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Rootstock effects on growth, reproduction and wood properties in hybrid larch (*Larix x eurolepis* Henry) and in some other *Larix* sp. grafting associations

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Abstract

Key message When grafting is used in breeding, the choice of the rootstock should not be underestimated. Its impact on grafted individuals can be either beneficial for reducing tree size or enhancing flowering such as in seed orchards or detrimental if it is a source of bias in clonal testing. This is demonstrated in an experimentation with *Larix* where the impact of grafting on the same or a different species rootstock is studied on several traits.

Context Grafting is heavily used by forest tree breeders to vegetatively propagate clones for establishment of clonal archives and seed orchards but also for clonal testing. Although of high importance in fruit trees and vines breeding, the selection of rootstocks in forest trees has drawn little attention.

Aims Our objective was to test the relative impact of rootstock and scion selection with contrasted characteristics on the performance of grafted trees.

Methods We performed three grafting experiments with larch (*Larix* sp.) combining either rootstocks and scions of the same species but with contrasted characteristics (high and low vigour and flowering capacity) or rootstocks and scions of the same and different species (homo- and hetero-plastic grafting). The performances of these combinations were monitored for over 10 years and compared for growth, wood properties, reproduction and some other traits.

Results The scion strongly affected performance but, in most cases, there was no significant interaction between scion and rootstock. Rootstock effects depended on the trait under consideration and the type of grafting. The choice of rootstock had little effect on wood properties. In case of homo-grafting, some significant rootstock effects were observed for growth although these effects were much weaker than those of scion and their relative weight decreased over time, making their practical importance minor. Notably, the mean performance of the grafted trees was unaffected by the vigour of the rootstocks or by their flowering capacities. In addition, the performance of individual clones was unaffected by the choice of clonal rootstock. Rootstocks had no significant effect on reproduction, whatever their vigour or flowering capacity. Flowering abundance was maximised when using scions from heavy flowering clones. When testing for different species grafting associations, the choice of rootstock had significant effects on multiple traits: hybrid larch rootstocks outperformed Japanese larch for growth traits but the latter

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yielded slightly but significantly delayed flushing and superior stem straightness. Additionally, European larch rootstocks led to heavier flowering than Japanese ones.

Conclusion The choice of the grafting type should be governed by breeders' objectives. Hetero-grafting should be preferred in cases where modification of traits such as tree size or production of flowers and cones is desired, as in seed orchard management. Conversely, no positive or negative impact on traits is wanted when evaluating genotype values for purposes such as clonal testing. In such cases, homo-grafting should be preferred to limit bias due to grafting.

Keywords Vegetative propagation, Rootstock-scion interaction, Seed orchard, Clonal testing, Diallel grafting design, Breeding, Homo-/hetero-plastic grafting

1 Introduction

Although grafted plants are commonly used in the cultivation of fruit trees and grapevines, grafting is not used as a mass-propagation tool for reforestation because of its cost. However, grafting and propagation by cutting are common practices in forest tree breeding to obtain genetically identical copies of trees. Grafting has a unique advantage over propagation by cutting because it allows multiplication of adult trees, thereby avoiding problems linked to loss of juvenility such as reduced rooting ability and plagiotropism (Mason 1984; Morgenstern et al. 1984). Consequently, grafting has become a preferred method for establishing clonal archives and clonal seed orchards. Indeed, grafting of adult trees usually accelerates flowering and fructification (Zobel and Talbert 1984) much more efficiently than the use of rooted cuttings and seedlings.

Vegetative propagation is also useful for genetic studies and breeding programmes to precisely estimate the genetic values of a set of genotypes and capture their full genetic variability. For most coniferous species, the only other way to evaluate adult trees is via progeny testing, which only gives access to the additive component (GCA: general combining ability) of the total genetic variance. Several authors have identified high correlations between clonal values and GCAs (e.g. Muranty et al. 1998; Partanen et al. 2011), making clonal testing particularly attractive for shortening breeding cycles because it avoids the sexual reproduction phase requested for progeny testing. Moreover, for species that are not readily amenable to vegetative propagation by cutting or that undergo rapid physiological ageing such as *Larix* (Peer and Greenwood 2001), grafting can be the only efficient way to establish clonal trials for adult trees and also for more juvenile specimens.

In contrast to the situation with fruit trees and vines, where it is well established that careful selection of the (inter-) rootstock is vital for optimal propagation of a variety (Warschefsky et al. 2016), the selection of rootstocks in forest trees has drawn little attention. However, there are at least two major exceptions. First, rootstock-scion compatibility is a general pre-requisite and has proven to be critical in species such as Douglas fir (Copes 1974, 1983; Darikova et al. 2011), for which 'universal' compatible rootstocks have been selected (Copes 1999). Secondly, the systematic use of an easily identifiable alternative species as rootstocks (exemplified by the use of Japanese larch rootstocks in European larch seed orchards) facilitates seed orchard management and secures the integrity of their base material against graft rejection. In other cases, rootstocks of forest trees are typically chosen only for their relative homogeneity, as noted by Jayawickrama et al. (1991).

An extensive body of research on fruit trees and vegetables (Giorgi et al. 2005; Soar et al. 2006; Warschefsky et al. 2016) has demonstrated the many benefits of grafting on appropriate rootstocks, which include improved control over scion development, earlier and more abundant flowering and fructification, improved product quality, and greater resistance to both pathogens and certain abiotic stresses. Several authors have postulated that similar benefits might be achievable in forest tree breeding. In seed orchards and clonal banks, the aims of grafting could be similar to those for fruit trees, namely to induce precocity in flowering, to stimulate both male and female flowering and fructification, and perhaps to enhance fruit/seed quality (e.g. Schmidtling 1983; Melchior 1987; Climent et al. 1997). Alternatively, the aim might be to limit tree size (e.g. Melchior 1987) to grant easier access to cones or fruits, or to facilitate orchard management (for example, by reducing the need for pruning) as suggested by Haines and Simpson (1994). A third objective could be to improve the adaptation of grafted trees to specific environmental conditions (e.g. Nitikin 1963; Monteuuis and Barnéoud 1991). In contrast, when grafting is used in clonal testing the aim is to minimise the influence of the rootstocks on scion growth and behaviour to avoid biasing estimates of clonal values; the absence of rootstock/scion interactions is important to guarantee stable ranking of clones.

Unfortunately, rootstock/scions interactions are complex (Goldschmidt 2014) and many contradictory findings have been reported in this area as demonstrated in the review of forest tree grafting by Jayawickrama et al. (1991). Effects are largely species-dependent but for any given species the rootstock's impact on scion behaviour also depends on several factors including its hetero-plasticity (or lack thereof) with respect to the scion (Bachiller 1990; Climent et al. 1997; Kita et al. 2018), its genetic origin (Hollis et al. 1979; Melchior 1987; Copes 1999), its age (Copes 1987; Perez et al. 2007, Greenwood et al. 2010) and its size (Greenwood et al. 2010). Literature results show that rootstock/scion interactions may or may not influence grafted plants' growth and behaviour for commonly studied traits including survival, growth, architecture, reproduction, disease resistance and wood properties (Jayawickrama et al. 1991).

The selection of appropriate rootstocks is thus a vital issue in forest tree breeding and there is a need to better estimate rootstock-scion interactions. Unfortunately, as shown by Jayawickrama et al. (1991), previously reported grafting studies on forest trees have several limitations including limited ambition of experimentation (few rootstocks/scions tested, short assessment duration) and the use of phenotypically/genetically un-characterised rootstocks.

To address these issues, a grafting plan was designed to investigate the reciprocal effects of hybrid larch (European × Japanese larch) scions and rootstocks and their interactions, addressing traits relevant to growth, wood properties and flowering. In a second set of trials, we investigated the impact of using another species as rootstocks. This paper presents the results of these experiments and seeks to answer three questions: (i) can we improve flowering management in larch (*Larix* sp.) seed orchards by selecting rootstocks that enhance reproduction and enable control over seed tree size?, (ii) are grafted plants adapted to clonal testing? and (iii) under what conditions should the same (homo-plastic grafting) or a different species for rootstock be preferred for grafting?

2 Material and methods

2.1 Experimental trials

2.1.1 Diallel grafting experimentation (homo-plastic grafting) (trial 1)

For this study, twelve clones of hybrid larch (*Larix x eurolepis* Henry) were selected from a clonal trial planted with 2-year-old rooted cuttings at Eclaches (Lat. 45°44′N, Long. 2°41′E, 1000 m a.s.l.) in 1984. Four classes of clones were selected representing high and low levels of vigour (denoted V and v, respectively) and male and female flowering capacity (denoted F and f, respectively). The selection criteria were total height at age 8 and observations of male and female flowering in 3 successive years. Flowering selection criteria included the proportion of ramets per clone bearing male and female flowers and the abundance of male and female flowers based on a subjective scoring system.

The 12 clones were vegetatively propagated by cutting in April 1992. Twigs were collected from a stock plant archive at INRAE-Orléans nursery. Rooted cuttings were grown for 4 years before serving as rootstocks. In March 1996, the 12 clones were side-grafted onto the same 12 clones following a full 12×12-diallel grafting design including self-grafting (Table 1). Out of 144 possible grafting combinations, 138 were successful.

Table 1 12×12 clone grafting plan: number of replicates per combination (trial 1)

Scion		10067	10071	10088	10091	10073	10078	10075	10077	10081	10108	10087	10111
Rootstock		**vf**[a]	**vf**	**vf**	**vf**	**vF**	**vF**	**VF**	**VF**	**VF**	**VF**	**Vf**	**Vf**
10067	**Vf**	0	0	1	2	1	3	0	0	2	0	1	0
10071	**Vf**	4	4	4	4	4	4	4	4	4	4	4	4
10088	**Vf**	4	3	4	3	3	4	4	4	4	3	4	4
10091	**Vf**	3	4	4	4	3	4	3	4	4	4	4	4
10073	**vF**	4	3	4	4	3	4	3	4	4	4	3	4
10078	**vF**	1	4	4	4	4	4	4	4	4	4	4	4
10075	**VF**	3	4	4	4	4	2	4	4	4	4	4	3
10077	**VF**	2	4	4	4	4	2	4	3	1	3	3	2
10081	**VF**	3	4	4	4	3	4	4	4	4	4	4	4
10108	**VF**	4	2	4	4	2	4	2	4	4	4	4	4
10087	**Vf**	4	4	3	4	4	4	4	4	4	4	4	4
10111	**Vf**	4	4	4	4	4	4	3	4	4	3	4	4

[a] v, V refers to vigour (low and high) based on total height at age 8 in the Eclaches trial/f, F refers to flowering capacity (low and high) based on average flowering score for 3 successive years of observations in the Eclaches trial

The grafted plants were field-planted in Beaumont-du-Lac (Lat. 45°45′N, Long. 01°50′E, 570 m a.s.l.) during the winter of 1997–1998. Plantation was conducted using an incomplete randomised block design with 8 blocks, single-tree plots, a maximum of 4 replicates per combination (rootstock/scion) and a spacing of 4×4 m.

2.1.2 Grafting experimentation with other species associations ('hetero-plastic grafting')

Impact on flowering (trial 2) Fifteen clones of hybrid larch (*Larix x eurolepis* Henry) chosen at random from our clonal bank were grafted onto 2-year-old seedlings in the spring of 1992. Rootstocks were produced from two commercial varieties, one of European larch (EL = 'Alsace' seed stand of alpine origin) and one of Japanese larch (JL = 'Hokkaido'). On average, 5 ramets were obtained per clone and rootstock. Trees were planted 1 year later at INRA nursery (Orléans) following a complete randomised block design (5 blocks; single-tree plots; spacing 3×3 m).

Impact on growth and wood properties (trial 3) Scions from 152 full-sib families of European (EL: 21), Japanese (JL: 44) and hybrid (HL: 87) larch, each represented by 12 individuals, were collected in an intra-/inter-specific diallel mating design trial (St-Saud, see Marchal et al. 2017 for details) in the winter of 2002. They were side-grafted on 2-year-old rootstocks from two species: Japanese larch (origin: 'Nagano Prefecture') and hybrid larch (origin: 'Les Barres' F_1-hybridisation seed orchard). Grafted trees were planted at 3×2.5 m spacing at Béchadergue, Peyrat-Le-Château (Lat. 45°49′N, Long. 1°44′E, 461 m a.s.l.) in early 2004. Trees were distributed according to an incomplete randomised block design with 44 blocks and three-tree linear row plots; each clone × rootstock combination was represented by 3 trees (1 on JL and 2 on HL rootstocks) planted in the same row plot. In total, 3598 trees were evaluated.

2.2 Observations and measurements

2.2.1 Diallel grafting experiment (trial 1)

Four observations of flowering were conducted in March on all trees, 6, 7, 10 and 12 years after grafting. Female catkins were counted in the first two assessments but subsequently became too abundant so a 4-grade scoring system was introduced (0: no flower, 1: 1–10 flowers, 2: 10–100 flowers and 3: > 100 flowers). Male flowers have been numerous since the first observation, so male flowering was scored as follows: 0: no flowers, 1 = up to 30 male strobili, 2 = 30–100 male strobili and 3: > 100 male strobili. A survey at age 10 revealed no flowering.

Total height (HT) was assessed regularly from age 4 to 10 after grafting. BH girth (C) was measured twice at age 10 and 18. Stem volume (V) was estimated from girth as described by Thill and Palm (1984). Pilodyn needle penetration (Pil) was recorded during winter at age 18 (at 1.3 m, over bark, same direction, 2–3 hits/tree). During the same winter, 5 mm diametrical increment cores were collected through the pith, axially sawn into 2 mm-thick radial boards, conditioned at room temperature and X-rayed for microdensitometry analysis (Polge 1966). Windendro® was used to obtain density profiles. Several home-made R scripts were used to delineate and date annual rings as well as early- and latewood, and then to compute annual ring parameters including ring width (RW), early- and latewood ring sizes (EW, LW), overall ring density (De) and early- and latewood density (DEW, DLW). Annual BH girths were reconstructed from the calculated annual ring widths assuming circular trunk areas and stable bark thickness. Microdensitometry profiles were also used to delineate heartwood from sapwood (based on the reduced earlywood density of sapwood), sometimes with support from colour differentiation observed directly on wood boards when the first criterion could not be used. The radial length and proportion of heartwood (HW and %HW, respectively) over the whole radius were then computed.

2.2.2 Grafting associations experiments

Impact on flowering (trial 2) Flowering was assessed each year up to 10 years after grafting by counting male and female strobili.

Impact on growth (trial 3) Growth was monitored regularly throughout this trial, but in this study we focus only on the measurements made 13 years after grafting and the bud flushing data obtained at age 6. The assessed traits included survival rate, bud flushing, total height and BH girth, stem straightness, drought crack frequency, heartwood proportion and overall wood density. Straightness was assessed using a subjective scoring scale ranging from 1 (heavily crooked) to 5 (straight). Terminal bud flushing was characterised by two operators working independently using a scoring scale ranging from 1 (dormant) to 5 (start of elongation). Survival and drought crack were recorded as binomial variables (0/1: alive/dead; 0/1: without/with crack). Ring parameters and heartwood size were determined by analysing increment cores collected at age 13 during winter as described above.

Access to the data The data and metadata description are available (Pâques 2024).

2.3 Statistical analysis

2.3.1 Diallel grafting experimentation (trial 1)

A first set of analyses tested clonal rootstock and scion effects and their interaction. Univariate analyses were based on a single-trait individual-tree linear mixed model with replicates as fixed effects and rootstock and scion clones as random effects; a spline-spatial random effect was added to account for micro-environmental effects. Residual maximum likelihood (REML, Patterson and Thompson 1971) was used to estimate the variance components for the random effects by using the function remlf90 in the R-package breedR (Muñoz and Sanchez 2020).

The impact of using different clonal rootstocks to evaluate clonal values was evaluated by comparing means with a Dunnett test using auto-grafts as controls. We hypothesise that self-grafting has a negligible effect on clonal performance even if we anticipate some trauma from grafting.

A second set of analysis used a similar model but tested for potential effects of rootstock and scion vigour and flowering capacity based on the vigour and flowering classes specified above. The means of four rootstock/scion groups (V/V, V/v, v/V, v/v and F/F, F/f, f/F, f/f) were compared using Tukey's test.

For flowering traits based on scores or numbering, chi-squared tests were used to test for effects of clonal vigour or flowering capacity.

2.3.2 Grafting associations experiments

In trial 2, pairwise *t*-tests were used to compare mean clonal numbers of flowers between the two rootstock species (R Core Team 2020).

In trial 3, raw data were first spatially adjusted for micro-environmental effects using the R-package breedR (Muñoz and Sanchez 2020). Analysis of variance was then used to test for significant scion and rootstock effects and their interaction. This was followed by pairwise comparisons between rootstock species using estimated marginal means (R Core Team 2020).

For binomial data (mortality, drought crack), a generalised linear model with a logistic function (R Core Team 2020) was used to test block, scion, rootstock and interaction effects.

3 Results

3.1 Trial 1: diallel grafting experimentation (homo-plastic grafting)

Although the site at Beaumont (trial 1) can be considered a low fertility site with high soil drainage, it is well adapted to hybrid larch because of regular rain across the growing season: survival was over 96% and individual tree volume up to 7 cm was slightly below half a cubic metre 18 years after grafting (Table 2).

3.1.1 Relative importance of rootstock and scion clonal effects on growth

Highly significant differences were observed between scion clones for all growth and growth-related traits (Fig. 1). Differences between rootstock clones were also present for all radial growth-related traits but not for total height, with lower levels of significance. The rootstock-scion interaction was not significant for height, girth or latewood size but did reach significance for the other growth traits. The rootstock effect never exceeded 4% of the total variance (0.4–3.9%) while the scion effect accounted for 7.7 to 43.8% of the total, being most influential on the proportion of latewood and total height. For

Table 2 Mean performance values in the diallel grafting trial (trial 1) 18 years after grafting

Traits	Codes	Units	Mean	Min	Max	CV (%)
Height[a]	HT	m	8.9	2.9	11.1	12.0
BH girth	C	cm	75.2	38.0	114.5	13.4
Heartwood radius	HW	cm	72.9	22.8	139.5	22.7
Heartwood proportion	%HW	%	68.4	36.8	86.6	10.9
Ring width	RW	mm	8.3	4.5	13.4	14.8
Earlywood width	EW	mm	6.7	3.6	11.6	15.9
Latewood width	LW	mm	1.6	0.7	2.8	19.5
Proportion of latewood	%LW	%	19.5	13.1	31.5	14.3
Pilodyn penetration	Pil	mm	29.5	22.5	35	7.0
Density	De	kg/m^3	386	294	478	6.3
Earlywood density	DEW	kg/m^3	301	213	387	7.0
Latewood density	DLW	kg/m^3	735	618	837	4.8

[a] Measured 10 years after grafting

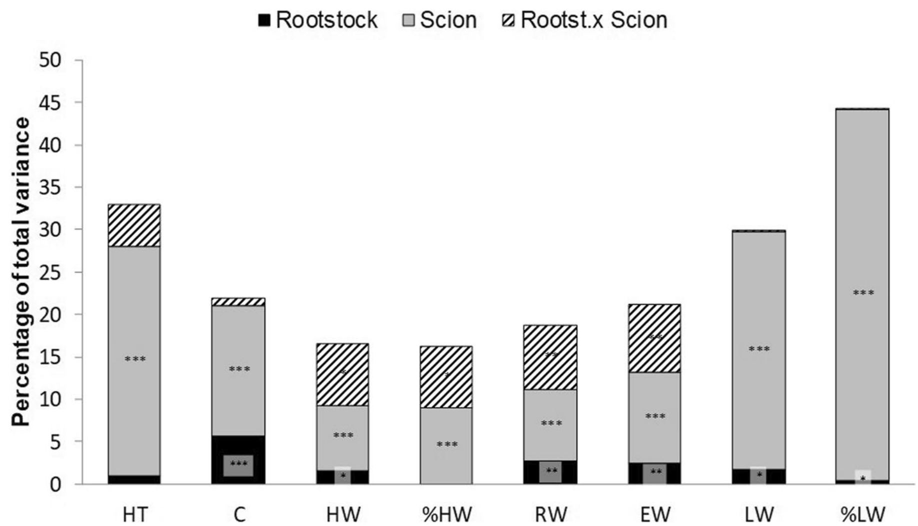

Fig. 1 Contributions of the rootstock, the scion and their interaction to the total variance in growth-related traits at Beaumont (trial 1, 10 years after grafting for HT; 18 years for other traits) (see Table 2 for the meaning of codes; *, **, *** = significant at the $p = 0.05$, 0.01 and 0.001 levels)

traits showing significant interaction effects, their contribution to the total variance was slightly less than that of scions.

The rootstock/scion effects clearly changed over time (Fig. 2). For total height, the rootstock and rootstock × scion effects remained stable over time but the scion effect increased steadily to over 25% of the total variance. For BH girth, all effects were more stable up to age 15 but the contribution of the scion always outweighed that of the rootstock and rootstock × scion interaction. Moreover, scion effects became substantially stronger with increasing age while rootstock × scion effects became weaker.

3.1.2 Relative importance of rootstock and scion clonal effects on wood properties

Scion was the only factor with significant effects on wood density and related traits (Fig. 3), accounting for over 40% of the total variance in wood density and pilodyn and 20% for other density components. The rootstock and rootstock × scion interaction contributions were negligible, accounting for less than 1.6% of the total variance.

3.1.3 Effect of rootstock vigour and flowering capacity on growth and wood properties of grafted material

The comparison of fast-growing (V) and slow-growing (v) rootstocks revealed that rootstock vigour had no

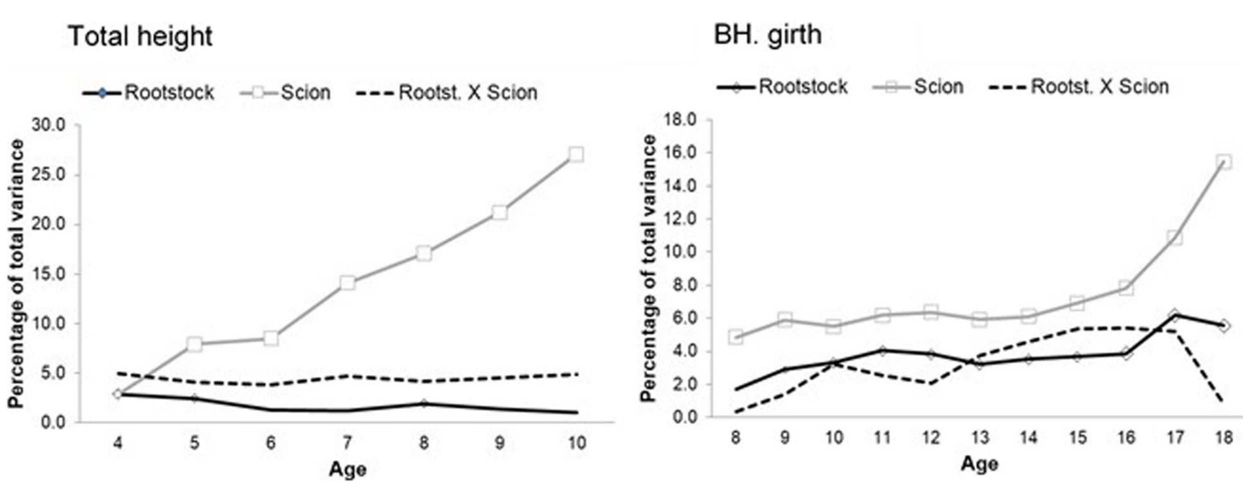

Fig. 2 Evolution of the contributions of rootstock, scion and their interaction to the total variance in the total height (left) and BH girth (right) in trial 1 over time. The size of the dots indicates the level of significance (no dot = not significant; small to large = significant for $p < 0.05$ to 0.001)

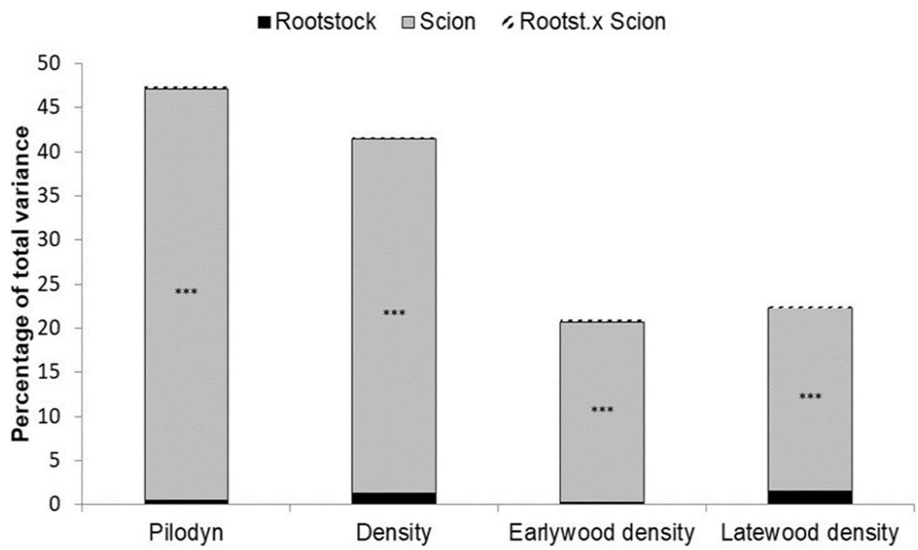

Fig. 3 Components of the total variance in wood density traits (trial 1, 18 years after grafting) (*, **, *** = significant at $p = 0.05$, 0.01 and 0.001 levels)

significant effect on traits other than mean annual ring width and latewood percentage at age 18, and its effect was always negligible relative to that of scion vigour (Table 3a). As shown in Fig. 4a, the performance of the different rootstock/scion vigour combinations always decreased in the order V/V > v/V > V/v > v/v.

Similarly, the comparison of high and low flowering capacity rootstocks (F and f, respectively) revealed no significant effect on any wood property other than pilodyn, for which the differences between the two flowering capacity classes were on the order of a few tenths of a millimetre (Table 3b). The effect of scion flowering capacity was generally much weaker than that of scion vigour, but was nevertheless important for several traits including height, latewood width and overall density. The rootstock/scion combinations with the highest scion flowering capacity (F/F and f/F) grew smaller and produced a slightly less dense wood with less latewood than the combinations with low scion flowering capacity (f/f and F/f; see Fig. 4b).

3.1.4 *Comparison of clonal performances using various rootstock clones and self-grafting*

The mean performances of the self-grafted clones were interpreted as their clonal values and used as references for Dunnett tests to compare their performance when grafted onto other clonal rootstocks. For every studied trait, no rootstock gave significantly better or worse results than self-grafted clones. Figure 5 illustrates this result for total height.

3.1.5 *Effect of clonal characteristics on flowering of grafted material*

At age 6, very few trees bore either male or female flowers (Fig. 6). One year later, all trees produced male flowers (albeit in limited quantities: 92.6% of trees had fewer than 30 flowers), but 94.2% of them displayed no female strobili. No flowering was observed in 2005 at age 10. Two years later at age 12, all trees produced male catkins quite abundantly and 90% of them had some female flowers albeit still in rather low quantities.

As shown in Table 4, neither the vigour nor the flowering capacity of the rootstock, separately or jointly, significantly affected male and female flowering with one exception: the use of a high vigour rootstock with low flowering capacity increased female flower abundance 12 years after grafting by around 10% compared to other combinations. Scion flowering capacity had the strongest effect on flowering, especially at early ages. High-flowering scions of low vigour (vF) tended to produce more trees with female flowers than other combinations: 19% more at age 7 and 7.3% more at age 12 (Fig. 7) when compared to the combinations with the lowest flowering at the same ages (vf and Vf, respectively). Vigour and flowering characteristics of both rootstocks and scions had no or little impact on flowering at age 12.

3.2 Trials 2 and 3: impact of grafting associations with other Larix species

3.2.1 *Flowering (trial 2)*

Flowering (both male and female) started 5 years after grafting onto rootstocks of both species. On average,

Table 3 Variance components (expressed as % of total variance) of the rootstock, scion and their interaction based on the analysis of 4 groups of rootstock/scion combinations: (a) clonal vigour classes (V/V, V/v, v/V and v/v) and (b) flowering capacity (F/F, F/f, f/F and f/f) (trial 1; age 18 for all traits except HT: age 10) (see Table 2 for explanation of codes)

(a) Vigour												
	Height	**Girth**	**Heartwood radius**	**Heartwood proportion**	**Ring width**	**Earlywood width**	**Latewood width**	**Latewood proportion**	**Pilodyn**	**Density**	**Earlywood density**	**Latewood density**
	HT	**C**	**HW**	**%HW**	**RW**	**EW**	**LW**	**%LW**	**Pil**	**De**	**DEW**	**DLW**
Rootstock	0.37 ns	1.97*	1.12*	0.004 ns	1.40*	0.97 ns	1.23*	0.01 ns	0.01 ns	0.64 ns	0.16 ns	0.33 ns
Scion	12.29***	4.22***	6.81***	3.40***	2.55**	1.01 ns	6.67***	4.87***	13.80***	6.98***	1.81*	4.39***
Rootst. x scion	0.01 ns	0.01 ns	0.01 ns	0.01 ns	0.01 ns	0.01 ns	0.01 ns	0.015 ns	0.01 ns	0.01 ns	0.01 ns	0.01 ns
Residual	87.33	93.80	92.06	96.59	96.04	98.02	92.10	95.12	86.18	92.38	98.03	95.26
(b) Flowering capacity												
	Height	**Girth**	**Heartwood radius**	**Heartwood proportion**	**Ring width**	**Earlywood width**	**Latewood width**	**Latewood proportion**	**Pilodyn**	**Density**	**Earlywood density**	**Latewood density**
	HT	**C**	**HW**	**%HW**	**RW**	**EW**	**LW**	**%LW**	**Pil**	**De**	**DEW**	**DLW**
Rootstock	0.83 ns	0.73 ns	1.20*	0.00 ns	0.45 ns	0.48 ns	0.01 ns	0.01 ns	2.37**	0.98 ns	0.72 ns	1.14 ns
Scion	3.31**	0.67 ns	0.34 ns	0.00 ns	1.46*	0.00 ns	12.26***	10.37***	0.62 ns	6.77***	0.28 ns	2.10 ns
Rootst. x scion	0.26 ns	0.01 ns	0.01 ns	0.00 ns	0.01 ns	0.00 ns	0.01 ns	0.01 ns	0.01 ns	0.01 ns	0.01 ns	0.01 ns
Residual	95.61	98.59	98.45	100.00 ns	98.08	99.51	87.72	89.62	97.00	92.24	99.0	96.75

*, **, *** = significant at $p = 0.05$, 0.01 and 0.001 levels

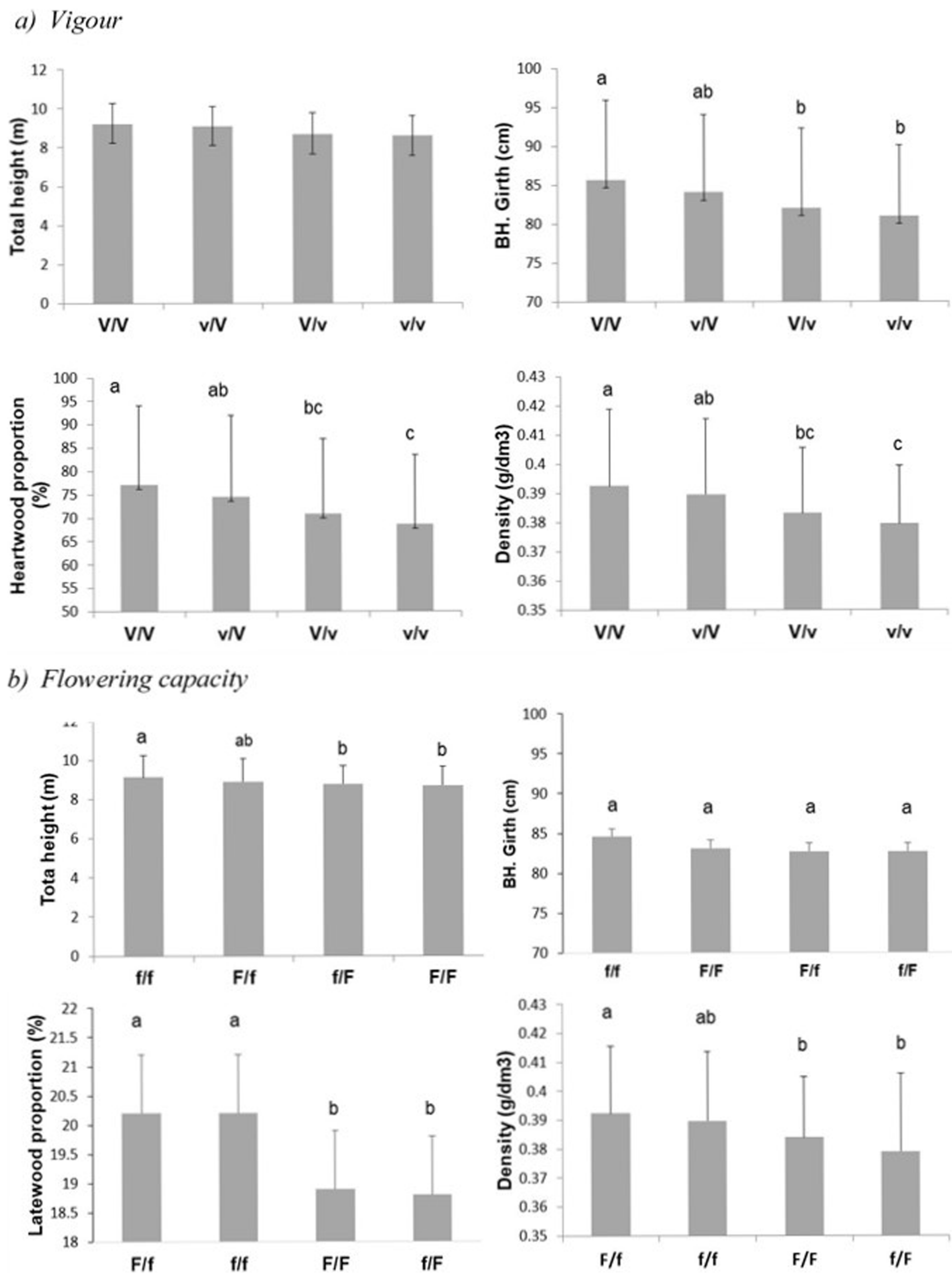

Fig. 4 Impact of rootstock and scion vigour (**a**) and flowering capacity (**b**) on selected traits (trial 1, age 18 except for HT, age 10). For both rootstocks and scions (rootstock/scion), V and v denote high and low vigour; F and f denote heavy and low flowering. Different letters indicate significant differences between rootstock/scion combination ($p \leq 0.05$)

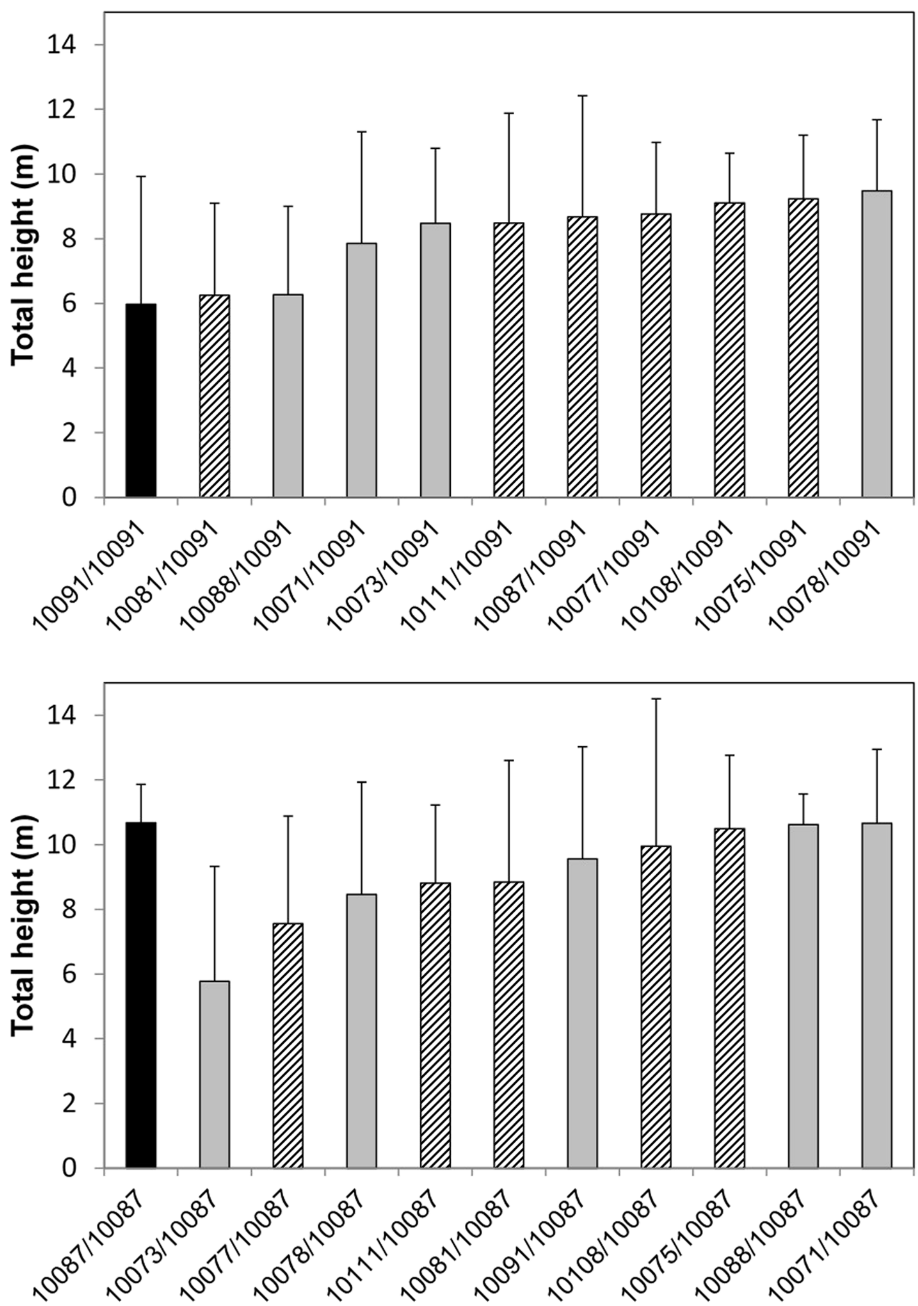

Fig. 5 Example of the mean performance of the poorest (10091) and best (10087) clones with respect to total height (trial 1, age 10) when self-grafted and when grafted onto other clonal rootstocks. Clone 10067 not included due to its low representation in the diallel design (black bar = self-grafted; dashed = grafting on high vigour (V) clones; light grey = grafting on low vigour (v) clones)

yearly flowering was higher on EL rootstocks than on JL ones (Fig. 8) but this difference was significant only once for female flowering (at age 6) and twice for male flowering (at ages 6 and 7). Over the full 10 years of observations, flowering on EL rootstocks was significantly higher than on JL, with scores of 41,455 ± 457 vs 34,445 ± 520 for male flowers (t-test p value = 0.014) and 10,410 ± 408 vs 6473 ± 333 for female flowers (t-test p value = 0.025). A modest scion × rootstock interaction was also observed: around 3–4 of the 15 hybrid clones produced more female and male flowers on JL rootstocks than on EL rootstocks.

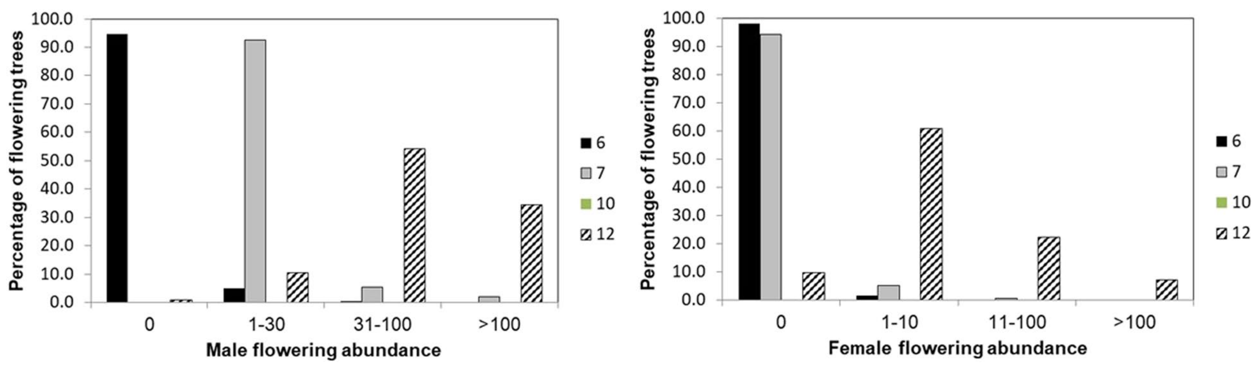

Fig. 6 Male (left) and female (right) flowering as a function of age (years), evaluated in terms of the percentage of trees bearing flowers (trial 1)

Table 4 Chi^2 test for the effects of rootstock or scion characteristics (V vs v, F vs f and their combination: VF, Vf, vF and vf) on male and female flowering at age 7 and 12 (trial 1)

Characteristics	Effects of	Age 7		Age 12	
		Male	Female	Male	Female
Vigour	Rootstock	1.12 ($p = 0.57$)	2.70 ($p = 0.269$)	2.56 ($p = 0.46$)	4.05 ($p = 0.26$)
	Scion	***7.81 (p = 0.02)***	1.66 ($p = 0.44$)	4.00 ($p = 0.26$)	1.25 ($p = 0.74$)
Flowering	Rootstock	1.656 ($p = 0.44$)	0.02 ($p = 0.99$)	4.18 ($p = 0.24$)	1.58 ($p = 0.67$)
	Scion	***28.09 (p < 0.001)***	***19.03 (p < 0.001)***	4.93 ($p = 0.18$)	1.70 ($p = 0.64$)
Vigour and flowering	Rootstock	4.95 ($p = 0.55$)	6.86 ($p = 0.33$)	15.70 ($p = 0.07$)	***22.41 (p = 0.01)***
	Scion	***64.5 (p < 0.001)***	***94.42 (p < 0.001)***	***28.06 (p = 0.001)***	13.32 ($p = 0.26$)

Figures in bold when effect significant at $p < 0.05$

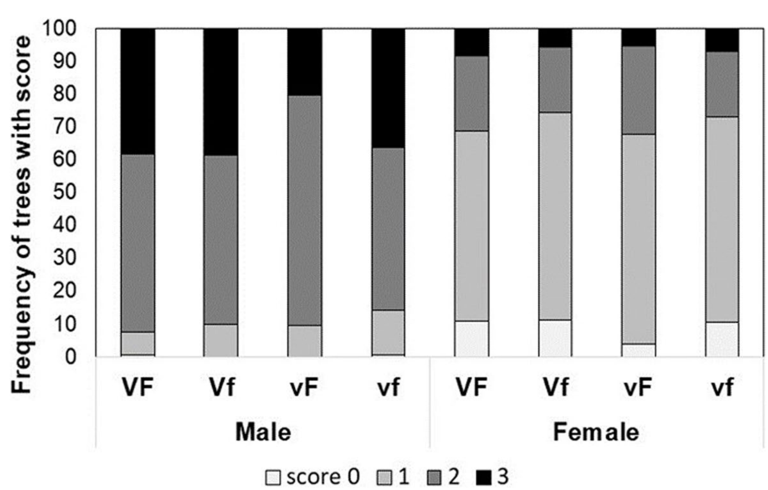

Fig. 7 Combined effect of clonal high (F) vs low (f) scion flowering capacity and high (V) vs low (v) scion vigour on male and female flowering (trial 1; age 12) (scoring scale: male: 0 = no flower/1 = 1–30/2 = 30–100/3 = > 100; female: 0 = no flower/1 = 1–10/2 = 10–100/3 = > 100)

3.2.2 Survival, flushing, growth and wood properties (trial 3)

Scion species had a significant effect on mortality (chi^2 test p value = 0.008) but no such effect was detected for the rootstock species or its interaction with the scion (Table 5). A similar result was obtained for the proportion of stems exhibiting drought cracking. Trees with HL scions had slightly lower mortality but a higher frequency of stems with cracks. Trees with JL scion on the reverse showed much less cracks whatever the rootstock used.

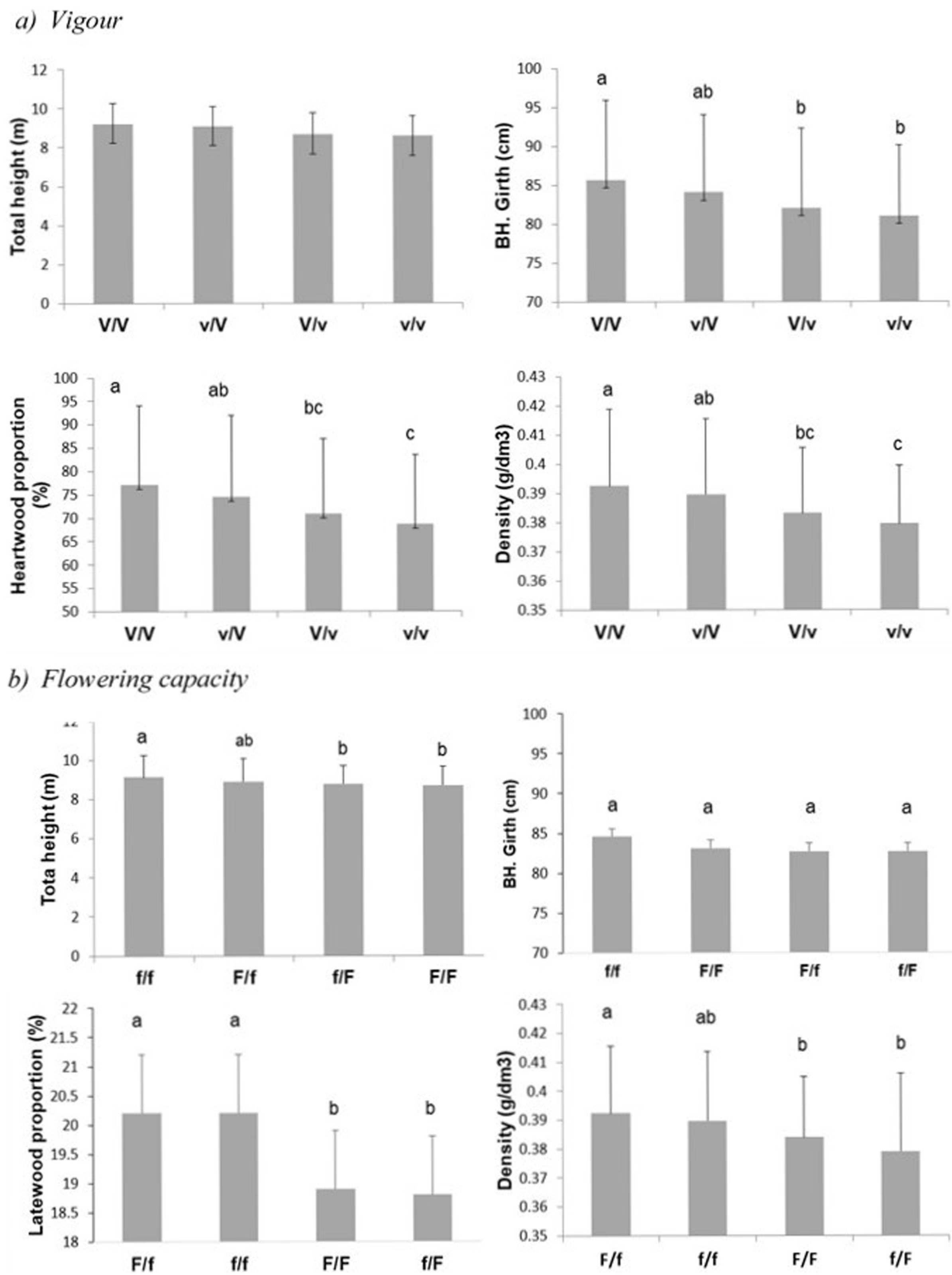

Fig. 8 Overall cumulated number of male (left) and female (right) flowers on European (EL) and Japanese (JL) larch rootstocks (trial 2)

Table 5 Rootstock/scion combination effects on the proportion of dead trees and trees with cracks. *p* values were determined using the chi2 test (trial 3, age 13 after grafting)

Combination rootst./scion	Mortality rate (%)	Drought crack (%)
HL/EL	18.8	25.1
JL/EL	22.0	18.3
HL/JL	21.4	5.6
JL/JL	17.0	5.1
HL/HL	17.3	24.9
JL/HL	14.9	26.1
p scion	***0.008***	***< 0.001***
p rootstock	0.09	0.923
p interaction	0.202	0.318

Figures in bold when differences are significant at $p < 0.05$

For terminal bud flushing 6 years after grafting, both the scion and the rootstock species had a significant effect (p values ≤ 0.001) but their interaction did not. Bud flushing was slightly more advanced in Japanese (score 2.9 ± 0.7) than in European (2.7 ± 0.7) or hybrid larches (2.6 ± 0.7). However, Japanese larch rootstocks tended to delay flushing (2.6 ± 0.7) when compared to hybrid larch (2.8 ± 0.7; p values < 0.001).

Both scion and rootstock species had a significant effect on stem straightness (p value < 0.001) with no significant interaction: Japanese larch had the straightest stems (score 4.0 ± 0.9), followed by European (3.9 ± 0.9) and then hybrid larches (3.6 ± 1.2). Japanese larch rootstocks tended to give better stem form than hybrid larch but the difference was negligible (3.8 vs 3.7).

Both scion species and rootstock had a significant effect (p value < 0.001) on growth traits but their interaction did not: growth was systematically and significantly improved when clones were grafted on hybrid larch (Table 6). For example, height was increased by between 4 and almost 8% on HL rootstocks compared to JL rootstocks and by 14 to over 16% for BH girth.

The results obtained for wood properties were trait-dependent. Both scion and rootstock choice had significant effects on latewood and heartwood proportions ($p < 0.001$) with no interaction. For latewood, the scion effect outweighed the rootstock effect but the opposite was true for heartwood. Trees grafted on Japanese larch rootstocks produced more latewood than on hybrid larch, but the reverse was again true for heartwood (Table 6). For overall wood density (and earlywood density; data not shown), only the scion had a significant effect ($p < 0.001$). For latewood density (data not shown), hybrid larch rootstocks gave a slightly denser wood.

4 Discussion

Grafting is a valuable vegetative propagation technique that has been used for many years in forestry breeding, mostly for clonal archive and seed orchard establishment but sometimes also for genetic evaluation (clonal testing). Knowledge of the potential for rootstock to modify tree structure and development is crucial in

Table 6 (a) Mean growth performances and (b) wood properties of EL, JL and HL clones when grafted onto JL and HL rootstocks (trial 3, age 13)

(**a**)

Combination rootst./scion	Height (cm)			BH girth (mm)			Ring width (mm)		
	Mean	SD	p.adj	Mean	SD	p.adj	Mean	SD	p.adj
HL/EL	1089.6	9.9		390.9	5.7		6.22	0.14	
JL/EL	1010.5	14.9	***1.07E – 05***	338.5	8.6	***3.54E – 07***	5.40	0.23	***0.0026***
HL/JL	1228.4	7.1		544.1	4.1		8.69	0.11	
JL/JL	1180.0	9.7	***5.82E – 05***	479.3	5.5	***1.05E – 20***	7.62	0.13	***0.0000***
HL/HL	1319.5	5.9		533.4	3.4		8.65	0.09	
JL/HL	1241.3	8.4	***2.88E – 14***	459.2	4.8	***5.86E – 36***	7.38	0.12	***0.0000***

(**b**)

Combination rootst./scion	Latewood proportion (%)			Density (kg/m^3)			Heartwood proportion (%)		
	Mean	SD	p.adj	Mean	SD	p.adj	Mean	SD	p.adj
HL/EL	20.6	0.4		405.4	2.9		50.8	1.0	
JL/EL	21.3	0.6	0.2925	399.1	5.3	0.2980	48.0	1.7	0.1592
HL/JL	16.8	0.3		383.8	2.3		59.0	0.8	
JL/JL	17.8	0.4	***0.0252***	387.4	2.9	0.3363	55.5	0.1	***0.0056***
HL/HL	18.2	0.2		396.4	1.9		57.1	0.6	
JL/HL	19.5	0.3	***0.0010***	402.2	2.6	0.0709	54.3	0.9	***0.0113***

Figures in bold when significant differences at $p < 0.05$

these contexts—modification could be beneficial in seed orchards if it improves desirable traits (e.g. survival, fructification) and/or facilitates orchard management (e.g. by increasing compatibility or reducing tree size). Conversely, modification is detrimental when conducting genetic evaluations because it may introduce bias through improvement or reduction of performances of grafted trees.

Trees grown from grafts are not equivalent to seedlings because their development is influenced by the close interaction (and/or complementarity) between rootstock and scion, including their differences in juvenility. Unfortunately, little is known about the physiological mechanisms underpinning grafted trees development as noted by Jayawickrama et al. (1991). We hypothesised that the use of rootstocks with specific characteristics (e.g. high vigour and/or flowering capacity) could affect the characteristics of the grafted trees. To evaluate these potential rootstock effects, we tested both homo- and hetero-plastic grafting on the basis that using a rootstock and scion from genetically distant species might stimulate beneficial complementary interactions. Accordingly, the forestry literature to date indicates that the rootstock effects achieved using hetero-plastic grafting (Schmidtling 1983; Climent et al. 1997; Darikova et al. 2013) are stronger than those for homo-plastic grafting (Haines and Simpson 1994; Jayawickrama et al. 1997).

Our study confirms that the impact of rootstock choice on grafted tree performance depends on whether the scion and rootstock are of the same or different species and also on the trait under consideration. However, some trends common to both homo- and hetero-plastic grafting were observed. In particular, highly significant scion effects were observed for all studied traits, whereas rootstock × scion interactions had no significant effects on any traits for hetero-plastic grafting and on most traits for homo-plastic grafting. These findings are consistent with previous reports (Haines and Simpson 1994; Jayawickrama et al. 1997) emphasising the role of scions and the lack of significant rootstock × scion interaction effects (ibidem, Sniezko 1986).

4.1 Growth traits

Significant rootstock effects were detected for all growth traits when using homo-plastic grafting, but their magnitude was small compared to the scion effects and declined over time. Consequently, no matter what trait was considered, the mean performance of individual clones (i.e. self-grafted trees) did not differ significantly from that seen when a scion of the same clone was grafted onto any of the 10 other clonal rootstocks included in the experiment. In addition, grafting onto a high vigour or high flowering capacity rootstock did not improve the growth performance of the studied clones when compared to grafting onto a low vigour or low flowering capacity rootstock. On average, the faster growing groups of trees were always those obtained by grafting with vigourous scions: growth performance decreased in the order V/V > v/V > V/v > v/v. However, scions with high intrinsic flowering capacity showed a slight (but mostly not significant) tendency to reduce growth performance, which decreased in the order f/f > F/f > f/F > F/F. This may suggest the existence of some growth-reproduction trade-off. Jayawickrama et al. (1997) sought to identify loblolly pine rootstocks that would reduce tree height in seed orchards but failed because rootstock choice had no effect in this case. Similarly, Haines and Simpson (1994) found that the impact of rootstock choice on height growth was much smaller than the scion effect in Caribbean pine.

Conversely, when associating different species for rootstock and scion, the choice of rootstock had a significant effect: trees grafted on hybrid larch rootstocks grew faster than those grafted on either European or Japanese larches. In parallel, hybrid larch rootstocks increased the size and proportion of heartwood, which was expected since heartwood development is directly linked to radial growth in *Larix* (Pâques 2001). Rootstock choice also affected some additional traits: hybrid larch rootstocks slightly advanced bud flushing and decreased stem form quality compared to Japanese larch. Well-known characteristics of hybrid larch (rapid growth (Greenwood et al. 2015; Marchal et al. 2017), early flushing (Pâques 2009)) as well as traits induced by rapid growth (e.g. high crookedness and large heartwood size) all appear to be 'transmissible' via grafting to scions of either European or Japanese larches. Such beneficial combination of advantageous complementary traits has previously been demonstrated by Han et al. (2018) in intergeneric grafting of Salicaceae (*Populus cathayana* on *Salix rehderiana* rootstocks) to enhance growth and drought resistance.

Hetero-plastic grafting obviously modifies growth as already shown in previous studies (Schmidtling 1983; Climent et al. 1997; Marchal et al. 2017; Kita et al. 2018), but also, some related morphological traits such as number of branches and needle length.

4.2 Wood properties

Rootstock choice had no significant effect on any of the studied wood properties no matter what type of grafting or species was used. The only exception was for the proportion of latewood. However, as for all other wood properties, the scion effect was much stronger.

To our best knowledge, very few published studies have explored the effects of grafting on wood properties. One of them (Anonymous 1963; cited by

Jayawickrama et al. 1991) found that in slash pine the wood specific gravity and tracheid length of scions were independent of the same traits in the rootstock. Marchal et al. (2017) studied the material used in trial 3 and showed that rootstock choice had little effect on wood density in hetero-plastic grafted trees.

Although a negative relationship between vigour and wood density is classically found in conifers (Pâques 2013), the use of fast-growing rootstocks (V) did not reduce wood density when compared to slow-growing alternatives (v) even when the rootstock and scion species differed (HL vs JL). Wood density (i.e. the dry matter weight per unit volume) is the result of a combination of processes: tracheid size through cell elongation and tracheid wall thickening through lignification. The finding that ring width (and thus volume) gain was at least partially rootstock-dependent suggests that scions may have strong effects not only on radial growth but also on cell wall deposition.

4.3 Flowering

As with growth traits, homo- and hetero-grafting had contrasting effects on male and female flowering. Rootstock vigour and flowering capacity had no significant effect on flowering when hybrid larch was grafted onto hybrid larch. The scion effect was determinant in this case; the best combinations for flower production used scions with a high flowering capacity (F). This confirms the findings of Hamaya et al. (1989) in their study on *Larix gmelinii*. Conversely, hetero-plastic grafts of hybrid larch onto European larch rootstocks produced more male and female flowers than grafts onto Japanese larch.

These findings are consistent with the contrasting results obtained on the one hand by Schmidtling (1983) and Climent et al. (1997), who observed strong rootstock effects on flower and/or cone production for hetero-plastic grafts, and on the other hand by Jayawickrama et al. (1997) who observed only weak rootstock effects in homo-plastic grafting of loblolly pine.

5 Conclusion

5.1 Homo-plastic grafting or hetero-plastic grafting?

Both types of grafting (homo- vs hetero-plastic) are equally efficient for vegetative propagation of forest trees: in *Larix*, the rate of successful grafting is the same whatever the species used. Nevertheless, as shown in this study, rootstock choice can have very important impacts on grafted tree performance depending on whether the rootstock species is the same as that of the scion or not. Careful rootstock selection may thus be important depending on the goals of the grafting programme.

For orchard management, hetero-plastic grafting should be preferred; the use of differing rootstock and scion species appears beneficial when seeking to enhance flowering (EL vs JL) or modify growth (HL vs JL). However, this should be avoided when performing genotype evaluations in clonal trials if the rootstock is susceptible to significantly modify performances as shown by hetero-plastic grafting. To avoid bias in genetic evaluation, homo-plastic grafting should be preferred. Even when using differing genotypes (for example, the high/low vigour and flowering capacity rootstocks examined in this work), the rootstock impact is low. Nevertheless ideally, a unique rootstock clone should be used in this context.

Little is known about rootstock-scion interactions in forest trees. Our results show that a deeper understanding of the physiological mechanisms underpinning such rootstock interactions is needed to more reliably guide rootstock selection for breeding issues.

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Authors' contributions
This research was achieved by L.E. Pâques from the conceptualisation of the experimentation, the analysis of data, up to the final writing of the manuscript.

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Data availability
The datasets analysed during the current study are available from recherche.gouv.data dataverse (https://doi.org/10.57745/WIJ60K).

Declarations

Competing interests
The authors declare that they have no conflict of interest.

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