18.8 (5.8)	48.4 (5.5)	25.0 (4.3)	5.9 (1.9)	0.7 (0.4)
1667	0.0 (0.0)	18.9 (3.8)	52.2 (2.3)	24.2 (2.9)	4.3 (0.8)	0.4 (0.4)
1111	1.3 (0.6)	15.4 (4.4)	50.1 (7.6)	26.5 (6.3)	5.4 (2.6)	1.3 (0.9)
833	1.8 (0.8)	14.8 (5.3)	35.5 (4.0)	35.5 (4.5)	9.2 (3.5)	3.1 (2.0)
500	6.7 (2.6)	18.6 (6.4)	40.3 (8.3)	15.6 (4.9)	11.9 (6.5)	7.0 (6.6)

Note: The numbers in the parentheses refer to standard errors of mean value for each branch insertion angle level; sph: Stems per hectare.

3.4. Effect of Planting Density on Diameter of Occluded Branch

The mean diameter of occluded branch was significantly negatively correlated with planting density (Table 3), and the mean occluded branch diameters of 500 and 833 sph were significantly larger than that of other planting density treatments. As to the frequency distribution of occluded branch diameters, more than 43% of occluded branches for each treatment showed a diameter of 10–19.99 mm, and no significant difference in the frequency was observed among them (Table 5). The main difference in the frequency distribution for the occluded branch diameters among the five planting density treatments occurred in the diameter classes of <10 mm and 20–29.99 mm. The frequency of occluded branches in the <10 mm diameter class tended to increase while that for 20–29.99 mm decreased significantly with increasing planting densities. At the stocking treatment of 3333 sph, more than half of the occluded branches were of a diameter smaller than 10 mm, and only 3.9% of the occluded branches was larger than 20 mm. For lower planting densities like 500 and 833 sph, more than 20% of the occluded branches were of a diameter larger than 20 mm. In addition, occluded branches with a diameter larger than 30 mm occurred only under three lower planting densities (500, 833, 1111 sph), and only under 500 sph did occluded branches with diameters above 40 mm exist.

Table 5. Frequency distribution of occluded branch diameter of *Betula alnoides*.

Planting Density (sph)	Frequency of Diameter Class (%)				
	0–9.99 mm	10–19.99 mm	20–29.99 mm	30–39.99 mm	≥40 mm
500	29.1 (3.0) ^{b}	49.2 (4.7) ^{a}	18.7 (3.5) ^{a}	2.0 (1.2)	0.9 (0.6)
833	31.6 (6.5) ^{b}	49.3 (5.8) ^{a}	15.6 (2.7) ^{a,b}	3.5 (1.5)	/
1111	40.2 (5.1) ^{a,b}	49.4 (2.7) ^{a}	9.5 (3.2) ^{b,c}	0.9 (0.6)	/
1667	37.7 (2.8) ^{b}	57.7 (3.3) ^{a}	4.6 (2.1) ^{c}	/	/
3333	53.1 (5.4) ^{a}	43.0 (4.6) ^{a}	3.9 (1.2) ^{c}	/	/

Note: The numbers in the parentheses refer to standard errors of mean value for each branch diameter class; Different superscript letters indicate a significant difference between planting density treatments at the 0.05 level; Analysis of variance was not conducted for diameter classes 30–39.99 and ≥40 mm since there was no data for treatments of high planting density; sph: Stems per hectare.

3.5. Models on Branch Occlusion and Knot Attributes

Generalized linear mixed models were used to explore the relationship between branch occlusion and knot attributes. As to the time of branch occlusion (OT), a log link function with a negative binomial distribution was applied to estimate it:

$$\ln(OT_{ptb}) = a_0 + a_1\ln(OBD_{ptb}) + a_2RDP_{ptb} + a_3SDGR_{ptb} \quad (1)$$

where a_0, a_1, a_2 and a_3 are parameter estimates (Table 1). The time of branch occlusion was correlated with the natural logarithm of occluded branch diameter (OBD), the radius of dead portion of knot (RDP) and the stem diameter growth rate during branch occlusion (SDGR). Other variables and random effects were omitted in the model due to their non-significance (Table 6). There was no significant trend in the raw residuals when plotted against independent variables OBD and SDGR (Figure 2A,C), while a remarkable decreasing trend was found for RDP larger than 55 mm (Figure 2B) and for predicted OT longer than 9 years (Figure 2D). Nonetheless, as RDP and OT exceeded the above values only in very few cases, the model was acceptable. The error statistics also showed that there was no obvious bias (Table 6), and the model explained 79.61% of total variance.

Table 6. Parameter estimates of the model for the time of branch occlusion, radius of dead knot, radius of knot and insertion angle.

Parameter	Estimate	Standard Error	T-value	Cl-Lower	Cl-Upper	Significance
Time of branch occlusion (Equation (1))						
Fixed parameters						
a_0	0.616	0.177	3.478	0.268	0.963	<0.001
a_1	0.198	0.044	4.453	0.111	0.285	<0.001
a_2	0.033	0.002	19.071	0.030	0.037	<0.001
a_3	−0.050	0.004	−13.398	−0.057	−0.043	<0.001
Φ	0.608					
Error statistics		E = 0.0000	$\|E\|$ = 0.3623		E^2 = 0.4996	

Table 6. *Cont.*

Parameter	Estimate	Standard Error	T-value	Cl-Lower	Cl-Upper	Significance
Radius of dead portion of knot (Equation (2))						
Fixed parameters						
b_0	2.010	0.139	14.474	1.738	2.282	<0.001
b_1	0.535	0.032	16.530	0.472	0.599	<0.001
Random parameters						
β_{ptb}	53.110	2.071	25.644	49.202	57.328	<0.001
Error statistics		$E = 0.0142$	$\|E\| = 4.7864$		$E^2 = 106.4202$	
Total radius of knot (Equation (3))						
Fixed parameters						
c_0	2.003	0.081	24.765	1.844	2.162	<0.001
c_1	0.678	0.017	40.059	0.645	0.711	<0.001
Random parameters						
γ_{ptb}	122.748	4.787	25.643	113.715	132.498	<0.001
Error statistics		$E = -0.0124$	$\|E\| = 8.1513$		$E^2 = 123.8880$	
Insertion angle of the occluded branch (Equation (4))						
Fixed parameters						
d_0	4.151	0.031	134.398	4.090	4.211	<0.001
d_1	−0.047	0.010	−4.776	−0.066	−0.028	<0.001
Random parameters						
γ_{ptb}	77.414	3.018	25.652	71.720	83.561	<0.001
Error statistics		$E = -0.01254$	$\|E\| = 6.5097$		$E^2 = 139.9267$	

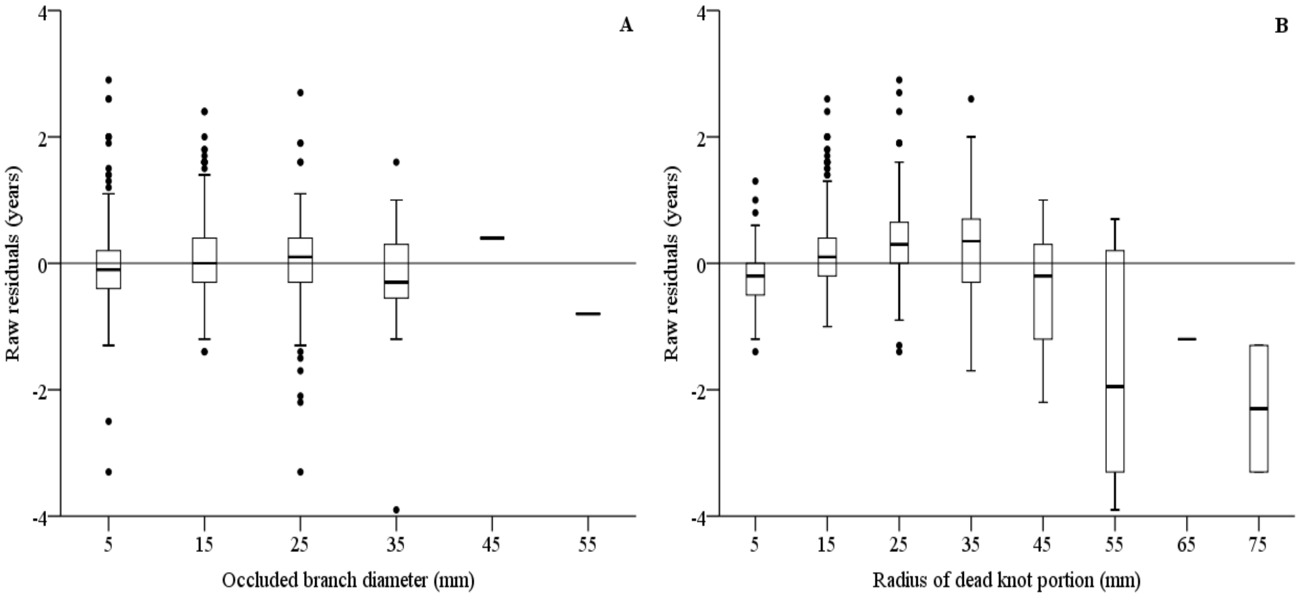

Figure 2. *Cont.*

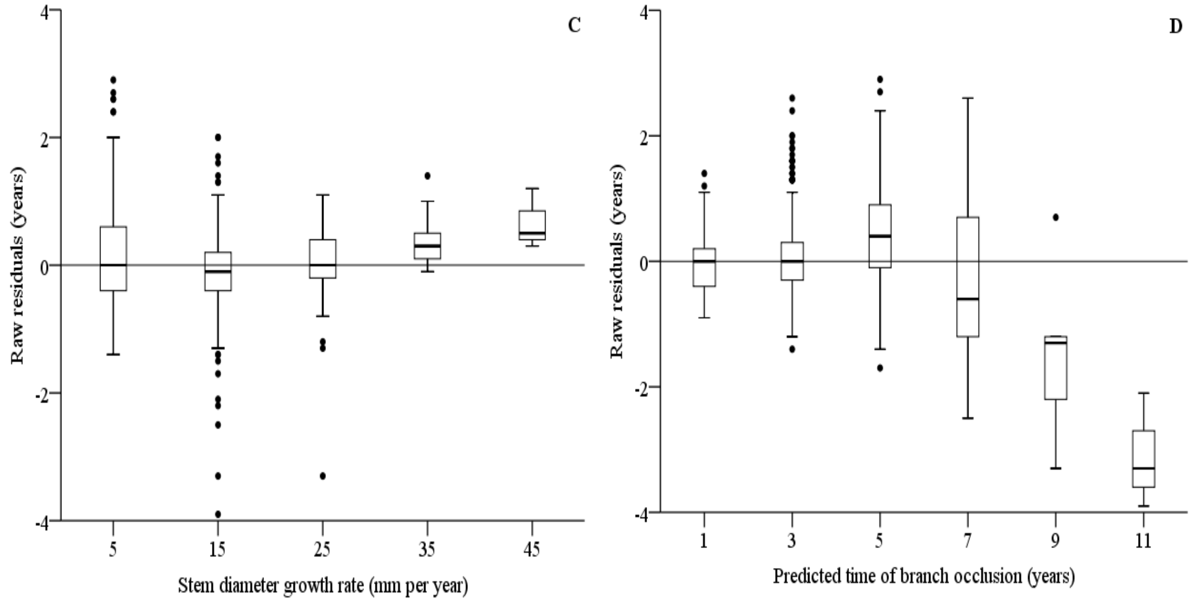

Figure 2. Raw residuals of the model for time of branch occlusion plotted against the independent variables (**A**, **B** and **C**) and predicted variables(**D**). The edges of the box are 25th and 75th percentiles; the vertical lines are drawn from the box to the most extreme point within 1.5 interquartile ranges; the transverse lines in boxes connect the medians.

The radius of the dead portion of the knot (RDP) was estimated using a log linear model with a normal distribution of response:

$$\ln(RDP_{ptb}) = b_0 + b_1\ln(OBD_{ptb}) + \beta_{ptb} \quad (2)$$

where b_0 and b_1 are the parameter estimates, β_{ptb} is the random effect at branch level (Table 1). The RDP was only correlated with the natural logarithm of OBD (Table 6). There was no significant trend in the raw residuals when plotted against OBD and predicted RDP (Figure 3). The error statistics inferred that some other factors were not included in the model (Table 6), and the model only explained 31.27% of total variance.

The total radius of knot (TRK) was modeled using a log-link function with a normal distribution of dependent variable:

$$\ln(TRK_{ptb}) = c_0 + c_1\ln(OBD_{ptb}) + \gamma_{ptb} \quad (3)$$

where c_0 and c_1 are the parameter estimates of the model and γ_{ptb} is the random effect at branch level (Table 1). The TRK was also only correlated with natural log-transformed OBD (Table 6). The error statistics showed there was some unexplained variation left (Table 6). No trend was found in the raw residuals when they were plotted against the predictor and predicted variables (Figure 4). The model explained 62.62% of the total variance.

The insertion angle (IA) of occluded branch was modelled in a log link function with a normal distribution of response:

$$\ln(IA_{ptb}) = d_0 + d_1 \ln(OBD_{ptb}) + \delta_{ptb} \quad (4)$$

where d_0 and d_1 were the parameter estimates, δ_{ptb} was the random effect at branch level (Table 1). The branch insertion angle was only correlated with the natural logarithm of OBD (Table 6). No trend in the raw residuals was found when plotted against independent and predicted variables (Figure 5). The error statistics inferred that there was still a considerable unexplained residual variation (Table 6). The model only explained 19.09% of total variance.

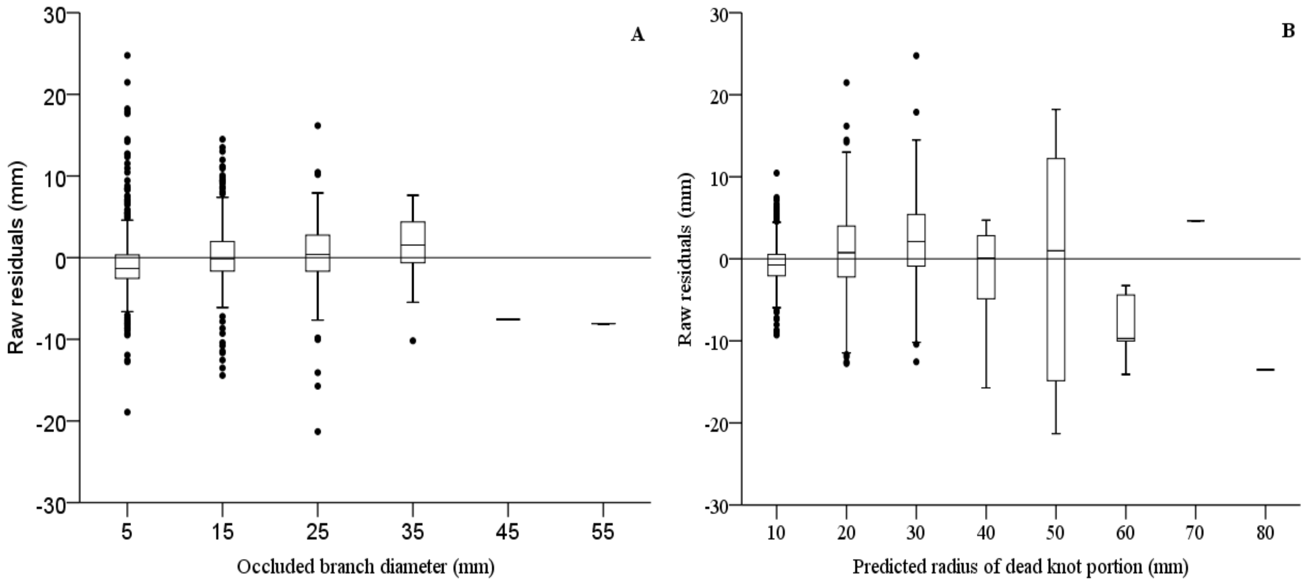

Figure 3. Raw residuals of the model on radius of dead portion of knot plotted against the independent variables (**A**) and predicted variables (**B**). The edges of the box are 25th and 75th percentiles; the vertical lines are drawn from the box to the most extreme point within 1.5 interquartile ranges; the transverse lines in boxes connect the medians.

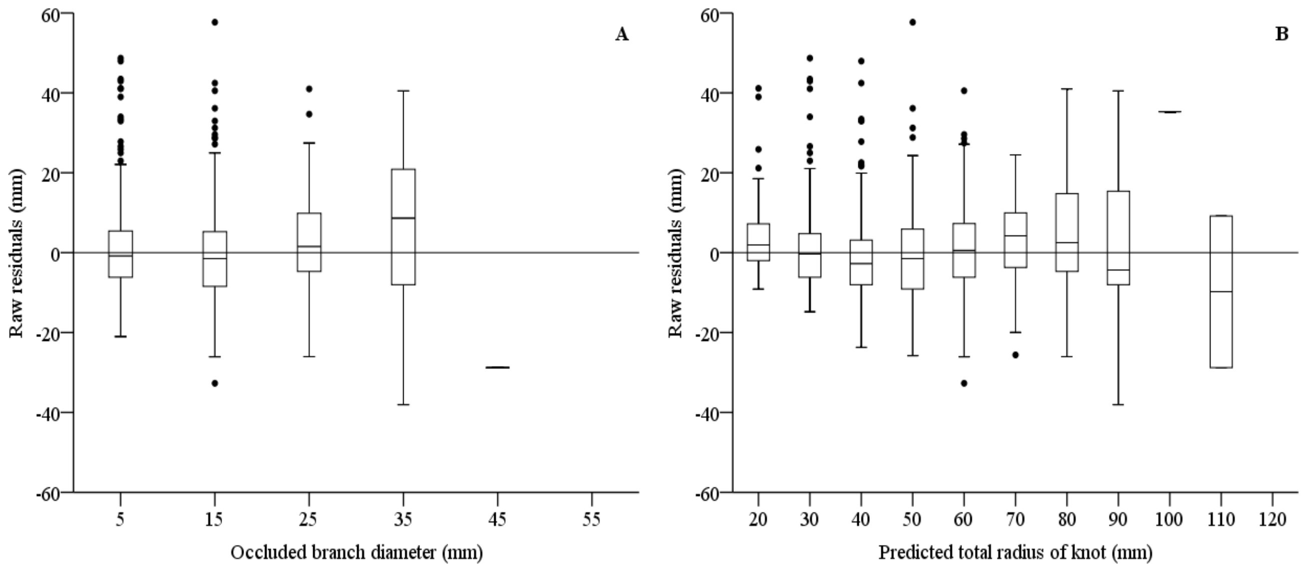

Figure 4. Raw residuals of the model on total radius of knot plotted against the independent (**A**) and predicted (**B**) variables. The edges of the box are 25th and 75th percentiles; the vertical lines are drawn from the box to the most extreme point within 1.5 interquartile ranges; the transverse lines in boxes connect the medians.

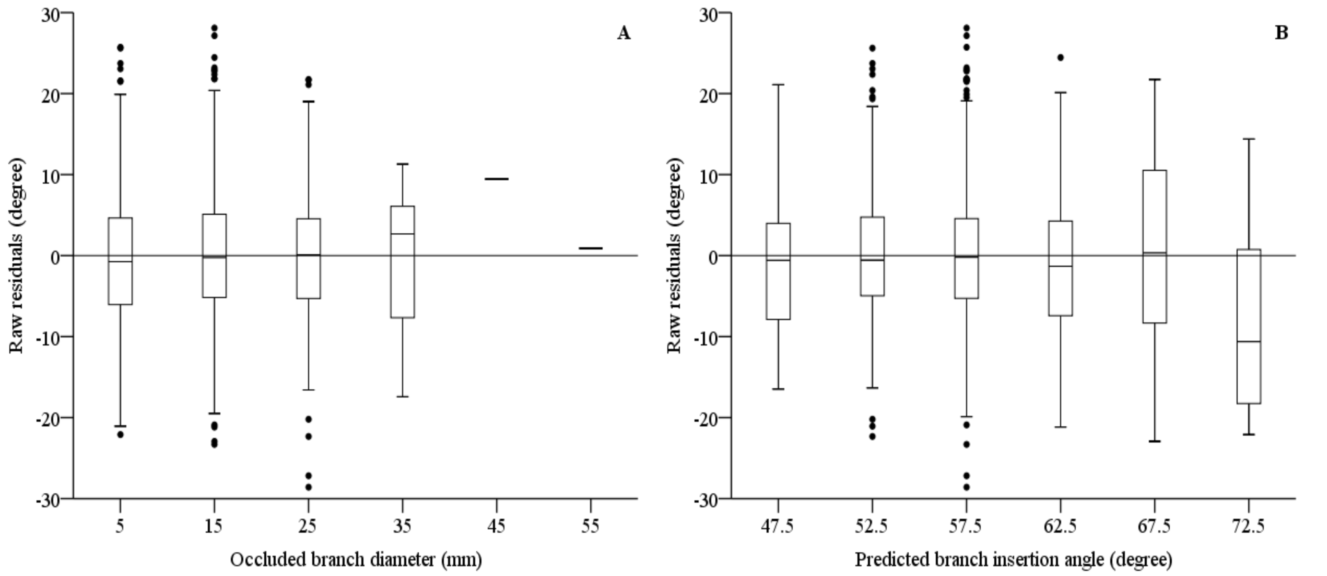

Figure 5. Raw residuals of the model on insertion angel of occluded branch plotted against independent variables (**A**) and predicted (**B**) variables. The edges of the box are 25th and 75th percentiles; the vertical lines are drawn from the box to the most extreme point within 1.5 interquartile ranges; the transverse lines in boxes connect the medians.

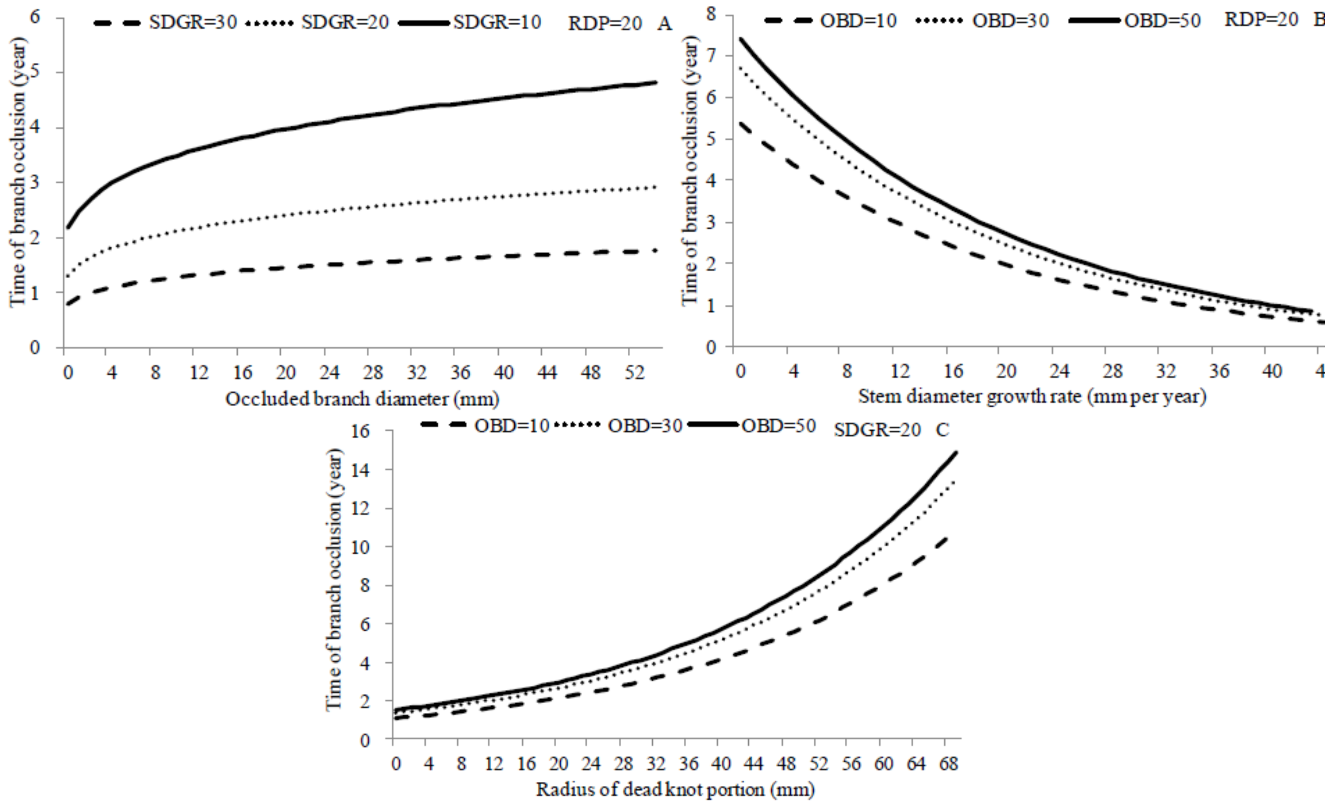

Figure 6. Predicted time of branch occlusion. (**A**) From three levels of stem diameter growth rates during branch occlusion (SDGR) and a radius of dead portion of knot (RDP) of 20mm plotted against occluded branch diameter (ODB) (Equation (1)); (**B**) from three levels of OBD and RDP of 20mm plotted against SDGR; and (**C**) from three levels of OBD and SDGR of 20mm year^{-1} plotted against RDP.

3.6. Simulations

Time of branch occlusion (OT), radius of dead portion of knot (RDP), total radius of knot (TRK) and insertion angle of occluded branch (IA) were simulated according to above equations (Figures 6 and 7). It was shown that the predicted OT increased with the increment of occluded branch diameter and RDP (Figure 6A,C), and trees with higher stem diameter growth rate (SDGR) occluded faster (Figure 6B). The occluded branch diameter influenced the simulated values of OT less than RDP and SDGR during the whole range of values from the sampled dataset. In addition, when the SDGR was larger than 20 mm year^{-1}, OT tended to be less than 3 years. Both RDP and TRK were significantly positively correlated with the occluded branch diameter (Figure 7A,B). The predicted IA decreased slightly with an increase in occluded branch diameter (Figure 7C). When the occluded branch diameter increased over the whole range of sampled values, the simulated RDP and TRK still increased markedly. However, IA did not decrease significantly when the occluded branches were larger than 15 mm in diameter.

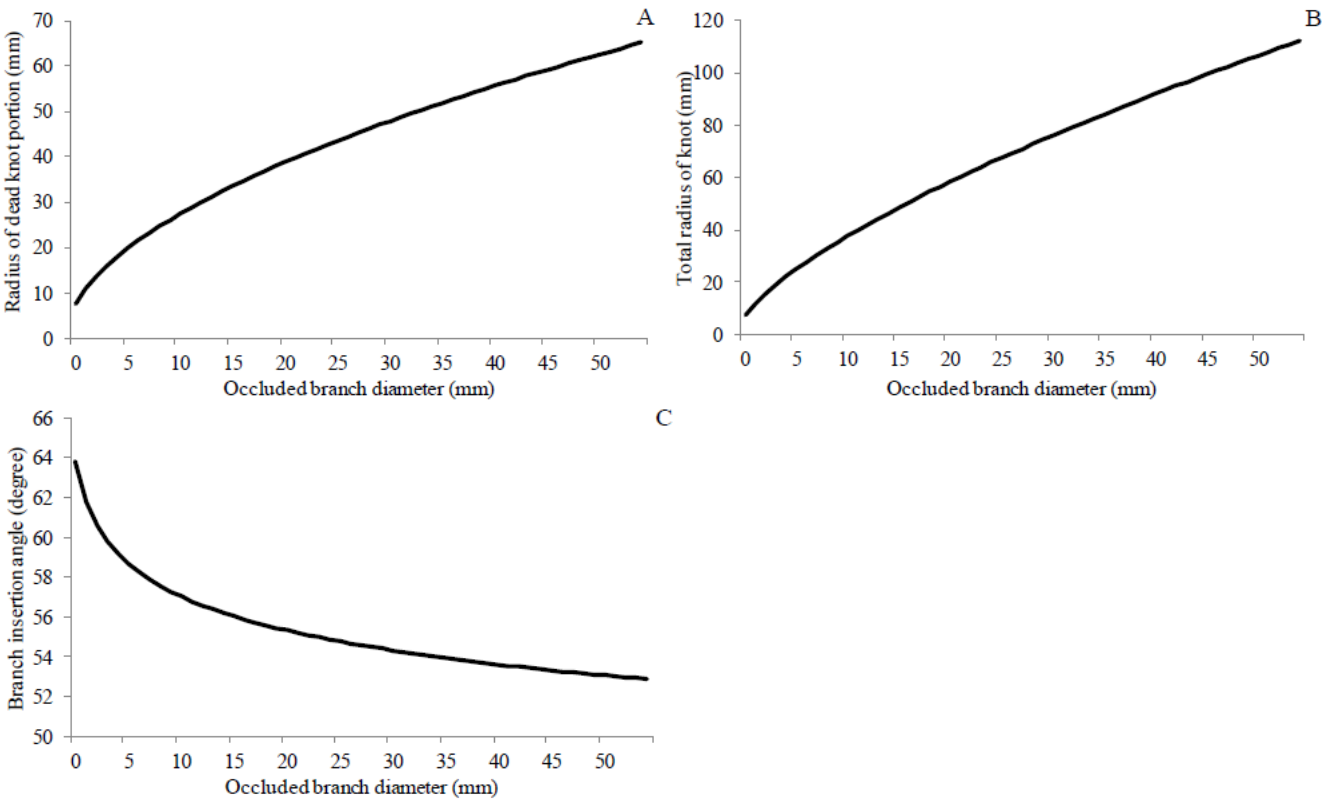

Figure 7. Predicted radius of dead portion of knot ((**A**), Equation (2)), total radius of knot ((**B**), Equation (3)) and insertion angle of occluded branch ((**C**), Equation (4)) plotted against occluded branch diameter.

4. Discussion

The results of the present study showed that the mean time of branch occlusion (OT) in *B. alnoides* increased slightly from 1.8 years to 2.3 years with decreasing planting density. This was different from Mäkinen's [2] study with *B. pendula* Roth in which the difference of occlusion time was not statistically significant from 7.6 years under 5000 sph to 10 years under 400 sph. This discrepancy may be attributed to differences between both species in their growth characteristics and the climate conditions. This could also be interpreted from the results of model building which showed that OT of *B. alnoides* was positively correlated with the diameter of occluded branches (OBD) and the radius of dead portion of knot (RDP), and negatively correlated with stem diameter growth rate at the knot position during branch occlusion (SDGR) (Equation (1) and Figure 6). This is consistent with studies on *Fraxinus excelsior*, *Acer peseudoplatanus* and *Fagus sylvatica* [18,19]. Generally, branches with large diameters often generate long dead branch stubs [18,30]. O'Hara and Buckland [20], Petruncio *et al.* [21] and Dănescu *et al.* [30] found that the branch occlusion time also increased with the increasing length of dead branch stub. This can explain the positive relationship between OBD and OT as well as RDP. As a whole, these results indicated that branch occlusion time could be effectively shortened by reducing the branch diameter and accelerating SDGR with silviculture and forest management measures.

Similar to the branch occlusion time, the mean radius of dead knots and the mean total radius of knot decreased significantly with increasing planting density in the present study. The prediction models showed that they were all significantly correlated with the diameter of occluded branches (Equations (2) and (3), and as inferred in Figure 6, large branches would form a large radius of knots after death. Hein and Spiecker [18] and Hein [19] also found that the radius of knot significantly increased with increasing branch diameter. Therefore, controlling diameter growth of branches is essential to reduce size of dead knot.

Significant decrease of the mean occluded branch insertion angle (IA) of *B. alnoides* occurred with increasing planting density (Table 3), but no significant difference was found for the frequency of IA at each angle level. Consistent with Hein's [19] study on *Fagus sylvatica*, the model of IA in the present study also showed a slight decrease with an increase of branch diameter (Figure 7), and the predictive power of IA was much lower. This may be due to the fact that only routinely measured parameters were taken into consideration when building the model. The present study revealed a large variability in IA of a tree or a stand which could be inferred from IA scales in Table 3 and standard errors of IA frequencies in Table 4, suggesting a possible influence of various factors, such as genetic control [31,32], tree social position in stand [33,34], *etc.* Thus the model of IA was of low reliability. Nonetheless, it seems not to be necessary to consider the effect of IA caused by planting density on the size of dead knot for *B. alnoides* since IA was not significantly correlated with OT (Equation (1)) and RDP (Equation (4)) in the present study.

Provided that OT and RDP were positively correlated with OBD, and a long OT and large RDP would greatly affect the quality of wood, controlling OBD through silvicultural measures is necessary for the production of high quality wood. In the present study, the mean occluded branch diameter decreased significantly with increasing planting density. Similar findings had already been recognized in previous studies not only for OBD in *Pinus sylvestris* [24] and *Picea abies* [25] but also for the diameter of dead or live branches in Douglas-fir [35,36], *Endospermum medullosum* [37] and *Eucalyptus pilularis* and *E. grandis* [38]. In addition, high density planting could significantly lower the percentage of large branches as shown in the present study (Table 5). This could be explained by the fact that planting with high density can intensify competitions among branches and trees for available growth space, nutrients, water and photosynthetically active radiation [15,39–41]. Therefore, high density planting is one of the effective measures to control branch diameter and subsequently reduce the size of knots of *B. alnoides* since it normally leads to small-sized branches which easily shed after death without long dead branch stubs.

However, a trade-off between SDGR and branch diameter should be considered when a planting density is selected. A two-phase silvicultural system may resolve this problem. On the one hand, since reduction of branch diameter with high planting density is at the cost of small-sized crowns, which may slow SDGR, thus affecting OT and stand rotation length, thinning in appropriate time is an efficient method to increase growing space, redistribute site resources to the remaining trees and increase their SDGR. Planting with a high density stock (e.g. 1667 sph) in combination with thinning for the purpose of crown release when branches have died up to a desired height on the trunk is an alternative strategy for production of high quality log in a short rotation for *B. alnoides* in southern China. While thinning needs extra investment, it is preferred from an economic point of view to delay the thinning to the time when stems reach a commercial size. On the other hand, artificial pruning is known as another effective method in controlling branch diameter and avoiding long dead branch stubs under natural pruning [18,21]. Since low density planting would increase mean branch diameter and frequency of large branch diameter in *B. alnoides*, artificial pruning is necessary for controlling the size of branches. Thus a combination of low density planting (e.g., 833 sph) and early artificial pruning is recommended for high-quality wood production of *B. alnoides*. Though planting with a low stock density could reduce the initial cost of plantation establishment, a high cost of artificial pruning is inevitable. A choice between these two strategies should depend on their investments and economic benefits, which cannot be quantified in the present study. Further studies on both silvicultural technics and economic analysis should be undertaken so as to verify which strategy is more appropriate for intensive management, and to establish a practical guideline for large-diameter and knot-free timber production of *B. alnoides* in southern China.

5. Conclusions

The present study demonstrated that planting *B. alnoides* with high stocking density could decrease significantly the mean occluded branch diameter (OBD), radius of knots, branch insertion angle and frequency of thick occluded branches. Branch occlusion time (OT) was also negatively related to planting density. The results of generalized linear mixed models indicated that branch occlusion and knot attributes were all closely correlated with OBD, small branches left small-sized stubs after death and needed short time to be occluded and produced knots of small size. While reduction of OBD was at the cost of stem growth, and OT was negatively correlated with stem diameter growth rate during branch occlusion (SDGR). A trade-off between SDGR and branch size should therefore be taken into account when two-phase silvicultural strategies with appropriate planting density are determined for large-sized clear-wood production of this species. The findings increase knowledge about the effect of planting density on knot attributes and branch occlusion, and are useful for foresters to make practical guidelines in valuable timber productions. Thus, planting at high stocking densities are beneficial for reducing the size of knot.

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Author Contributions

Jie Zeng, Zhigang Zhao and Chunsheng Wang designed the experiment. Chunsheng Wang, Zhigang Zhao, Ji Zeng, Junjie Guo, Wenfu Guo performed the experiments and collected the data. Chunsheng Wang and Sebastian Hein analyzed the data. Chunsheng Wang, Sebastian Hein, Johanna Schuler and Jie Zeng contributed to writing the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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