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**SOME INSIGHTS ON HYBRIDS IN
FOREST TREE IMPROVEMENT**

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SUMMARY

Biological features of crossability of species, viability of hybrid offspring and vegetative propagability determine feasibility of hybrid breeding and deployment programmes. Their economic success depends on their superiority in growth and adaptation to particular sites as well as in log-, wood- and product characteristics over the parent and other species. The question "To hybrid, or not to hybrid?" needs critical appraisal.

Recent New Zealand experience with eucalypt, pine and poplar hybrids provides an introduction to a comparison of hybrids in these genera, world-wide. The particular biological features of each genus, particularly crossability of species and ease of multiplication by cuttings, with or without problems of ageing and rejuvenation, have strongly influenced the use of hybrids and also the nature of forest management in these genera.

First-generation hybrids generally have the most desirable features for commercial deployment but long-term breeding and deployment strategies have often not been well developed. Some of the features of recurrent selection for general combining ability, reciprocal recurrent selection and derivatives of these strategies have been revisited and an alternative strategy combining elements of both, proposed. Hybrids are genetic dead-ends, best deployed as vegetatively-propagated clones under well thought-out breeding objectives.

INTRODUCTION

My first encounter with interspecific hybrids was in Zambia in 1960, while assessing young species and provenance trials of eucalypts. In some plots of Zambian-sourced seedlots of *Eucalyptus grandis*, I kept finding a few trees, much bigger in diameter than the rest and which had a silvery bark, unlike *E. grandis* at that age (I can visualise these monsters, even now!). These were natural hybrids of *E. grandis* x *E. tereticornis*. Later Dick Danks successfully made the hybrid by controlled pollination (Shelbourne and Danks, 1963).

Such obviously superior natural hybrids make a big impact on the forester and they have often been the initial basis of successful hybrid eucalypt plantations, as in Brazil and Africa (eg. Delwaulle, 1988; van Wyk, 1990; Brandao *et al.*, 1984).

Further development of successful hybrid breeding and deployment depends on a number of overlapping factors, including:

- *crossability of the two species
- *feasibility of controlled pollination
- *viability of hybrid offspring
- *vegetative propagability of mature hybrids, or of juvenile hybrid material
- *feasibility of F1, F2 or backcross hybrid seed production
- *costs of breeding and deploying hybrids
- *gains in different traits from hybrids, versus from improvement of pure species

There is a long and expensive development process between identifying a promising hybrid species combination and creating a sustainable hybrid breeding and deployment programme. The question, “to hybrid or not to hybrid” is an important one, considered here. A comparison of the application of hybridisation in three genera, *Eucalyptus*, *Pinus* and *Populus*, both in limited New Zealand (NZ) experience and worldwide, and some revisiting of strategic aspects of hybrid breeding and deployment, are covered in this paper.

NEW ZEALAND CASE STUDIES

The only practical experience we have had with eucalypt hybrids in NZ has been with *E. grandis* x *E. nitens* (Shelbourne *et al.*, 1999). We compared 8 pair-cross hybrid families of *E. grandis* (female parent) x *E. nitens* (pollen parent) of central Victorian provenances and another 8 pair-crosses with *E. nitens* pollens of southern NSW origin, and open-pollinated families from all male and female parents. Crossing was done by Brian Pierce, CSIR, Nelspruit, S. Africa on his *E. grandis* clones using our NZ-collected pollens. Two- and a half years after planting, there was little difference in mean height and DBH between the hybrids and the *E. nitens* open-pollinated families (the *E. grandis* material performed poorly and was evidently not well adapted). However, when we compared the distributions of height and diameter, it was clear that there was a high proportion of poorly-grown trees in the hybrids and that the distributions were highly skewed. Subsequently, by age 5 years, the better hybrid trees have come to dominate the stand in the single-tree-plot trials, largely because of their dense, healthy crowns which do not suffer from defoliation by *Mycosphaerella cryptica* and *Kirrimyces eucalypti*, two leaf fungi that affect *E. nitens*.

Two things seem to have happened: firstly, the hybrid families contained a high proportion of ‘faulty’ genotypes which died or became suppressed in the first two years from planting; secondly, the ‘normal’ hybrid genotypes (on the warm, low-altitude test sites) have an advantage over *E. nitens* because they are not affected by fungal leaf disease. Further experience with *E. nitens* in Northland at ages of 8-12 years on similarly warm, low altitude sites with higher rainfalls have shown up serious health problems with *E. nitens*, especially with the Victorian provenances, which may indicate its basic maladaptation to these sites (Shelbourne, Low and Smale, unpubl.).

It is nearly impossible to propagate adult trees of *E. nitens* from (juvenile) coppice shoots. In contrast, *E. grandis* is easy to propagate. Preliminary propagation of the hybrid by coppice from one-year-old seedlings (Aimers-Halliday, *et al.*, 1999) was quite successful, but not from coppice shoots from stumps of felled 2-year-old trees. We have recently successfully grafted scions from 5-year-old selected hybrids onto *E. nitens* rootstock with the hope of propagating cuttings and tissue cultures from juvenile shoots to be induced from these.

In this small programme, 7 years from initial controlled pollination, we have, as yet, been unable to produce enough stock of ‘normal’ hybrid individuals to properly evaluate this hybrid. The relatively low frequencies of normal individuals in hybrid families means that a plantation stand of hybrid clones needs to be created by vegetative means. Economic as well as biological factors come into the picture; the costs of developing propagation techniques to produce research stock for testing is high and for a commercial system, even higher. We need to test the hybrid in plantation stands on a variety of sites; we also need to evaluate wood and kraft pulping properties (basic wood density at age 2 ½ years is the same for *E. nitens* and the hybrid).

Eucalyptus nitens is the most widely-grown eucalypt for pulp in NZ. Where there are many (eucalypt) species to choose from, it is arguably more cost-effective and ecologically safer to introduce and test different species that promise acceptable pulping properties and choose well-adapted, fast-grown provenances, than to develop this hybrid. We are, in fact, also following this path, and have confirmed the good performance of a well-tried alternative for these warm sites, *E. fastigata*, as well as finding a relatively untried newcomer, *E. globulus* ssp. *maidenii* which promises well.

Interspecific hybridisation has not yet had much application with *Pinus radiata* in NZ. This species makes up 90% of the exotic forest estate and only crosses readily with *P. attenuata*. This hybrid has been established recently in trials as 15 polycross progenies of *P. attenuata* female parents, mated with a *P. radiata* pollen mix. Female parents of *P. attenuata* were selected from the four best provenances from southern Oregon. A pollen mix of 15 selected progeny-tested *P. radiata* parents was crossed with 15 *P. attenuata* clones, and open-pollinated progenies of these parents from a seed orchard were also included, as a control. The hybrid progeny trials were planted on cold, semi-continental sites in the South Island in 1998. This hybrid has had limited use in California and Oregon, extending the range of *P. radiata* into colder, snow-prone sites with more continental climates.

There are unconfirmed reports of *P. radiata* being crossed with *P. tecunumannii*, *P. patula* and *P. greggii*. A few hybrid offspring were produced from NZ crossing between *P. radiata* and the southern provenances of *P. muricata* in the 1980s but crosses with the northern provenances did not yield any seed. There are exciting possibilities in future of overcoming barriers to crossing between *P. radiata* and the other closed-cone pines through somatic hybridisation and other molecular-based methods.

The Cedros and Guadalupe provenances of *P. radiata*, which are genetically distinct and much slower-grown than the mainland provenances, both cross freely with the Californian provenances, and the F1 hybrids grow at about the same rate as the latter. Separate small breeding populations of each island population are being maintained as future gene resources.

Other potentially valuable hybrids for application in NZ exist among the cypresses. These species include 17 species of *Cupressus* and 6 species of *Chamaecyparis*. *Cupressus macrocarpa* (from Monterey, in California) and *C. lusitanica* (from Central America) are grown in modest quantities, mainly by farm foresters. *Chamaecyparis lawsoniana* is used in shelterbelts, and hybrid clones of *Ch. nootkatensis* x *C. macrocarpa* (Leyland cypress) and with *Ch. nootkatensis* x *C. lusitanica* (Ovens cypress) have been widely used, also mainly for shelter. These hybrids have the advantage of easy vegetative propagability and better resistance to cypress canker, which affects the two cypresses and *Ch. lawsoniana*. These two genera generally produce low density, naturally-durable, stable and easily-worked timber with a pleasing appearance. *C. macrocarpa* and *C. lusitanica* are seen as a potential substitute for native NZ kauri, *Agathis australis*, with a possible potential market in Asia as a substitute for Hinoki, *Ch. obtusa*. Members of both genera appear to cross sufficiently readily to make them a valuable gene pool for creating various species combinations. In the case of the UK-produced Leyland and Ovens hybrid clones, cutting propagation is easy, without apparent physiological ageing effects. Both *C. macrocarpa* and *C. lusitanica* are being propagated by cuttings in NZ and some clones of each species tested and released for clonal forestry deployment. Breeding programmes based on recurrent selection for general combining ability (RSGCA, Allard, 1960) have been advanced to a second-generation breeding population in both species.

Poplars are the principal species planted in NZ for erosion control and shelter but are not used for wood production to any significant extent. Some nine clones which are disease, wind and possum-resistant have been selected and tested, and are commercially available and another 10 clones are held by Regional Council nurseries. These are all interspecific hybrids amongst *Populus deltoides*, *P. nigra*, *P. maximowiczii*, *P. yunnanensis* and *P. trichocarpa*. No development of breeding populations of poplar species has ever been undertaken in NZ. However, following a recent review of the NZ breeding programme and the international literature (Shelbourne and Wilkinson, unpubl.; Shelbourne, unpubl.) systematic introduction and breeding population development of certain poplar species is accepted as a necessary basis for future development of pure-species and hybrid breeding, and is planned to start with *P. trichocarpa* (L. Fung, pers. com.).

COMPARISON OF INTERSPECIFIC HYBRIDISATION IN PINES, EUCALYPTS AND POPLARS

It is instructive to compare the role of hybrids in these three important genera and this brings out the way in which the various limiting factors, outlined earlier, have moulded their development.

Poplars

With poplars, the beginning of genetic improvement long predates that of pines and eucalypts; Stout and Schreiner(1927) started breeding and selecting interspecific hybrids in the 1920s yet poplar clones had been selected long before this. Lombardy poplar may have arisen as a natural hybrid between *P. nigra* and fastigate *P. nigra* var. *thevestina* as early as the 17th century (Wilkinson, 2000). Undoubtedly the distribution and genetic structure of natural populations of poplars have been strongly influenced in Europe and Asia by mankind over thousands of years and clonal propagation has reinforced this influence. Poplar interspecific hybrids like I 214 (between native *P. nigra* and American *P. deltoides*) were created and released by Giacometti in Italy before World War 2.

The key feature of poplars that lent themselves to selection and breeding were their ease of propagation and their ease of crossability between species, including crossing within and between Sections, such as the black and balsam poplars (*Aigeiros* and *Tacamahaca*). In addition, heterosis of inter-species crosses is a widespread phenomenon. Even controlled pollination is very easy and fast in poplars by cutting off branches from flowering trees and keeping these in a greenhouse during pollination, yielding seed after only a few weeks. One characteristic that has seriously inhibited the use and movement of seed is its short period of viability, which in practice made trading seed and seed introduction of poplars to other countries difficult or even impossible. The flora and fauna accompanying the fluffy seed makes strict quarantine necessary as well. The ease of cutting storage, transport and propagation encouraged the introduction of selected clones, both of pure species and hybrids, rather than introduction of seed in the form of progeny and provenance seedlots.

1). Lindsay Fung, HortResearch, Palmerston North

Rapid multiplication by cuttings, combined with some not-so-visionary forest planning has resulted in the entire poplar plantation resource of countries like France and Italy being composed of a handful of clones, often hybrids, despite the development of genetically broad-based breeding programmes. These monocultures have greatly increased the risks of widespread biotic and climatic damage and have reduced the range of wood properties and potential products. New Zealand has similarly relied heavily on a few imported and locally developed hybrid clones which are, of course, genetic dead-ends to further breeding.

It is curious and unfortunate that the biological features of poplars such as propagability and crossability between species have contributed to unwise deployment of too-few clones and, in many cases, rather haphazard hybridisation without a proper breeding strategy. There are, however, some notable exceptions to this, which will be considered later.

Pines

Pines have generally proved difficult or even impossible to propagate by cuttings from mature ortets, though propagating from young seedlings by cuttings or tissue culture has proved feasible for many species. In *P. radiata*, often in association with the development of control-pollinated seed orchards, multiplication by cuttings from hedged stool beds of full- or half-sib families has become an important, in some cases the most important source of commercial planting stock in NZ, Australia and Chile.

For interspecific hybrid pines, the first ever mass production of control-pollinated seed in tree species was of *P. rigida* x *P. taeda* in Korea. Recently Westvaco Corporation, in the eastern U.S.A., has been planting F2 hybrid seedlings derived from open-pollinated clonal seed orchards of F1 hybrids. However, the best-developed hybrid programme in pines is that of the Queensland Forest Research Institute and Department of Primary Industry forests where the *P. elliottii* var *elliottii* x *P. caribaea* var *hondurensis* (PEE x PCH) hybrid has been developed, tested and finally deployed to replace the slower-growing PEE in southeastern Queensland. F1 hybrid seed is produced from clonal seed orchards and clonal archives of PEE by controlled pollination. A few families, where seed set was good, have been deployed as seedlings but most are multiplied by juvenile cuttings from hedged stool beds, much as for *P. radiata*. F2 hybrid seed has also been produced (with good seed set) in open-pollinated orchards of F1 clones. Within-family variability of F1 and even F2 families has not proved to be much greater than that in within-species crosses and has not proved a problem in commercial plantations. Clonal forestry is now at the stage where it is being applied as the deployment method of choice for selected and tested F1 hybrid clones, with up to 2500 ha. of clones planted per year.

These PEE x PCH hybrids grow faster than PEE and with better-than-intermediate growth rate to PCH on most SE Queensland sites but are not well-adapted to the poorest sites where PEE continues to be used. The growth superiority of the hybrids combines adequate resistance to cyclone wind-throw with good bole straightness and the hybrids have intermediate wood properties to the pure species. Like most interspecific hybrids, the PEE X PCH hybrid's advantages are a combination of ecological and adaptive complementarity and some heterosis, with intermediacy in other traits such as wood quality.

The within-family variability of pine hybrids, at least for the PEE x PCH combination, seems to be generally acceptable, making multiplication of juvenile seedling families by vegetative propagation a viable deployment method. Cutting propagation from hedged stools, which can

be periodically replaced by newly-germinated (and rejuvenated) seedlings as well as better families, forms a sustainable and reliable means of deploying these hybrids. As yet, clonal forestry with pines and pine hybrids is fraught with some risk, as maintaining juvenility of clones, by hedging or tissue-culture cold-storage, may not be possible on an indefinite basis. At present, it seems that embryogenesis and cryogenic storage of clones is a potentially reliable way of maintaining juvenility indefinitely.

Clonal forestry with hybrids, as with pure species, has the promise of greater genetic gains in different traits from exploiting general (hybrid) combining ability (GHA) (i.e. additive gene effects) in crosses between species, as well as additional gain from within-family selection of clones. This potentially uses all the genetic variance, including specific hybrid combining ability (SHA) and other forms of non-additive variance. Equally important, demonstrated at least with *P. radiata*, most wood and end-product related traits show very high heritabilities. The resulting within-clone uniformity and thus predictability of the processing and product performance of clones may prove to be the most valuable feature of using clones, even outweighing the value of higher gains.

Eucalypts

In eucalypts, the main limiting factor in the practical use of hybrids lies in their ability to be propagated vegetatively from the stump sprouts of mature trees, and the vegetative vigour of such propagules. Production of control-pollinated hybrid seed and seedling planting stock in commercial quantities has never, I believe, proved feasible, although where a species like *E. globulus* is the maternal parent, there are sufficient seed per capsule (30) to make control-pollinated seed production a practical possibility. Most, if not all commercially-planted eucalypt hybrids are propagated as clones from selected mature ortets initially, and these are induced to produce juvenile coppice shoots for propagation. Such clones can be maintained as stools from which juvenile cutting material can be harvested at regular intervals. Mature ramets in clonal tests can also be propagated in the same way after a period of clonal testing. Propagation by this method is not possible for many species such as *E. nitens*, and it could be expected that the capacity for coppicing and cutting propagation would be intermediate to that of the parents. This was borne out in the *E. grandis* x *E. nitens* hybrids in NZ and S. Africa.

Hard-to-propagate species like *E. nitens* can often be propagated from very young seedlings and it is possible that family forestry or even clonal forestry according to a pine model might be feasible, though is not being practiced commercially, to my knowledge.

Even relatively easily-propagated species often vary greatly in propagability between families and clones, and such variation is the source of increased costs of eucalypt clonal and cloned hybrid deployment. Vegetative propagability for production of eucalypt hybrid clones is therefore a key limiter of the use of potentially-valuable hybrid combinations.

Crossability of species is obviously another key factor. It is generally determined by taxonomic distance in eucalypts. The large proportion of genetic "junk" we found in the *E. grandis* x *E. nitens* crosses may be typical only of a cross between two species that are rather too distantly related for easy hybridisation.

BREEDING STRATEGIES FOR INTERSPECIFIC HYBRIDS

This is an area in which I have had some interest since 1991-92, when I was working on breeding strategies with CSIR Forestek in South Africa. I proposed strategies for the main pine and eucalypt species, for the PEE x PCH hybrid and also for the *E. grandis* x *E. urophylla* hybrid (Shelbourne, unpubl.). I was also involved at this time in predicting gains from the use of cloning in the breeding population as well as for clonal forestry deployment (Shelbourne, 1992), both of which are relevant in hybrid breeding strategies. I proposed using a strategy of recurrent selection for general combining ability (RSGCA) in the breeding populations (BPs) of each parent species, rather than the reciprocal recurrent selection (RRS) strategy proposed for the *E. grandis* x *E. urophylla* hybrid by Vigneron (1991) in the Congo Brazzaville. I believed that RRS was at a severe disadvantage in requiring a cycle of GHA testing (i.e. mating each pure species parent with, preferably, a standard set of testers of the other species) to enable **backwards** selection of parents in each species, to re-mate within each pure-species BP. This backwards selection, to be effective, would reduce effective population size (status number) of each pure-species BP, quite drastically. While hybrid crosses used to estimate GHA could be made, as Vigneron suggested, in a partial factorial or some similar design, and serve as a hybrid production population (HPP), their parents could not be selected for GHA contemporaneously. It would be necessary to make a further round of hybrid crosses among the best parents, selected on GHA, to gain the full benefits of GHA testing in the HPP. This would be followed by a cycle of clonal testing of selected members of these families. This would all add up to a very long drawn-out and expensive programme.

I believed that improvement of the parent species BPs by RSGCA would be effective in preselecting parents for hybrid crossing for traits where GHA and GCA were well correlated and which had high heritability within species, and not detrimentally change these traits where they were not. Growth and adaptive traits with lower heritability and applicable to parent species in their own environments, might be expected to show lower correlations between GCA and GHA. By crossing the very best parents in the respective species BPs and then selecting amongst resulting hybrid families on GHA, and amongst clones within families for remaining GHA and SHA, good gains in all traits, including those where GHA and GCA were poorly correlated, should be realised.

Garth Nikles in a review paper (Nikles, 1992), discussed these strategies and proposed a modified RRS scheme. Instead of using backwards selection in the parent species BPs, he proposed using **combined forwards** selection in intra-population crosses. GHA information would be derived from hybrid crosses amongst all parents of each species (used to generate a hybrid production population) and combined in an index with GCA information (from intra-species crossing) and individual phenotype to select new BP parents in each species. This scheme, which he called "RRS with forwards selection" (RRS-SF), has the advantage of requiring about the same cycle time as RSGCA, while giving some scope for moulding each species' BP according to the ability of parents to combine well with the other species. It still requires all parents in species BPs to be intermated with a sample of parents of the other species. In early 1993 I summarised all these strategies in flow charts (Shelbourne, 1993).

Stephano Bisoffi (Bisoffi, 1989; Bisoffi and Gullberg, 1996) has described the implementation of an RRS strategy for breeding and production of *Populus deltoides* x *P. nigra* hybrids, which, I believe is the only advanced operational hybrid breeding programme for tree species using RRS. He selected 300 *P. deltoides* parents from provenances introduced earlier from the U.S.A., but for the native *P. nigra*, a survey of Italian native populations located a further 300

parents, far from existing plantations (which were often of hybrids). RRS involved polycrossing with *P. nigra* males onto *P. deltoides* females, and the use of six *P. deltoides* female testers to progeny-test the *P. nigra* males (poplars are dioecious). This is a classic RRS strategy, made more complex by the dioecious nature of poplars.

I have come, if not full circle, at least to recognise that hybrid family performance, particularly for growth and adaptive traits may be, to a large degree, unpredictable from within-species breeding values. Dieters and Nikles (1998) have shown no correlation between breeding values of PEE parents within PEE (GCA), and those estimated from crossing with PCH (GHA), for DBH and tree volume, though this result may be equivocal because of the selected nature of the PEE parents. Further information on the breeding values of the PCH parents is promised. I am not aware of other evidence of this lack of correlation. Intuitively, it makes good sense, especially where the hybrid combines species, widely differing in adaptation and which are genetically distant, such as the *E. grandis* x *E. nitens*, *Populus trichocarpa* x *P. deltoides* and PEE x PCH species combinations. However, it might be expected that other morphological and wood quality traits would show additive behaviour and could be usefully selected in the pure species BPs. The loss of effective population size that seems implicit in a true RRS strategy, as well as the problem of two cycles of breeding to one of the HPP, militate against the use of classical RRS. An RRS-SF strategy is more acceptable on these grounds yet its selection for GHA is very "diluted" in the pure species-breeding populations.

An alternative could be to use RSGCA-improved breeding populations of each species, selected minimally for growth rate but more intensively for wood quality and end-product traits and traits like bole straightness and branching, where phenotypic selection would be effective. A hybrid production population of a large number of hybrid crosses and parental combinations, with large numbers of trees per family, could serve to select between hybrid families as a GHA progeny test and as a source of hybrid genotypes for selection. Followed later by cloning the best of these in clonal tests, this would form a source of hybrid clones for deployment. This will cope with the possible unpredictability of hybrid performance at both family-mean and clonal levels and will allow intensive selection for GHA and SHA effects in the HPP. In the following generation of the pure-species BPs, the parents of each species of the **previous** generation that showed outstanding performance in hybrid crosses in the HPP can be used again for intra-species crossing, alongside forwards selections, which will improve the hybrid combining ability (GHA) of each parental species population.

Much attention and emphasis has been given in designing hybrid breeding strategies to maximise heterosis for potential gains in growth rate. The RRS scheme, in particular, addresses this criterion. In contrast, I think that the role of complementarity, often unpredictable, as well as the generation of new combinations of genes that are adapted to sites and pathogens rather unpredictably may be more important than classical single-trait heterosis. Useful wood and utilisation properties from each parent species can also be combined in the hybrid. Selecting for product-related traits is also likely to be more profitable in adding value to the crop, whether it is grown on short rotations for pulp or on longer rotations for higher value products, than chasing cubic metres of mean annual increment. Wood quality and related processing and product traits (like stiffness and stability of solid wood) are likely to become important selection criteria which are also likely to be strongly inherited, and to be predictable from parental (within-species) breeding values. These factors may make the classical RRS strategy unnecessary. Proper definition of breeding objectives for F1 hybrids (i.e., the important elements of the production system from nursery to market) may be even more important for hybrids than pure species because of their dead-end nature.

CONCLUSIONS

1. F1 interspecific hybrids are genetic dead-ends and they are always at least one step removed from the improved parental species populations. They cannot lead to cumulatively improved populations unless advanced-generation hybrids or introgression are practicable.
2. Vegetatively-propagated clones, where biologically feasible, are the best way to deploy hybrids as they can exploit all the genetic variance, with other attendant advantages of clonal forestry, particularly higher gains and within-clone uniformity.
3. The costs and complexity of hybrid breeding and deployment are high, and introduction, improvement and deployment of a single species is likely to be cheaper, simpler, more rapidly implemented and more easily sustainable.
4. Easy species crossability and vegetative propagability of hybrids can be a trap that results in neglect of proper species introduction, provenance testing and breeding-population development. This can hinder development of new and better hybrids.
5. Definition of breeding objectives (i.e. elements of profitability for the whole production system) and corresponding selection criteria are particularly important for hybrids.
6. Breeding and deployment strategies need to be tailored to the biology of the hybrid. Neither RRS, RSGCA or RRS-SF seem to be entirely satisfactory for hybrids.

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