Genetic relationships between wood density components and cambial growth rhythm in young coastal Douglas-fir[1]

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To better understand the genetic control of wood formation in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), and to assess the potential impact of selecting for increased wood density on adaptation of trees, genetic relationships of wood density, and its components, with cambial growth rhythm traits were examined in a 15-year-old progeny test. Timing of diameter growth during the 1987 growing season was available from an earlier study, and wood formation traits were estimated by X-ray densitometry of increment core samples. Wood formation traits were under weak genetic control ($h_i^2 < 0.20$). Lengths of earlywood and latewood formation were mostly determined by the timing of latewood transition. Overall core density was negatively correlated with the dates of cambial growth initiation ($r_A = -0.41$) and latewood transition ($r_A = -0.62$), and positively correlated with the date of cambial growth cessation ($r_A = 0.40$). As a result of these relationships, higher wood density was associated with a longer duration of cambial growth ($r_A = 0.67$) and a slower rate of wood formation ($r_A = -0.37$). All density components showed similar relationships with cambial phenology and wood formation traits. Selection for increased wood density is expected to cause only a slight extension of the cambial growth period, but it would also cause an earlier transition to latewood formation, negatively affecting growth rate.

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Pour mieux comprendre le contrôle génétique de la formation du bois chez le sapin de Douglas (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), et afin d'apprécier l'impact potentiel, sur le niveau d'adaptation des arbres, de la sélection en fonction d'une plus forte densité du bois, les relations génétiques ont été étudiées entre, d'une part, la densité du bois et ses composantes et d'autre part, les caractères d'allure de la croissance cambiale. Ces études ont été réalisées à partir d'un test de descendances âgé de 15 ans. Les données concernant le début et la fin de la croissance saisonnière en diamètre étaient disponibles à partir d'une autre étude, alors que les caractères de formation du bois ont été mesurés à l'aide de la densitométrie aux rayons X sur des carottes de sondage. Les caractères de formation du bois étaient sous contrôle génétique faible ($h_i^2 < 0,20$). Les périodes de formation du bois de printemps et du bois d'été étaient principalement déterminées par le moment de la transition vers la formation du bois d'été. La densité globale des carottes était négativement corrélée à la date de début de la croissance cambiale saisonnière ($r_A = -0,41$) et à celle de transition vers la formation de bois d'été ($r_A = -0,62$), alors qu'elle était positivement corrélée à la date de fin de la croissance cambiale saisonnière ($r_A = 0,40$). Il découle de ces résultats qu'une plus forte densité du bois se retrouvait associée à une plus longue période de croissance cambiale ($r_A = 0,67$) et à un taux plus lent de formation du bois ($r_A = 0,37$). Toutes les composantes de la densité du bois affichaient des relations similaires avec la phénologie du cambium et les caractères de formation du bois. Il est prévisible que la sélection pour une densité du bois accrue produira seulement une faible extension de la période de croissance cambiale. Toutefois, cette sélection produira aussi une transition plus hâtive vers la formation de bois d'été, tout en affectant négativement le taux de croissance.

[Traduit par la rédaction]

Introduction

In temperate conifers, seasonal changes in cambial activity influence both cell size and cell wall thickness (Gordon and Larson 1968; Brown 1970). Thus, strong relationships between wood density and cambial growth rhythm traits (i.e., phenology and rate of cambial activity) are expected in these tree species (Mergen et al. 1964; Smith 1978; Dodd and Power 1986).

Knowledge of genetic relationships between wood density and cambial growth rhythm traits is important for understanding the physiological mechanisms of wood formation and the degree to which the phenotypic relationships between these traits are under genetic control, as well as for tree-

breeding purposes. Undesirable genetic correlations between wood density and cambial growth rhythm traits could cause serious problems for tree breeders, because growth rhythm is important to adaptation (Dietrichson 1964). If, for example, wood density is negatively correlated with date of cambial growth initiation (i.e., trees with earlier cambial growth initiation have higher wood density), selection for increased wood density would result in increased susceptibility to cambial damage from spring frosts. Frost damage in the cambium could cause incomplete lignification of xylem cells and increase the risk of snowbreak in trees (Kennedy 1961; Dietrichson 1964).

Because of the difficulty of measuring cambial phenology, relationships between wood density and cambial phenology traits have been studied in only a few cases (Worrall 1970; Cown 1976). From these studies, it appears that the relationships between wood density and cambial phenology are quite complex. Overall wood density results from three interacting components, earlywood density, latewood density,

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and latewood proportion, and it has been hypothesized that these components are affected by different physiological factors during the process of wood formation (Worrall 1970; Nicholls and Wright 1976). Presumably, in temperate conifers, cambial division is reactivated by shoot growth in the spring, and earlywood is formed until shoot elongation stops, at which point latewood formation commences and continues until cambial growth ceases in late summer (Wareing 1958; Savidge and Wareing 1984). Because cell diameter and cell wall thickness are affected by the rate of cambial division, it might be expected that earlywood and latewood densities are primarily related to the rate of cambial growth during their respective formation periods. Similarly, latewood proportion might be expected to be mostly determined by the length of the latewood formation period. Knowledge of the correlations between wood density components and wood formation traits (i.e., date of latewood transition, lengths and rates of earlywood and latewood formation) may help in understanding the relationships between overall density and cambial phenology.

In 1987, cambial phenology data were collected from 60 open-pollinated coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) families growing on a single test site in western Oregon (Li 1990; Li and Adams 1994). X-ray densitometry of increment cores collected from the same trees in summer 1988 provided wood density profiles for the 1987 annual ring, as well as for the entire core. In this paper, cambial growth phenology and wood density traits in these trees are compared to (*i*) estimate the extent of genetic control of wood-formation traits; (*ii*) determine the genetic relationships of overall core density and its components with cambial phenology and wood-formation traits; and, (*iii*) examine the potential effects of selection for increased wood density on individual cambial phenology traits.

Materials and methods

Plant material

The families included in this study are growing in a progeny test plantation near Eugene, Oreg. (45°58'N, 123°18'W, elevation 274 m). The mother trees, located in nearby stands (150–450 m elevation) in the central Oregon Coast Range, are part of the first-generation selections in the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program (Silen and Wheat 1979). The families were planted as two 30-family sets, each set comprising a separate randomized complete block experiment with four replications. Families in each block were originally represented by a four-tree noncontiguous plot, with trees assigned to planting spots at random, at a spacing of 3.05 × 3.05 m. Trees were 15 years old from seed in 1987, when the measurements were made. At that time, survival of trees in these two sets was about 85%. Most mortality, however, occurred during the first 2 years after planting and dead seedlings were replaced with seedlings from the same families. The replacements were not measured in this study. At the end of the 1987 growing season, average height and diameter at breast height (DBH; 1.37 m) of the study trees were about 11 m and 14 cm, respectively. Crown closure had already begun, with the lowest living branches in all trees between 1 and 3.2 m above ground level.

Measurements and derivation of traits

Cambial phenology data for the 60 families during the 1987 growing season were obtained by Li (1990). Diameter growth at breast height was monitored on a weekly basis with a high precision caliper, by measuring the distance (approximated to the nearest 0.01 mm) between two thumbtacks located on opposite sides of the stem. Trees were measured from the week of March 26, before detectable growth began, until the week of October 16, when no further diameter change could be detected. To minimize the effect of stem shrinkage due to water loss during the day, all measurements were done before 10:00. The distance between the thumbtacks and lowest living branches on each tree was also recorded to adjust, if necessary, for the effect of live crown position on cambial phenology traits.

Cumulative diameter growth curves were generated for each tree from the weekly diameter measurements. The dates at which 5 and 95% of the diameter growth was completed estimated dates of initiation and cessation of diameter growth, respectively. The length of the cambial growth period was estimated as the difference in the number of days between the dates of cessation and initiation of diameter growth. Because the distance between the sampling point and the base of the live crown did not differ significantly among families (Li and Adams 1994), cambial phenology traits were not adjusted for crown position.

To estimate wood density traits, a 5 mm diameter increment core sample, extending from pith to bark, was taken from the same spot where diameter growth was measured one growing season earlier (Vargas-Hernandez and Adams 1991). Intraring density information across each core sample was obtained by using a direct scanning X-ray densitometry system (Hoag and McKimmy 1988). Ring density and its components (i.e., earlywood density, latewood density, and latewood proportion) for the annual ring formed in the 1987 growing season, as well as average values of these components for the whole core, were calculated from the X-ray density profiles. The point in the ring where density equals the average of the minimum and maximum density values for that ring was used as the criterion to separate earlywood from latewood (Green and Worrall 1964).

Wood-formation traits were estimated by comparing, for each tree, the cumulative diameter growth curve in 1987 with the densitometric profile for the ring formed in the same year. The approximate date of latewood transition was assumed to occur at the time when the percentage of cumulative diameter growth was identical to the percentage of earlywood in the annual growth ring (Vargas-Hernandez 1990). This method assumes that total ring width obtained from the core sample is closely correlated to total diameter growth obtained from the growth curves. A plot of ring width against total diameter growth showed that these traits were linearly related ($r = 0.76$). Several factors could have contributed to this imperfect correlation, including asymmetric diameter growth around the stem, differences among trees in the amount of phloem production, and differences in shrinkage of the core samples. Nonuniform diameter growth around the stem is the most likely cause of the correlation being lower than expected. Diameter growth was estimated from measurements that included cambial growth on two sides of the tree, whereas ring width was estimated using only one side. Phloem growth, on the other hand, is normally less than 10% of the total annual xylem growth, and it is not expected to differ much among trees (Grillos and Smith 1959). Similarly, radial shrinkage of the core samples at 10% moisture content has been estimated to be only around 3% (Erickson 1955; Kennedy 1961). Because of the imperfect relationship between ring width and diameter growth, the error in estimating the date of latewood transition on an individual tree basis may be large. Nevertheless, residuals of the regression of ring width on total diameter growth were randomly distributed among families, so that estimates of family means for the date of latewood transition are likely to be unbiased.

The lengths of the earlywood and latewood formation periods in 1987 were estimated as the number of days from initiation of diameter growth to the date of latewood transition, and from the date of latewood transition to cessation of diameter growth, respectively. In addition, the rates of earlywood and latewood formation in the 1987 annual ring were calculated by dividing earlywood width and latewood width by the lengths of their respective formation periods.

TABLE 1. Form of the variance and covariance analyses for wood density, cambial phenology, and wood formation traits

Source of variation	df*	Expected mean squares[†]
Sets	$s - 1$	$\sigma_w^2/k + \sigma_e^2 + b\sigma_{f(s)}^2 + f\sigma_{b(s)}^2 + bf\sigma_s^2$
Blocks within sets	$(b - 1)s$	$\sigma_w^2/k + \sigma_e^2 + f\sigma_{b(s)}^2$
Families within sets	$(f - 1)s$	$\sigma_w^2/k + \sigma_e^2 + b\sigma_{f(s)}^2$
(Block × families) within sets (plot error)	$(f - 1)(b - 1)s$	$\sigma_w^2/k + \sigma_e^2$
Within-plot error	$\sum_{i=1}^{t}(n_i - 1)$	σ_w^2

*s, number of sets; b, number of blocks per set; f, number of families per set; n_i, number of trees in plot i; t, total number of plots in the experiment.

[†]σ_w^2, within-plot variance; σ_e^2, plot to plot variance; $\sigma_{f(s)}^2$, variance among families in sets; $\sigma_{b(s)}^2$, variance among blocks in sets; σ_s^2, variance among sets; k, harmonic mean of number of trees per plot for all sets. For covariance analyses, cross products are used instead of mean squares.

TABLE 2. Estimates of population means ($\bar{X}$), phenotypic (P) and genetic (A) coefficients of variation (CV), and individual-tree (h_i^2) and family (h_f^2) heritabilities for wood formation traits in the 1987 annual ring

Trait	$\bar{X}$	Range*	CV (%) P	CV (%) A	h_i^2	h_f^2
Date of latewood transition[†]	177	170–187	5.67	1.81	0.10±0.05	0.22±0.08
Length of the earlywood formation period (days)	71	65–81	13.61	3.83	0.08±0.06	0.18±0.10
Length of the latewood formation period (days)	48	38–58	21.28	9.17	0.19±0.06	0.32±0.08
Earlywood formation rate (mm/day)	0.059	0.049–0.068	22.03	7.57	0.12±0.07	0.24±0.10
Latewood formation rate (mm/day)	0.042	0.033–0.049	22.65	8.27	0.13±0.07	0.26±0.09

NOTE: Values for individual-tree and family heritabilities are estimates ± SE.
*Differences among families were significant ($p < 0.05$) for all traits ($n = 60$).
[†]Number of days after January 1.

Data analysis

All variance and covariance analyses were performed on a plot-mean basis using a random-effects model (Table 1). Missing values for three plots (of a total of 240) were estimated according to Steel and Torrie (1980). Within-plot variances and covariances, as well as the harmonic mean for number of trees per plot were estimated separately by pooling individual-plot values. Components of variance and covariance were estimated from the appropriate mean squares and cross products (Namkoong 1979).

To determine the genetic control of wood formation traits, individual-tree (Falconer 1981) and family heritabilities (Vargas-Hernandez and Adams 1991) for these traits were estimated assuming a coefficient of genetic relationship of one third among progeny within open-pollinated families (Campbell 1979). Standard errors for heritability estimates were calculated following Osborne and Paterson (1952). The genetic relationships of wood density and its components with cambial phenology and wood formation traits were analyzed by estimating their respective genetic correlations (and standard errors) as in Becker (1984). Expected changes in cambial growth rhythm traits resulting from selection on overall core density were explored by estimating and comparing the correlated responses of individual growth rhythm traits (Falconer 1981). In these calculations, we assumed parent trees are selected on the basis of the performance of their open-pollinated progenies and then are mated at random to produce improved offspring (Vargas-Hernandez and Adams 1991).

Results and discussion

Genetic control of wood formation traits

Analysis of variance showed significant differences ($p < 0.05$) among families in date of latewood transition and lengths and rates of earlywood and latewood formation (Table 2). Thus, despite the error in estimating date of latewood transition, it was possible to detect family differences in this trait and all the traits derived from it. All the wood-formation traits, however, had low coefficients of genetic variation. In addition, they had low estimates of individual-tree ($h_i^2 < 0.20$) and family ($h_f^2 < 0.32$) heritabilities, indicating they are under weak genetic control. The levels of genetic variation and magnitudes of genetic control observed for these traits are similar to those found by Li and Adams (1994) for cambial phenology traits (initiation, cessation, and duration of cambial growth) in the same families.

The average date of latewood transition during the 1987 growing season was June 27 (i.e., 177 days after January 1; Table 2); this date is about 1 month earlier than the earliest average date of transition estimated by Emmingham (1977) for several provenances of young Douglas-fir growing on different sites in Oregon (measured directly in 1971 using the "pin-pricking" method). Assuming the method used in our

TABLE 3. Estimates of genetic correlations between overall wood density traits at age 15 and cambial (diameter) growth phenology and wood formation traits in the 1987 growing season

Wood density trait	Date of diameter growth		Date of earlywood–latewood transition	Length of formation period*	Formation rate[†]
	Initiation	Cessation			
Earlywood density	−0.24 (0.22)	0.51 (0.31)	−0.43 (0.24)	−0.32 (0.28)	−0.22 (0.27)
Latewood density	−0.48 (0.22)	0.15 (0.35)	−0.75 (0.22)	0.63 (0.18)	−0.37 (0.28)
Latewood proportion	−0.46 (0.26)	0.28 (0.35)	−0.66 (0.25)	0.65 (0.20)	−0.42 (0.28)
Overall core density	−0.41 (0.20)	0.40 (0.30)	−0.62 (0.20)	0.67 (0.28)	−0.37 (0.23)

NOTE: Standard errors of estimates are given in parentheses.

*Refers to the length (days) of the formation period for the corresponding wood density trait. In the case of latewood proportion (LP), the correlation is between LP and the length of the latewood formation period.

[†]Refers to the formation rate (mm/day) of the corresponding wood density trait. In the case of LP, the correlation is between LP and rate of latewood formation.

study provides a fairly reliable estimate of mean latewood transition date, differences between the two studies in date of latewood transition may be due to differences in seed source, year to year variation, or tree age. Emmingham (1977) reported differences of 10–20 days in the average date of latewood transition among provenances growing on the same plantation site, with seed sources from drier areas having earlier dates of latewood transition. As to differences between years, Kennedy (1961) reported a large variation in date of latewood transition from one growing season to the next, even in the same population of Douglas-fir. In addition, Cregg et al. (1988) found that latewood transition in loblolly pine (*Pinus taeda* L.) occurred 3–4 weeks earlier in a growing season with a relatively dry summer, than in a growing season with average precipitation. According to the precipitation records for the area where the progeny test in the current study is located, rainfall in 1987 was below average. Total rainfall during the first 6 months of 1987 was 83% of the average precipitation in that period for the last 15 years, and total rainfall in the period April–June was only 56% of the average in that period for the last 15 years. The possibility that low rainfall caused the early date of latewood transition is supported by the fact that diameter growth in these families also ceased about 1 month earlier (Li and Adams 1994) than in the populations studied by Emmingham (1977), although stem shrinkage at the end of the growing season may have contributed somewhat to an earlier estimate of the date of cambial cessation in our study trees. Differences in age might also contribute to differences in the date of latewood transition. Trees in the populations studied by Emmingham (1977) were 2–4 years younger than trees in this study and, because the proportion of latewood in temperate conifers normally increases with age (Zahner and Oliver 1962; Larson 1969), including this Douglas-fir population (Vargas-Hernandez et al. 1994), it might be expected that older trees would have earlier dates of latewood transition.

Of the 4 months of cambial growth in 1987 (Li and Adams 1994), approximately 2.5 months (71 days) corresponded to earlywood formation, and 1.5 months (48 days) to latewood formation (Table 2). Families varied, however, by 17 days in the mean date of latewood transition, 16 days in the length of the earlywood formation period, and 20 days in the length of the latewood formation period. These ranges are about twice as large as the family range in duration of cambial growth (10 days; Li and Adams 1994).

The estimated average rate of earlywood formation (0.059 mm/day) was greater (by about 40%) than the average rate of latewood formation (0.042 mm/day) (Table 2). In contrast, Emmingham (1977) found a nearly constant rate of cambial growth over the entire growing season.

Genetic interrelationships among wood density components, wood formation traits, and cambial phenology

Estimated genetic correlations of wood density and its components with wood formation and growth rhythm traits in 1987 were similar, regardless of whether wood density traits were based on the 1987 annual ring alone, or on the entire core sample. This is not surprising, however, because genetic correlations among wood density traits at different ages are strong in these materials (Vargas-Hernandez and Adams 1992); in this case, genetic correlations among wood density traits in the 1987 annual ring and their respective values for the entire core varied from 0.73 to 0.94. One goal of this study was to examine the potential impact of selection for increased wood density (based on information from the entire core) on individual cambial phenology traits. Thus, only genetic correlations of overall core density and its components with wood formation and growth rhythm traits are discussed.

Estimated genetic correlations of overall core density and all its components with dates of diameter growth initiation and latewood transition were negative (Table 3). This indicates that families with higher wood density tend to have earlier dates of diameter growth initiation and latewood transition. Wood density traits were more strongly correlated with the date of latewood transition than with the date of diameter growth initiation, suggesting that despite the positive genetic association between initiation of cambial growth and latewood transition ($r_A = 0.52 \pm 0.28$; mean ± SE), timing of latewood transition is more important in determining wood density. This seems logical, because an earlier date of latewood transition would increase the length of latewood formation at the expense of reducing the length of earlywood formation, which would result in a higher proportion of latewood in the ring. This is especially so in these data, where Li and Adams (1994) found little family variation for date of cambial initiation or for total length of cambial growth. As might be expected, the strongest genetic correlations involving the date of latewood transition were found with latewood density ($r_A = -0.75$) and latewood proportion ($r_A = -0.66$).

Although overall core density and its components were

positively correlated with date of cambial growth cessation, the standard errors of these estimates were large. Nevertheless, the combined tendency for wood density to increase with both earlier initiation and later cessation of diameter growth, resulted in moderately strong positive genetic correlations between wood density traits and the length of their respective formation periods (e.g., the genetic correlation between overall core density and length of the growing season was 0.67). The only exception was the estimated correlation between earlywood density and length of the earlywood formation period, which was weakly negative. The positive genetic correlation between overall core density and length of the growing season, therefore, was due to the positive correlations of latewood density and latewood proportion with length of the latewood formation period. Similar relationships were reported by Kennedy (1961), and Nicholls and Wright (1976). Moreover, as in those earlier studies, the length of the latewood formation period was negatively correlated with the length of the earlywood formation period ($r_A = -0.77 \pm 0.23$), indicating again that the longer period of latewood formation was primarily due to an earlier latewood transition date, rather than to a later cessation of cambial growth.

Estimated genetic correlations of overall core density and its components with their respective rates of formation were all weak (and of similar magnitude to their standard errors), but negative. Negative correlations between these traits were not unexpected, because overall core density had a negative genetic correlation with bole diameter at age 15 (Vargas-Hernandez and Adams 1991). The stronger genetic correlations found between wood density traits and the length of their respective formation periods, as compared with their rates of formation, suggest that the length of the formation periods is more important in affecting wood density and its components. This interpretation, however, should be made with caution, because of the interrelationships between length of the formation periods and rates of formation (i.e., rates of formation were estimated using length of the formation period in the denominator, so these traits are not independent). Besides, the magnitude of the standard errors associated with the correlation estimates are large enough to indicate that differences between the magnitudes of these estimates could be due entirely to sampling error.

The negative relationship observed between wood density and growth rate may be primarily due to differences among families in the time of latewood transition, because a moderately positive genetic correlation ($r_A = 0.67 \pm 0.21$) was found between the overall rate of wood formation and date of latewood transition, indicating slow-growing trees tended to switch earlier to latewood production. Because families did not differ significantly in crown position, earlier latewood initiation may primarily be associated with earlier onset of internal water stress in smaller trees, owing to their inability to compete with larger individuals. Brix (1972) and Cregg et al. (1988) suggested that increased water stress can promote the initiation of latewood production, presumably through its effects on the physiological activity of the crown.

Implications of selection for wood density on cambial growth rhythm

Despite the moderate genetic correlations between overall density and cambial phenology traits observed in this study, only weak correlated responses in cambial phenology are expected from selection to increase wood density. This is primarily due to the low heritability and limited amount of variation observed in cambial phenology traits.

Based on the data presented in this study, mating of the top 20% of parents selected for greater overall density would result in progeny with an average cambial growth period 2 days longer than in progeny resulting from crosses among all parents prior to selection. Both an earlier initiation and a later cessation would contribute to the extended period of cambial growth. The extent to which this small increase in the length of the cambial growth period may influence adaptability, however, is unclear. Dietrichson (1964) found that when southern provenances of Scots pine (*Pinus sylvestris* L.) are grown in Norway, they experience greater cambial frost damage and snowbreak frequency than local provenances, presumably because the extended growth period of southern sources results in incomplete lignification of the outer latewood zone at the time frosts occur. Cambial growth periods of southern provenances, however, were more than 2 weeks longer than the average growth period for local sources. In addition, Dietrichson's study was conducted in a harsher climate than normally experienced in the Oregon Coast Range.

Selecting for increased overall wood density would accelerate the transition from earlywood to latewood formation. Using the same selection intensity indicated above, date of latewood transition in the progeny of the selected parents would be expected to occur 2 days earlier than in the population prior to selection. This would increase the length of the latewood formation period at the expense of the earlywood formation period, negatively affecting the rate of diameter growth.

Given the time and cost of measuring cambial phenology traits, it is not likely that these traits will be included in tree improvement programs for Douglas-fir in the Pacific Northwest. Nevertheless, genetic correlations between wood density and cambial phenology do not appear to be very strong, so even if the intensity of selection for increased wood density were relatively high, the impact on cambial phenology is not expected to be great. The intensity of selection applied for increasing wood density, however, is not likely to be large, otherwise gains in volume growth would have to be sacrificed (Vargas-Hernandez and Adams 1991). In addition, selection for increased volume growth is not expected to have much effect on cambial phenology, because genetic correlations between volume growth and cambial phenology traits also appear to be weak in this species (Li and Adams 1994).

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