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Review article

A critical review of larch hybridization and its incidence on breeding strategies

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Summary — Hybrid larch *(Larix* X *eurolepis* Henry) superiority over the parental species *(Larix decidua* Mill. and *Larix kaempferi* (Lamb.) Carr.) has been described by many tree breeders. This superiority concerns not only growth characteristics but also several economically important traits.

In the literature, there is some ambiguity regarding the 3 following concepts : hybridization, hybrid superiority and heterosis. In particular, the superiority of hybrid larch has been claimed in many studies as due to heterosis. A detailed review of published results does not permit a decisive opinion on the subject as most of the results are based on punctual and limited observations.

The interest in hybridization is not restricted to hybrid vigor but also includes combination and transfer of favorable characteristics. Several larch improvement strategies based on inter- and intra-specific hybridization are discussed. Reciprocal recurrent selection seems particularly attractive. Nevertheless, none of the present strategies, including the F_1 generation as a breeding population, can be excluded. Precise knowledge on genetic properties of traits selected for are required before any firm recommendation can be made.

There is an urgent need for well designed, long-term experiments set up on several sites to obtain more insight into these delicate questions. Use of a two-level factorial mating design is recommended, in particular to avoid some of the approximations made in past experiments. Moreover, valuable information on genetic parameters, e.g. combining ability, heterosis, will be gained at both intra- and inter-species and intra- and inter-population levels and may help tree breeders in their choice of a more efficient hybridization strategy for the improvement of larch.

larch – hybridization – improvement strategies – heterosis

Résumé — Hybridation des mélèzes : revue critique et incidence pour l'amélioration. *La supériorité du mélèze hybride (*Larix *X* eurolepis *Henry) sur ses espèces parentes (*Larix decidua *Mill. et* Larix kaempferi *(Lamb.) Carr.) a été reconnue et décrite par de nombreux auteurs. Elle ne se limite pas à la croissance mais concerne aussi divers caractères économiques importants.*

Une confusion existe cependant dans la littérature entre trois notions : hybridation, supériorité de l'hybride et hétérosis. En particulier, cette supériorité du mélèze a été assimilée dans de nombreux cas à un effet d'hétérosis. Une revue minutieuse de la littérature ne permet pas cependant dans l'état actuel de nos connaissances de confirmer ou d'infirmer ce rapprochement car les résultats publiés résultent souvent d'observations ponctuelles et partielles.

Il est rappelé que l'intérêt de l'hybridation ne se limite pas à la seule vigueur hybride. Diverses stratégies d'amélioration des mélèzes par hybridation inter-spécifique (et intra-spécifique) sont briè-

vement discutées. La sélection récurrente réciproque présente de nombreux avantages. Cependant aucune voie, y compris celle utilisant la génération F_1 comme population d'amélioration ne peut être a priori *rejetée tant qu'une connaissance précise des propriétés génétiques du matériel étudié (en particulier, le rapport dominance/additivité) n'est acquise sur les caractères concernés par l'amélioration.*

En vue de répondre aux diverses questions posées, la mise en place de dispositifs expérimentaux rigoureux, multisites et conçus pour des observations à long terme apparaît comme une priorité. Afin d'éviter certains écueils d'expériences antérieures (choix du matériel parental de référence), le recours à un plan de croisement factoriel à 2 niveaux est recommandé. Des informations précieuses sur les paramètres génétiques (capacités à la combinaison, hétérosis, etc.) pourront être obtenues aux niveaux intra- et inter-spécifiques et intra- et inter-populations et devraient permettre d'orienter le travail des améliorateurs.

mélèze – hybridation – stratégies d'amélioration – hétérosis

Introduction

The transfer of European larch (*Larix decidua* Mill.) seed sources from their native range (the Alps) to more lowland areas has not been successful in France. Several provenance tests have shown its poor adaptation, slow growth, and canker susceptibility (Lacaze and Birot, 1974; Ferrand and Bastien, 1985, Schober, 1985) when cultivated at lower elevations. On the other hand, Japanese larch *Larix kaempferi* (Lamb.) Carr., an exotic species from Hondo Island, Japan, initially appeared to be a promising successor to European larch with fast juvenile growth and canker resistance. However, its requirement for moisture during the vegetative period restricts it to more limited oceanic sites. Even so, the *Larix* genus remains very attractive for its silvicultural advantages, namely light-tolerant species, no plantation problems, fast juvenile growth, relatively short rotation, and the high quality of its timber.

A hybrid between the European and Japanese larch (*Larix* X *eurolepis* Henry) first described in 1919 by Henry and Flood (1919) opened new perspectives for larch tree improvement programes. The hybrid was advocated for its outstanding growth performance, usually described as heterosis, it has subsequently been received with some reserve by European countries. Contradictory results have been published on its heterotic response.

This paper will first discuss the results published on hybrid larch with special reference to hybrid vigor, and then will consider possible alternative hybridization strategies which could benefit from the heterotic response.

Hybrid larch and hybrid vigour

Hybridization work on larch has mainly been concerned with inter-specific crosses; only minimal interest has been shown in intra-specific crosses. Various possible crosses between species of the *Larix* genus have been reported throughout the world, but the most economically important ones currently concern hybrids between European larch and Japanese larch, and between the Japanese larch and the Korean larch (*Larix gmelinii* Rupr.). In Europe, only the former is cultivated and will be discussed.

Hybrid larch has been extensively planted in regions such as Scotland (> 55,000 ha. by 1980) (Destremau, 1987) and Denmark, but at present it is nearly absent in

French forests for various reasons, the principal cause being the lack of reforestation material.

Inter-specific hybridization of larch has long been cited for its positive heterotic effect, a property it shares with other forest trees such as poplars, eucalyptus and pines. The superiority of hybrid larch as regards morphological and phenological characteristics, growth traits, wood properties and physiological parameters has been illustrated (Matyssek, 1986). In addition, it seems to be much more resistant to larch canker (*Lachnellula willkommii* (Hartig) Dennis) (Keiding, 1980) than many of the European larch populations.

Table I presents some of the most significant results presented in the literature on hybrid larch growth performance involving various types of hybrid progenies (control or open pollinated families), as well as diverse sources of parental material to which they are compared. These include either provenances (natural or artificial) or families. The results are normally positive, though highly variable, irrespective of the various ages of the tested material and contrasting regions in Europe that they originate from. When Hybrid larch height growth is generally found to be much more significant vis-à-vis European larch than vis-à-vis Japanese larch.

Positive traits in hybrid larch other than growth are also outlined in Table II. Results are presented as the relative ranking of the hybrid when compared to the parental species. The hybrid generally ranks higher for several important characteristics such as stem form and wood mechanical properties. However, the hybrid ranks only intermediate for several wood physical properties. Wood volume shrinkage and heterogeneity in particular could well be negative aspects of hybrid

Table I. Superiority (expressed in %) of hybrid larch over parental species for total height.

Age	*Hybrid*	*E.L.*	*J.L.*	*Parental material*	*Author*
2	4 FS	19-39	–	3 FS fam. artif. prov.	Nilsson (1959)
5	14 FS	15-58	–	20 FS fam. Sudetan prov.	Vincent [1] (1972)
7	3 SO	33-40	–	1 Sudetan prov.	Vincent [1] (1965)
7	4 FS	40-55	–	3 FS fam. Sudetan prov	Reck
		2-13		4 OP fam. (best one)	(1977)
7	7 FS	7-50	–	1 artif. prov.	Keiding
		8-33	–		(1962)
8	1 SO	42		1 Sudetan prov.	Nanson [1]
			35	1 artif. prov.	(1978)
15	1 SO	26	–	1 Polonica prov.	Bellon (1967)
21	1 SO	19		1 Sudetan prov.	Ferrand [1]
			9	1 prov.	(1985)
22	8 FS	4-19		1 artif. prov.	Keiding (1980)
	20 FS	–	3-32	1 prov.	
33	1	12		1 artif. prov.	Gothe
			7	1 prov.	(1987)

E.L. = European larch; J.L. = Japanese larch; [1] = only first author mentioned; prov. = provenance; fam. = family; artif. = artificial; FS = full-sib family; OP = open pollinated family; SO = seed orchard progeny.

Table II. Relative ranking of the hybrid X eurolepis (H.L.) compared to the parental species.

Character	*Age*	*E.L.*	*J.L.*	*H.L.*	*Authors*
Flushing	5	2	3	1	Lacaze [1] (1965)
Stem form	8	1	3	2	Nanson [1] (1978)
	13	3	2	1	Lacaze [1] (1974)
	21	2	–	1	Reck (1977)
Branching	13	3	2	1	Lacaze [1] (1974)
	17	1	–	2	Reck (1977)
Wood density (Po/Vs)	8	1	3	2	Nanson [1] (1978)
	15	1	–	2	Reck (1977)
	15	1	3	2	Deret [1] (1979)
	28	3	2	1	Reck (1980)
Volume shrinkage	8	3	1	2	Nanson [1] (1978)
	15	2	1	2	Deret [1] (1979)
	28	3	1	2	Reck (1980)
Mechanical properties	15	2	3	1	Deret [1] (1979)

E.L. = European larch; J.L. = Japanese larch; 1 = best material; [1] = only first author mentioned.

larch (Bastien and Keller, 1980). Some contradictory results (*e.g.*, for stem form, branching habit, wood density) also exist between experiments. These will be discussed later.

Hybrid larch's reciprocal, *Larix* X *leptoeuropea* Dengler, has not received the same amount of attention, although the Dunkeld hybrid from which all the hybridization work on larch originates was produced from this formula. In a German experiment, (Gothe, 1987), at 33 years this hybrid showed a slight advantage in height growth but a slight loss in diameter growth compared to its reciprocal *Larix* X *eurolepis*. Results from other published studies do not permit a conclusion to be made regarding the superiority of one over the other. Nevertheless, the success of the hybrid X *eurolepis* seems more due to favorable conditions of artificial pollination than to its real superiority over its reciprocal.

Heterosis or hybrid vigor, commonly defined as the superiority of the hybrid over the mean performance of both parents (Falconer, 1960) is more often redefined by tree breeders as its superiority over its best parent. Moreover, while crop breeders take pure inbred lines as their reference point, forest tree breeders actually work if not at the species level, then at least at the population level or at best with individuals which are presumably highly heterozygous.

Two criticisms may be levelled at these different concepts. First, by only comparing hybrids to the best parent, it is clear that several hybrid families will be neglected and only part of the potential gain connected with heterosis will be obtained (Schmitt, 1973). Second, study at the species or population level might be sufficient to show advantages of hybridization, but is of little use for advanced selection and above all for interpretation of heterosis.

As mentioned previously, results presented in Tables I and II show some inconsistency in the observed level of "heterosis" for height growth-rate; in addition there are some contradictory results for various traits.

Apart from the restrictions of some of the experimental designs from which these results were obtained, it should be stressed that the parental material with which the hybrid progenies are compared is, in several cases, represented by provenances to which the parents of the hybrid do not even belong or by full-sib families with which the hybrid families share no common parent. This raises the question of the choice of the reference parental material, which in many cases can only be considered to be the best material available and not necessarily adapted to the specific test sites.

In addition, comments made by Schmitt (1973) cited by Reck (1977) concern the hybrids themselves. He points out that due to the difficulties of control pollination, hybrid heterosis has very often been described on an individual basis rather than for a population of individuals, so that general conclusions on heterosis of larch can hardly be drawn.

The majority of the results given in Table II concern young material, with the oldest data available from plantations of mid-rotation age. The question should be raised as to whether this early superiority of hybrid material continues and therefore constitutes true heterosis, or whether it is just a temporary faster initial phase of growth. An illustration of the latter situation was given by Namkoong (1963) for a hybrid between Loblolly and Longleaf pines. The answer to this question has not been clearly determined but is of prime importance in tree breeding.

Analysis of periodic growth increments made by Gothe *et al.* (1980) and Gothe (1987) in a German experiment indicated that from an age of $\approx$ 20 yr, the hybrid shows a slight reduction in its absolute production advantage, but a strong reduction in its relative production advantage over the progenies of the pure parent species. Results presented by Keiding (1980) and Reck (1980) support this view that the growth superiority of the hybrid is at its greatest during the first 10 yr. This opinion is also upheld by Scamoni (1977) but data collected from a French experiment (Ferrand and Bastien, 1985) is not in agreement with these results. At age 26, the hybrids retained not only their absolute but also their relative superiority in volume production over the parental species.

There is at present no clear answer to the question of a durable superiority over time of the hybrid over its parents. This uncertainty, however, points to urgent need for proper experimental designs for long-term observations. Nevertheless, without taking into consideration other possible advantages of the hybrid, it seems clear that a faster initial growth rate with a consequently shorter rotation and a hypothetical final higher total wood production should be sufficient to justify a hybridization program for larch.

Another question for which no relevant information has been presented so far concerns heterotic stability over a range of environments. Most of the results presented in Tables I and II are from experiments on one site only. It would be necessary to test for genotype X environment interaction to define conditions in which hybrid superiority occurs and to interpret its causes (combination of characteristics, hybrid habitat). Several examples in the forestry literature illustrate this problem. Hyun's results on poplar hybridization (Hyun, 1974) show that the hybrids tested show heterosis only in certain specific environmental conditions. Inter-provenance hybridization work with Norway spruce in Sweden also indicated that the hybrid (between Central European and Swedish populations) was superior in growth to both parents only at the latitudes of the northern parent. This was attributed to the combination of better growth ability of the southern parent with the frost hardiness of the northern parent (Nilsson, 1974). Similar behavior could also be observed in larch hybrids including *Larix siberica* (Nilsson, 1959). On the other hand, several studies can be cited in which no relationship between heterosis and environmental quality could be found (Owino and Zobel, 1977; Roman-Amat, 1984).

As suggested by Keiding (1962), part of the superiority of hybrid larch could be explained by its greater drought resistance and in general by its higher degree of "fitness". Its advantage over the parental species would therefore "show up more clearly under more adverse conditions in respect of climate and site". Experiments on a range of sites currently being undertaken in France by INRA will hopefully answer some of the questions.

The continuing superiority of hybrids due to "heterosis" over several generations has received little attention in forestry. Depending on which factors determined heterosis, reduction in hybrid vigor (if the cause was dominance or overdominance) or continuation of vigor (combinations of genes with additive effects, hybrid habitat) in the F_2 and following generations can be expected (Wright, 1976). Epistasis might, however, modify the reduction in vigor. A greater variability in the F_2 compared to the F_1 material can be expected. However, in a study with *Pinus rigida* X *taeda*, Hyun (1976) noted no significantly different performance in the F_2 compared to the F_1 generation and no significant increase in variability. Similar observations have been reported by Nikles (1981) for other species. The result led Hyun (1976) to recommend use of F_2 generation material (wind pollinated progeny from F_1 plantations) for commercial plantations of this pine hybrid in lowland regions of South Korea.

The growth of F_2 generation material of hybrid larch has not been well documented although F_2 seedlings are widely used in Scotland. Difficulties encountered in the production of F_1 generation reproductive material on a commercial scale necessitate this option. Rohmeder and Schonbach (1959) found "that F_2 and backcross hybrids of Japanese X European larch grew vigorously but did not possess the same degree of hybrid vigor as F_1 hybrids" (cited from Wright, 1976). Other examples have been given by Vincent and Fer (1965) and Lacaze and Birot (1974). Although they compare F_1 and F_2 progenies derived in a different fashion, it is interesting to note that F_2 progenies still show superiority over the pure parental species but to a lesser degree than the F_1 progenies and show a comparable variability.

The greater uniformity of the F_1 generation progeny over the parental progenies has also been recognized as an advantage in favor of hybrids. This was the main conclusion drawn by Lacaze and Birot (1974) where the F_1 hybrid larch progeny tested was characterized by a remarkable homogeneity for most of the traits studied. Similar conclusions were drawn by Ferrand (1986) for height measured at the nursery stage, but more recent observations on the same hybrid families indicate that this conclusion should be modified with respect to hybrid formula and characteristics. Reck (1977) found a similar situation amongst both the most homogeneous and the most heterogeneous families. Selection and breeding for uniformity of growth do not have the same degree of importance as in crop breeding, since thinning is a common practice in commercial forestry. Nevertheless, breeding for uniformity could be of importance in areas with a low stocking intensity type of forestry. For other economic traits such as wood quality, homogeneity would constitute a definite improvement.

Hybrid larch and hybridization programs

Tree improvement programs for larch benefit from several characteristics inherent in the *Larix* genus. Among those which are of special interest to the tree breeder are its great potential for inter–species crossability (no major barriers), its relatively precocious (10 yr) ability to produce abundant flowering, its monoecious character, its suitability for vegetative propagation, and the ease of its establishment in plantations.

Growth traits, stem and crown habits (basal sweep, stem straightness, branching habits), wood quality, and pest resistance (*e.g.,* larch canker) are the main selection criteria. Wide soil adaptability and growth uniformity are also of importance.

A great deal of genetic variability exists for these traits in larch. Recent results from 2 international European larch provenance experiments (Lacaze and Birot, 1974; Schober, 1985, 1987) have stressed the importance of the choice of seed origin for reforestation. Amongst the most promising for cultivation at low elevations are origins from the Sudetan mountains (280-620 m), Central Poland (150-650 m), and some northeastern Austrian alpine origins. The first two are favored for their growth capacity and canker resistance, while the third shows excellent stem form.

Japanese larch also shows variability but no particular recommendation as regards origin has been made. Fast juvenile growth and high resistance to larch canker are two of its most valuable characteristics. Experiments with other larch species have usually been limited in Europe to arboreta. Potential advantages through hybridization could be obtained from crosses with *Larix sibirica* for cold resistance (Nilsson, 1959) and with *Larix laricina* for its presumably good adaptation to wet soils (Ferrand, 1986).

Interest in hybridization lies in 3 main areas : first, heterosis for a given characteristic; second, combination of traits leading, for example, to better adaptation (*e.g.,* growth and drought resistance), including those traits which might be negatively associated through linkage or pleiotropy; and lastly, transfer of a favorable characteristic, (*e.g.,* pest resistance) from one population to another, where it might have been lacking. A higher degree of fitness of the hybrids and uniformity can also be considered important properties (Keiding, 1962).

Most of the work on larch inter-specific hybridization presented in the literature describes heterotic success obtained from mainly random crossing of individuals, and its early evaluation through sexual or vegetative propagation. A short-term breeding strategy using early tests might give rapid and substantial gains (Table II, with the previously-noted reservations). In this way, INRA is testing in France some 600 hybrid families over a range of potential sites for larch. Preliminary results indicate that there are several families with juvenile growth rates comparable to other vigorous species such as Douglas fir and an apparent wide soil adaptability.

Rational use of the parental populations and their evaluation through hybridization as described above will depend on basic knowledge of gene action for the characteristics used in selection. Management of the F_1 hybrid generation as a breeding population and its possibly successful exploitation through F_2 generation also depends on these genetic properties. Systematic studies of general and specific combining abilities of the genetic material for the main traits of interest, through well designed multisite experiments will be necessary to determine the relative proportion of dominance to additivity of the traits, their level of inheritance and correlations, and their stability over time and space.

There would appear to be no such studies for larch. It is, however, currently assumed but without any rigorous proof that "heterosis" for growth traits is unpredictable unless specific crosses are made, suggesting they would depend on non-additive gene action (Keiding, 1980; Reck, 1977; Vincent and Machanicek, 1972). Nilsson's conclusions (1959) suggest, however, that the action may be predominantly additive. Stem form, on the other hand, would depend on additive effect according to Keiding (1980). No information is available for other traits.

A strategy using complete or partial factorial designs with or without reciprocal crosses would be recommended. The size of the breeding populations (hundreds of trees) and their structure (as mentioned above, at least 3 European larch populations are of interest to us) as well as technical constraints connected with artificial control pollination (*e.g.*, irregularity of flowering, flower damage by frost, non-matched flowering times, pollen conservation, low full seed set per cone) will definitely restrict the mating design to a manageable number of parents. A two-level diallel (Hinkelmann, 1974) or better suited to our purposes, a nested population diallel or factorial mating design such as that used by Park and Gerhold (1986) in a Scotch pine inter-population hybridization study seem promising. These designs could give valuable preliminary information on combining abilities and heterosis at both family and population levels. Moreover, some important trends on intra-specific hybridization potential could also be obtained. A restricted selection of widely contrasting parents (*e.g.*, 5) per population, so as to avoid any *a priori* elimination of individuals, except those which are canker-susceptible, would be recommended.

According to the mode of gene action, alternative strategies have been proposed for the development of hybridization programs, and in particular to take advantage of heterosis (Namkoong, 1979; Falconer, 1981). When much of the genetic variance is additive for the traits selected, classical recurrent selection should be most efficient. Selection could occur either in the parental populations prior to hybridization, used in this case for trait combinations or transfer, or after hybridization in the F_1 generation or most likely a combination of both levels. When non-additive gene action effects prevails, inbreeding–outcrossing methods could be more efficient than selection methods without inbreeding.

Investigations on inbreeding–outcrossing possibilities in larch hybridization have been conducted in Denmark by Keiding (1968). His results, based on a limited number of crossings between two non-inbred European larch parents and a few number of first-generation selfed (S1) parents of Japanese larch, show that non-negligible supplementary gains (5–10%) and uniformity for total height can be obtained in this manner compared to normal (no selfing) inter-specific crossing. However, this approach requires extensive and systematic progeny testing.

However, inbreeding of larch through self-pollination is usually expressed by severe deleterious effects such as reduction of full seed set, low seed germination, high mortality, reduced vigor, crooked growth, lack of apical dominance and reduced fertility (Dieckert, 1964) though some progenies show remarkable uniformity and contain some fast-growing trees. Development of the technique requires continuous inbreeding over several generations to increase genetic divergence between parental populations. Selfing up to the third generation (S3) has proved to be possible with Douglas fir (Orr-Ewing, 1976); but this is a rather unique example in forestry. Its feasibility with larch beyond the second generation of selfing is not known so far.

The Reciprocal Recurrent Selection (RRS) strategy has been little used in forest tree breeding but was recommended by Conkle (1970) and Hyun (1976) for pine hybridization. Its efficiency for tree breeding is not known, but promising results with maize have been obtained (Moll and Stuber, 1971; Eberhart, 1977).

The RRS strategy combines several advantages which might be compatible with a general larch improvement program, as long as heterosis exists and is connected with non-additive gene effects. The advantages are the following :

– Development of crosses with high specific combining abilities; at each generation, high performance specific crosses can be selected and regenerated for commercial forest application. F_1 progenies may be conserved for a further possible exploitation in F_2 generation.

– Parental species populations are maintained separately and are simultaneously genetically improved. This aspect is particularly important, as individual species and the hybrid have their own interest, and separate individual programs might not be developed because of limited budgets and facilities. Intra-species selection performed in this manner might not be as efficient as classical recurrent selection in each species, as illustrated by Moll and Stuber (1971) with maize.

– Inbreeding deleterious effects due to selfing are avoided.

– Inbreeding depression of intra-species population crosses does not reduce gain in the hybrid product (Namkoong, 1979) though control of inbreeding level is recommended if continuous progress in parental species populations is to be achieved.

– An important gain in time is obtained, since before release of selected hybrid material is made, an extra-generation for selfing is not required as for the inbreeding-outcrossing strategy.

However, irrespective of the strategy selected, biological constraints such as the large number of crosses which must be made and tested and unpredictable flowering mean that improvement cycles will be long (as with many other forest tree improvement programs). Early flower induction and development of reliable juvenile tests — especially for early detection of heterosis — could be very rewarding in shortening generation intervals.

Hybrid larch and its commercial utilization

Selected hybrids can be prepared for commercial utilization through mass propagation by either sexual or vegetative methods. To take maximum advantage of non-additive effects, bi-clonal orchards using parents which show a high degree of specific combining ability should be used. Direct vegetative multiplication of specific crosses themselves can be used as an alternative, especially when there is a shortage of seed.

Both methods are feasible and have already been adopted by several breeding programs. Yet, to use them efficiently and to determine their place in breeding strategies first requires clear responses to several important questions. The objective of this chapter is not to make a complete review of the literature on these two topics as much of the work, especially on vegetative propagation, is not published and is evolving rapidly, but to give an overview of the general question that tree breeders are faced with.

Sexual mass propagation

Bi- or pauci-clonal orchards have been planted in most European countries with varying success (Keiding, 1970, Steinmetz *et al.*, 1987; Nanson, personal communication). Failures are mainly attributed to frost damage of strobili (Ferrand, 1988), to irregular flowering, and most of all to general non-overlapping phenology between European and Japanese larch (Mitchell, 1958) resulting in a low proportion of true hybrid seed. Low number of full seed per cone is also a major handicap.

Poor results have been recorded in France with a hybridization orchard, which has been successful in Denmark. Separation of the two parent clones in different orchards, mechanical pollen collection in one and mass-supplemental pollination in the other, is a solution that is currently being tested in France (Steinmetz *et al.*, 1987). Selection of parents with matching phenology could be another solution in the absence of any bad correlations with economic traits, and in particular with heterosis.

With the hypothesis that the hybrid X *eurolepis* and its reciprocal X *leptoeuropea* are equivalent in terms of general perfomance, one question remains on the respective role of both parental species as male or female genitors in the orchard. No general answer can be formulated. A precise knowledge of the individual clones phenology and their ability to produce male and female gametes is required as well as their level of autosterility. A better understanding of the incompatibility barriers resulting in the observed low rate of full seed is also needed.

Use of F_2 generation material from selected F_1 generation hybrid plantations would be an economical way of getting around these problems as long as this solution meets selection objectives.

Vegetative propagation

Vegetative propagation by means of rooting cuttings has been attempted in several countries with variable results depending on clone identity, age and treatment of the stock plants and cultivation conditions (John, 1979; Mason, 1984; Cornu and Nanson, personal communication). Multiplication of young seedlings from selected hybrid families (bulk propagation) or of single individuals selected at a later stage are presented as alternative solutions (Bonnet-Masimbert *et al.*, 1987). No recommendation can be made as long as precise and concordant indications on genetic (*i.e.*, feasibility of very early selection of heterotic families, level of intra-family genetic variability, minimum requirement of genetic diversity in forest plantations), physiological (*i.e.*, influence of physiological age on rootability and cutting growth habit, rejuvenation opportunities), technical, and economic (*e.g.*, acceptable multiplication rates, size of clonal park) parameters are not known.

Conclusions

A hybridization strategy based on selecting outstanding crosses showing up in random matings amongst individuals might be suitable for short-term hybridization programs whose main objective is a quick release of hybrid material for reforestation. Such programs are under way in many European countries for inter-specific hybridization of larch.

Long-term improvement programs will require a better management of genetic resources including breeding within pure species populations. Several hybridization breeding strategies exist. It is not possible to recommend any single strategy since there is still a lack of basic genetic information. Initially studies of hybrid behavior in long-term, multisite, well designed experiments with appropriate parental references should be established. These would investigate the role of heterosis in actual hybrid growth superiority, conditions of its manifestation, and its stability over sites and time. Choice of an adequate mating design (for example a nested population factorial) should give precise indications on inheritance patterns.

Inter-specific hybridization of larch might be interesting even in the absence of heterosis but this consideration does not preclude preliminary research on genetic parameters.

There are a number of options available for the mass propagation of selected hybrids, and given the present state of our knowledge none, even use of F_2 generation material, can be rejected.

In many cases, economic considerations will be a limiting factor and any progress in reducing the generation interval through early flower stimulation and development of juvenile tests for heterotic response coupled with quick vegetative propagation should be given the highest priority.

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