only to indicate an average degree of non-additivity on a population basis.

Some possibilities for utilizing interpopulation specific combining abilities are indicated from the 7 × 8 polycross experment. Five population SCA estimates for height were relatively large, i.e., the absolute values exceeded twice their respective standard errors; four of these estimates were positive and were larger than GCA values. Also, three of the large SCA estimates were associated with the pollen mixture of the Belgian population. For example, a desirable SCA for 3-year height growth may be identified by 240 FRA × 318 BEL from the 7 × 8 factorial population polycross. It is not the highest SCA, but the progenies have better quality in other Christmas trees traits. One method of capturing these non-additive effects is to identify desirable specific combining ability pairs, and then vegetatively propagate them to produce planting stock. Perhaps, successive rooted cuttings of juvenile plants as described by Armson *et al.* (1980) may be used.

Regardless of these SCA effects however, it is clear that the largest differences among the hybrid families were due to additive effects of the two parents in combination, since a general lack of useful specific combining ability was found. Therefore, conventional breeding techniques that utilize general combining ability seem appropriate for breeding of Scotch pines of different provenances for juvenile height and needle length.

Acknowledgements

We thank Dr. J. W. Wright, Michigan State University (retired), for making the Scotch pine plantation available for breeding and for helpful suggestions on the early version of this manuscript. We are also thankful to the nursery owners, Messrs. J. Carino, F. Strathmeyer, and the State of Pennsylvania for providing spaces in their nurseries.

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Strobilus Production in a Clonal White Spruce Seed Orchard: Evidence for Unbalanced Mating

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(Received 11th November 1985)

Summary

Two important genetic objectives of clonal seed orchards are the minimization of self-fertilization and the production of seed reflecting the genetic diversity of all represented clones. As part of a study of the mating system of a clonal seed orchard of white spruce, *Picea glauca* (Moench) Voss, male and female strobilus production was investigated during two successive years. Within years, one third of the clones produced the vast majority of the male and female strobili; clonal means of male and female strobilus numbers were positively correlated; and the seed germination rate was negatively correlated with clonal male strobilus numbers. The results are concordant with the hypothesis that a few clones make a disproportionally large genetic contribution to the seed crop of a given year, and that clones which produce the largest numbers of male strobili also yield seed resulting from higher than average levels of self-fertilization. Between years, clone means of female strobilus numbers are negatively correlated, suggesting that the genetic diversity of the seed crop may be significantly increased by combining the seed harvest of the two separate years. If upheld by genetic marker studies of the mating system, the results imply that white spruce seed orchards should be monitored for strobilus production levels, and if necessary, modified mechanically or hormonally to foster more equitable flowering.

Key words: seed orchard, *Picea glauca* (Moench) Voss, male strobili, female strobili, mating pattern, gamete production, self-fertilization.

Zusammenfassung

Zwei wichtige Ziele von Klon-Samenplantagen sind die Minimierung der Selbstbefruchtung und eine Samenproduktion, die die genetische Vielfalt aller repräsentierten Klone widerspiegelt. Als Teil einer Studie über die Pollenverteilung bei Weißfichten [*Picea glauca* (Moench) Voss] in einer Klon-Samenplantage wurde die Produktion männlicher und weiblicher Blüten während zweier Jahre untersucht. Jeweils innerhalb eines Jahres produzierte ein Drittel der Klone den Großteil der männlichen und weiblichen Blüten. Die Durchschnittswerte der Anzahl männlicher und weiblicher Klon-Blüten waren positiv korreliert, und die Keimrate des Samens verschiedener Klone war mit der Anzahl männlicher Klon-Blüten negativ korreliert. Die Ergebnisse stützen die Hypothese, daß nur wenige Klone den genetischen Hauptbeitrag zur Samenproduktion eines Jahres leisten, und daß Klone, die die höchste Anzahl männlicher Blüten produzieren, Samen hervorbringen, die das Resultat überdurchschnittlich hoher Selbstbefruchtung sind. Vergleicht man die beiden Jahre, so sind die Durchschnittswerte der Anzahl weiblicher Klon-Blüten negativ korreliert, was darauf hinweist, daß die genetische Vielfalt

der Somenproduktion durch Kombinierung der Samenernte verschiedener Jahre erhöht werden kann. In Verbindung mit genetischen Untersuchungen des Pollenverteilungssystemes ergibt sich auch, daß Samenplantagen in Bezug auf die Höhe der Blütenproduktion kontrolliert werden sollten. Falls nötig, sollten sie verändert werden, um ein ausgeglicheneres Blühen zu fördern.

Introduction

The establishment of clonal seed orchards from selected trees provides an important mean of producing genetically improved seeds for reforestation. Genetic priniciples associated with the design of seed orchards have been discussed by many forest geneticists (Woessner and Franklin, 1973; Hadders and Kokki, 1975; Adams and Joly, 1980; Moran, Bell and Matheson 1980; Shen, Rudin and Lindgren, 1981; Müller-Starck, 1982; Müller-Starck, Ziehe and Hattemer, 1983). Besides minimizing self-fertilization, one of the most important genetic criteria of orchard design is the production of seeds which reflect the diversity present in all represented clones. This goal is best achieved when all clones contribute equal numbers of male and female gametes to the seed crop. The extent to which existing clonal seed orchards conform to this objective has only recently been questioned (Shen, Rudin and Lindgren, 1981; Müller-Starck, 1982; Griffin, 1982; Müller-Starck, Ziehe and Hattemer, 1983; Ross, 1984), and it is presently not clear whether the problem of unequal gametic contributions is a general one for all forest tree species. The limited data on strobilus production levels suggests that at least for *Pinus radiata, P. sylvestris, Picea mariana,* and *P. glauca,* unbalanced strobilus production may be an obstacle to achieving random mating in seed orchards (Griffin, 1982; Ross, 1984; Nienstaedt and Jeffers, 1970; O'Reilly, Parker and Barker, 1982).

While genetic analysis of the seed crop can provide detailed information about the mating pattern, information on potential male and female gametic contributions may also be gleaned by studying production levels of male and female strobili (Nienstaedt and Jeffers, 1970; O'Reilly, Parker and Barker, 1982). Assuming that genetic contributions of clones are correlated with the numbers of strobili they produce, this approach can reveal the potential for departure from equal male and female gamete contributions to the seed crop by the different clones in the orchard. Departure from equal gamete contributions may also occur due to non-overlapping flowering phenologies of clones, embryo and gametophytic selection, mortality of ramets, and localization of clones into small blocks.

As part an ongoing investigation of the mating pattern of a clonal seed orchard of white spruce [*Picea glauca* (Moench) Voss], we present an analysis of male and female strobilus production levels during two successive years. After accounting for ramet numbers and orchard design, strobilus numbers represent one gross feature of the orchard which is relatively easy to assess. Clonal differences in the production of strobili (as a result of variation in both number of ramets and numbers of strobili per ramet) are potentially important in determining the mating pattern, as it is expected that there should be a close correspondence between strobilus and gamete production levels. Moreover, previous studies in clonal seed orchards indicate that variability in strobilus production among clones can be pronounced (see above). Future publications will examine the relationship between variability in strobilus production, estimates of gamete contributions, and self-fertilization rates of separate clones in the orchard. The objectives of the present study were to: (1) examine the level of variability in the production of male and female strobili among years, among clones, and within clones; and (2) relate the observed variation in strobilus production to potential gamete contributions by clones, and to potential clonal self-fertilization rates.

Materials and Methods

The work described here was conducted in the Glencairn seed orchard, located near Glencairn, Ontario, and operated by the Ontario Ministry of Natural Resources (Latitude 44°15'N, Longitude 79°50'W). The orchard is comprised of blocks, each containing from two to eleven ramets of twelve clones. Nine blocks, outplanted in 1973, were chosen for study because they contained the majority of trees flowering during the two years of the study. Among the nine blocks are thirty-three clones and a total of 694 trees. Twenty-five of the clones occur in two or more blocks.

Counts of male strobili on all 694 trees were made in late May of 1984 and 1985, while counts of female strobili were made in mid-August of these years. To count strobili, an observer walked around the tree, and counted all male (or female) strobili with a hand-held tally meter. A ladder was sometimes necessary to count the uppermost strobili on the taller trees. Because counts of strobili were distributed as log-Poisson random variables, all statistical tests were made after log squareroot transformation of the data. The transformations restored normality and homogeneity of variances to the distributions.

Seeds used in the germination tests were obtained in early August of 1984, and were ripened according to the procedures outlined by Winston and Haddon (1981). The germination tests were conducted with 20 seeds from each of two ramets per clone for all 33 clones, giving a total of 1330 seeds. The sets of 20 seeds were each placed in separate petri dishes, on moistened filter paper in an illuminated growth chamber (16 h day, 25° C). Germination of seeds

Figure 1. — Proportional contribution of the one third most productive clones to the yearly total of male and female strobili in nine orchard blocks. Numbers in diagrams refer to clones.

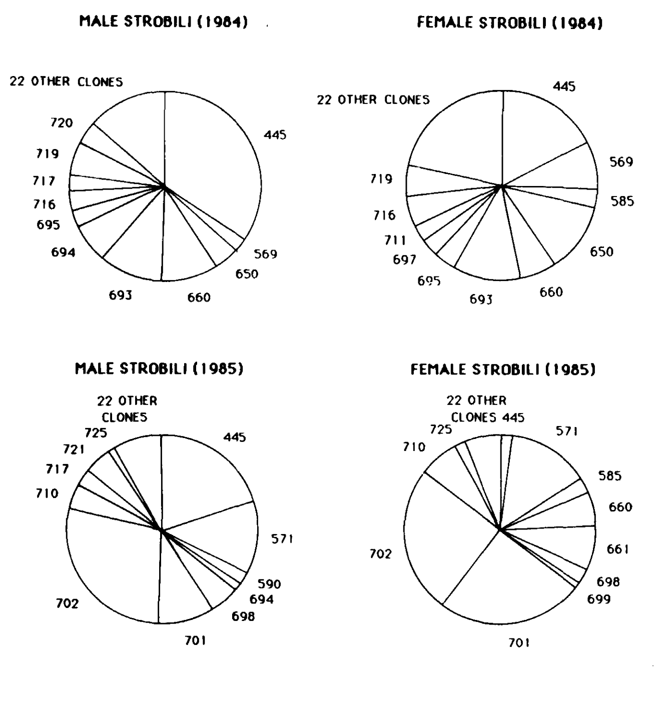

Table 1. — Mean levels of male and female strobilus production, mean ramet height, and seed germination in clones of the Glencairn white spruce seed orchard.

Clone	Number of ramets	Mean number of male strobili per ramet (se) 1984	Mean number of male strobili per ramet (se) 1985	Mean number of female strobili per ramet (se) 1984	Mean number of female strobili per ramet (se) 1985	Mean height in cm (se)	Seed germination[a] (%)
445	55	970(84)	682(86)	669(53)	7(3)	556(13)	32.5
569	28	161(32)	53(16)	619(74)	1(1)	432(26)	40.0
571	19	6(3)	1265(318)	122(38)	157(55)	332(28)	27.5
585	18	1(1)	7(6)	356(58)	28(14)	277(23)	72.5
590	5	15(8)	285(97)	44(29)	8(3)	174(16)	80.0
594	6	137(67)	7(4)	498(183)	2(2)	339(57)	65.0
648	10	290(107)	47(8)	497(114)	11(11)	383(46)	47.5
650	69	93(26)	48(8)	369(36)	2(1)	257(10)	47.5
660	16	964(173)	5(1)	804(539)	0(0)	374(29)	50.0
661	17	33(20)	91(23)	49(13)	97(26)	377(32)	57.5
667	7	96(56)	9(5)	232(44)	18(12)	186(19)	55.0
669	6	78(78)	4(2)	72(57)	20(11)	232(44)	50.0
693	39	422(68)	1(1)	622(86)	0(0)	273(15)	65.0
694	34	301(57)	67(11)	95(15)	2(2)	310(20)	55.0
695	27	164(40)	64(22)	301(73)	6(4)	273(21)	72.5
697	18	151(39)	29(11)	356(65)	4(3)	254(20)	17.5
698	6	1(1)	1509(487)	1(1)	90(60)	327(39)	80.0
699	9	3(2)	158(37)	61(16)	30(12)	251(34)	50.0
700	6	200(73)	4(4)	218(67)	0(0)	227(38)	70.0
701	53	8(1)	351(64)	39(7)	102(21)	290(16)	65.0
702	36	1(0)	1430(135)	126(23)	145(41)	310(15)	80.0
710	38	8(3)	200(31)	30(7)	40(10)	299(13)	62.5
711	34	35(10)	41(12)	165(26)	3(3)	222(13)	70.0
716	25	214(52)	1(1)	417(60)	1(0)	376(19)	57.5
717	21	220(44)	253(39)	7(2)	4(2)	398(16)	37.5
718	7	0(0)	84(32)	2(1)	16(6)	270(32)	65.0
719	23	374(90)	48(11)	546(76)	0(0)	351(22)	72.5
720	14	406(134)	89(49)	181(38)	0(0)	314(26)	45.0
721	17	99(23)	465(83)	185(24)	10(8)	360(21)	35.0
722	7	48(16)	193(49)	648(114)	2(2)	433(24)	77.5
723	7	286(88)	3(2)	203(58)	0(0)	257(26)	65.0
725	8	106(36)	221(92)	356(66)	40(40)	314(31)	77.5
726	14	238(58)	19(7)	222(34)	0(0)	341(28)	35.0

[a] Percent seeds germinating out of N = 40 per clone.

Table 2. — Analysis of variance of strobilus production in the Glencairn seed orchard.

Source of variation	SS	df	MS	F	Variance component %
(a) Male strobili (1984):					
Clones	345.12	32	10.79	30.40***	58.3
Error	234.50	661	0.35		41.7
Total	576.62	693			
(b) Female strobili (1984):					
Clones	136.55	32	4.27	19.16***	46.4
Error	147.22	661	0.22		53.6
Total	283.77	693			
(c) Total strobili (1984):					
Clones	738.45	32	23.08	29.80***	57.8
Error	511.90	661	0.77		32.2
Total	1250.35	693			
(d) Male strobili (1985):					
Clones	353.60	32	11.05	28.05***	56.3
Error	260.42	661	0.39		43.7
Total	614.02	693			
(e) Female strobili (1985):					
Clones	314.44	32	9.83	28.35***	56.6
Error	229.08	661	0.35		43.4
Total	543.52	693			
(f) Total strobili (1985):					
Clones	1048.06	32	32.75	42.75***	66.5
Error	506.40	661	0.76		33.5
Total	1554.46	693			
(g) Height (cm):					
Clones	50.3	32	1.57	12.25***	34.9
Error	84.8	661	0.13		65.1
Total	135.1	693			

*** $P < 0.001$

was recorded as the percentage of the 40 seeds from each clone which developed to or beyond 0.5 cm of radicle extension within 1 month of the start of the test.

Tree heights were obtained directly with a tape measure held from the base to the apex of the tree. Heights were measured in 1984 only. Height data were log transformed to provide homogeneity of variances among the distributions for the different clones.

Results and Discussion

Whole orchard variation between years in strobilus numbers

The two years differed tenfold in magnitude of total female strobilus production. In 1984, there were 211,430 female strobili on the 694 trees, while in 1985, only 21,530 were produced. In contrast, total male stobilus production showed less variation between years with 155,650 and 185,100 strobili in 1984 and 1985, respectively. White spruce, like other conifers is known to undergo large year to year fluctuations in flowering. The year 1984 can be regarded as a mast year (*sensu* SILVERTOWN, 1980) for this species in Ontario.

Variation between clones in strobilus numbers

In both years, one third of the thirty-three clones produced the vast majority of male and female strobili (*Figure 1*). This dominance in strobilus production by a few clones is attributable to a combination of two factors; certain clones: (1) produced larger numbers of strobili per ramet; and (2) are represented in the sampled blocks by more ramets (*Tables 1* and *2*). From 46—66% of the observed variation in strobilus numbers per ramet is associated with differences between clones (*Table 2*).

Correlations between clonal means of two characters ($\overline{x}$ and $\overline{y}$) were calculated as

$$\text{Corr}(x,y) = \text{Cov}(x,y)/[V(x)V(y)]^{1/2}$$

where $\overline{\text{Corr}}$, $\overline{\text{Cov}}$, and $\overline{V}$ refer to the correlation, covariance, and variance of true clonal, means respectively. Estimates of the variance among clonal means were obtained from one-way analysis of variance. Estimates of the covariance of true clonal means between two characters were obtained using a similar procedure for the summed values of the two characters in each individual, and the formula (Kempthorne, 1969)

$$\text{Cov}(x,y) = (1/2)[V(x+y) - V(x) - V(y)].$$

The correlation between true clonal means of male and female strobilus numbers in 1984 was 0.60 ($P < 0.01$), and in 1985 was 0.59 ($P < 0.01$). The correlation among true clonal means of male strobilus numbers between 1984 and 1985 was -0.24 ($P > 0.05$), and among female strobilus numbers between 1984 and 1985 was -0.62 ($P < 0.01$).

Several inferences about the gametic contributions of clones in 1984 and 1985 can be drawn from these findings: (1) certain clones dominated in the contributions of male and female gametes to the seed crop within a given year; (2) there was a tendancy for clones which dominated one year as male gamete contributors to also do so as female gamete contributors during that same year; (3) there was no consistent year to year variation as to which clones dominate as male gamete producers; (4) clones which dominated as female parents in one year were unlikely to do so in the next.

Inferences about clonal variation in the rate of self-fertilization are more problematical since these require not only information on production of pollen but on its fate as well. If it is assumed that a clone's contribution to the pollen cloud is proportional to the number of male strobili it produces, and that this pollen settles out at random (on self- and outcross female strobili) once it has been dispersed, we would expect clones with the larger contributions to the male strobilus crop (and, hence, to the pollen cloud) to produce more self-pollinated seed, resulting in larger percentages of empty seeds, lower germination rates, and increased levels of inbreeding depression (Mergen, Burley and Furnival, 1965; Fowler and Park, 1983; Park, Fowler and Coles, 1984). Data from the germination experiments supports this expectation (*Table 1*). We observed a significant negative correlation between the log of clonal male strobilus numbers in 1984 and percent germination of seed collected that year ($r = -0.40$, $P < 0.05$). The potential for higher selfing rates in clones which produce the majority of the orchard's pollen is significant in light of the tendency for these clones to also be the most productive of seed. Data on clonal self-pollination rates (e.g. obtained via application of marker gene methods) are required to substantiate this suggested trend.

Variation between clones in tree height and its relationship to stobilus numbers

Some of the variability in strobilus production among clones is correlated with variability among clones in tree height. Approximately 35% of the variation in height is associated with differences among clones (*Tables 1* and *2*). The correlations between true clonal means of height and cone numbers are significant for male strobili [Corr(height, male) $= 0.47$, $P < 0.05$ in 1984 and Corr(height,male) $= 0.32$, $P = 0.05$ in 1985] but insignificant for female strobili [Corr(height,female) $= 0.31$, $P > 0.05$ in 1984 and Corr (height,female) $= -0.22$, $P > 0.05$ in 1985]. A portion of the variance among clones in male (but not female) strobilus production, therefore, is associated with among-clone variation in height. This conclusion is reinforced by considering the partial correlations between true clonal means of male strobilus numbers in 1984 and 1985, controlling for the influence of height [Corr(male,male.height) $= 0.47$, $P < 0.05$], and between true clonal means of female strobilus numbers in 1984 and 1985, controlling for the influence of height [Corr(female,female.height) $= -0.59$, $P < 0.01$]. That controlling for the influence of height has little influence on the magnitude of the correlation between years for female strobilus production, but doubles the magnitude of the correlation between years for male strobilus production, further supports the conclusion that the taller clones will show a tendency to contribute more male gametes to the seed crop each year.

Correlation between male and female strobilus numbers within clones

Within clones, male and female strobilus production also showed variation. In 1984, 17 of the 33 clones exhibited significant positive correlations between male and female strobilus numbers (*Table 3*). In 1985, only three of the 33 clones exhibited positive correlations between male and female strobilus numbers, while one showed a negative correlation (*Table 3*). These results suggest the potential for higher rates of self-pollination within the crowns of the more productive seed producing trees in the mast year, 1984.

Table 3. — Correlations between numbers of male and female strobili for clones in the Glencairn orchard in 1984 and 1985.

Clone	Number of ramets	Correlation between numbers of male and female strobili in: 1984	1985
445	55	0.41**	-0.26
569	28	0.47*	-0.17
571	19	-0.03	0.10
585	18	0.22	0.63**
590	5	0.65	0.81
594	6	0.74	0.49
648	10	0.97**	0.21
650	69	0.29*	-0.05
660	16	0.66**	--a
661	17	-0.42	-0.19
667	7	0.82*	0.72
669	6	0.60	-0.44
693	39	0.80**	-0.13
694	34	0.64**	0.34*
695	27	0.91**	0.11
697	18	0.79**	0.32
698	6	-0.68	-0.05
699	9	0.28	-0.06
700	6	0.99**	--a
701	53	0.12	-0.24
702	36	0.19	0.01
710	38	0.38*	-0.34*
711	34	0.33*	0.13
716	25	0.75**	0.15
717	21	0.65**	0.36
718	7	-0.26	0.79*
719	23	0.55**	0.06
720	14	0.52	0.15
721	17	0.77*	-0.34
722	7	0.48	0.32
723	7	0.97**	--a
725	8	-0.07	-0.04
726	14	0.49	--a

* $P < 0.05$
** $P < 0.01$

a Correlation coefficient could not be calculated due to zero production of strobili.

Conclusions

Assuming that clonal gametic contributions to the seed crop are proportional to clonal strobilus numbers, our findings suggest that the gametes of certain clones will dominate the genetic composition of the seed crop, and that both male and female gametes will contribute to this dominance. These findings have several potential genetic consequences for orchard seed production. The genetic diversity of the seed crop is reduced over that expected assuming random mating among clones, and the rate of self-fertilization of certain clones relative to that of others potentially is increased. Both factors will probably lower the expected genetic gain to be made by breeding the clones.

From a management perspective, the problem of reduced genetic diversity in the seed crop may be addressed in a number of ways. Since different clones dominate female strobilus production in different years, the genetic diversity of seeds may be significantly increased by combining the seed crops of two or more years. Alternatively, hormonal treatment of orchard clones (MARQUARD and HANOVER, 1984) may, by increasing male and female strobilus numbers, bring about more equitable production levels.

The potential problem of higher self-fertilization rates in trees and clones producing larger numbers of male strobili is more difficult to solve. It could be addressed by increasing the number of male strobili of other clones, thereby increasing the proportion of non-self pollen in the pollen cloud. Alternatively, clones producing exceptionally high levels of inbred seed could be excluded from use as sources of seed.

Strobilus production levels represent only one factor which potentially influences the mating system of clonal seed orchards. Other factors such as flowering phenology, wind direction, gametophytic selection, clone number, clone mortality, and clone placement probably interact with strobilus production to influence the genetic composition of orchard seed crops. Electrophoretic analysis of the clones and the 1984 and the 1985 seed crops is, therefore, essential to reveal the importance of strobilus production alone on the genetic composition of the seed crop. In particular, it will be important to determine the degree to which clones producing the majority of male strobili contribute the majority of male gametes to the seed crop, and the extent to which such clones self-fertilize at higher rates than those clones which produce less pollen.

Acknowledgements

Financial support from the Natural Sciences and Engineering Research Council of Canada Strategic Grants Programme and the Ontario Ministry of Natural Resources is gratefully acknowledged. We thank JAMES V. HOOD and R. MARIE RAUTER for facilitating our studies at the Glencairn orchard. CREMILDA DIAS and JANET WYMAN provided excellent technical help. Dr. WILLIAM CHELIAK provided helpful advice throughout the course of this investigation.

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Phenology, Height Increment, and Cold Tolerance of Alnus glutinosa Populations in a Common Environment[1])

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(Received 11th November 1985)

Summary

Progenies of 48 natural populations of black alder [*Alnus glutinosa* (L.) GAERTN.] were compared on the basis of height increment in the second growing season, date of budburst, date of budset, spring frost injury, winter cold injury, and laboratory-determined freezing tolerance. Budburst occurred in all populations before the beginning of the frost-

[1]) Journal Article No. 7160 of the Pennsylvania Agricultural Experiment Station. This research was supported by U.S. Department of Agriculture Cooperative Regional Project NE-27. The authors wish to acknowledge the generous cooperation of R. B. Hall, Iowa State University.

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