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GRAFTING IN CONIFERS: A REVIEW

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Abstract

Grafting is one of the vegetative propagation methods most commonly used worldwide to preserve genotypes and increase germplasm production. The method involves the insertion of a scion from one individual plant into a rootstock from another individual to form a single plant. It has been widely used in fruit trees and hardwoods, but much less so in conifers. Grafted trees are used to establish asexual seed orchards for producing forest germplasm and thus yield genetically improved seed on a large scale. Sprouting processes (callus formation) in the grafted plant are affected by several factors, the most important of which are the technique used, grafting season, phenological and physiological state of the scion and the rootstock, taxonomic affinity between the organs, age of buds and rootstocks, microclimatic conditions of the site where the grafts are maintained, and genetic, anatomical and histological differences between the grafted organs. On the other hand, graft incompatibility can be caused by extrinsic or intrinsic factors. Grafting is also used to rejuvenate mature trees (upper buds), and it is possible to shorten the process by applying growth promoting hormones. Good results have been achieved with conifers in grafting tests conducted in the United States and some parts of Europe and Asia; however, successful grafting and survival of conifer grafted rootstocks have not yet been achieved in Latin American countries.

Key words: Vegetative propagation, Conifer grafts, Asexual seed orchards, Forest genetic resources, Compatibility-incompatibility of grafts.

Introduction

Forest genetic resources are socially, scientifically, environmentally and economically important worldwide. About 31% of the earth's surface is covered by forests, of which 93% are natural and 7% are planted forests. The total number of tree species in the world is between 80,000 and 100,000, representing 12% of the total biodiversity on earth (FAO, 2014). The growing demand for forest products, as well as changes in forest land use and the effects of climate change have led to forest degradation (Chidumayo & Gumbo, 2013) and to an increase in timber deficit in some countries, such as the US, where wood imports have had to be increased (Fiedler *et al*., 2001). The appropriate use of forest genetic resources will help preserve, improve and propagate species of high commercial value, providing the industry with the timber resources it requires (Neale & Kremer, 2011; Vargas *et al*., 2013; FAO, 2014; Burney *et al*., 2015).

Grafting is the union of two plant organs, a scion, bud or plectrum (aerial part) and a rootstock (underground part), which continue to grow, thus generating a single plant (Gil *et al*., 1986; Iglesias *et al*., 1999). Some authors believe that grafting has been used for more than 3,400 years and that it was practiced by Eurasian peoples (mainly in Mesopotamia), as well as by the ancient Hebrews; however, the existing evidence is unclear (Mudge *et al*., 2009). Nevertheless, the first documented evidence of the use of grafting techniques dates back more than 2,000 years in China, mainly involving species of importance for producing fruit; a large body of literature shows that successful grafting was achieved in some species (González, 2004).

Propagating forest species through grafts enables the preservation of desirable genotypes of high commercial or ecological value; likewise, forest diversity can be maintained and loss of genetic variety can be prevented or reduced (Zobel & Talbert, 1984; Vargas *et al*., 2004). Pike *et al*., (2018) pointed out the importance of identifying superior individuals that are resistant to attack by pests and diseases, and of propagating such individuals by grafting. Once the scions of the superior individuals are grafted, it is possible to establish asexual seed orchards (ASOs) (Matziris, 2000; Koskela *et al*., 2014). ASOs can be used to preserve genotypes and produce high quality seed (Wright, 1976; Zobel & Talbert, 1984; Matziris, 2000; Vargas *et al*., 2004), thus enhancing the success of reforestation programs and commercial forest plantations, as successful establishment of plantations will help mitigate the degradation of natural forests (Fiedler *et al*., 2001; Martínez & Prieto, 2011; Aparicio-Rentería *et al*., 2013; Thompson *et al*., 2014). The first large-scale study of conifer grafting was carried out in Corsica in 1820 (Jayawickrama *et al*., 1991). However, the establishment of ASOs by grafting conifers for breeding programs did not acquire great importance until the late 1940s in Sweden (Lindgren *et al*., 2008).

Information about the intrinsic and extrinsic factors that influence graft survival in conifers is scarce (Gil *et al*., 1986; Jayawickrama *et al*., 1991; González, 2004). The objectives of the present study were therefore to review the documentary information on the development of grafting techniques in coniferous species and to report on the current use of these. The overall aim was thus to contribute to improving the propagation of clones of desirable conifers, especially the genus *Pinus*, which is one of the most important timber-producing groups worldwide (Martínez & Prieto, 2011; Vargas *et al*., 2013; Burney *et al*., 2015).

The following main topics related to coniferous grafting are addressed in this review article: grafting techniques, taxonomic and anatomical affinity of the organs used for grafting, age of the rootstock and scion, hydric and hormonal stress, effects of cellular and vascular structures (parenchyma, meristematic cells, cambial zone, resin channels, xylem and phloem), effects of temperature, greenhouse vs. non-greenhouse conditions, microenvironment of the graft zone, protection of the grafted area, fungi and possible diseases, prior treatment of the rootstock and scion, and care of the plants after grafting. Owing to the scarcity of information on the factors influencing the compatibility of grafted conifers, the present review also includes some reports on other gymnosperm and hardwood species, which may support future investigations on conifers.

Use of grafting to establish asexual seed orchards (ASOs) of the genus *Pinus:* Grafted trees are the main source of vegetative material used to establish ASOs of different forest species of interest, in which it is possible to carry out controlled pollination, with the aim of generating genetic gains in the progeny obtained through controlled crosses in the orchard (Nienstaedt, 1965; Zobel & Talbert, 1984; Jaquish, 2004). Likewise, ASOs can be used to produce seeds of species that only flower once in a while (Martín & González, 2000; Prieto & López, 2006; López *et al*., 2011).

Establishment of ASOs enables vegetative material of high genetic quality to be used as scions and thus produce grafts that may be converted into second generation orchards, or even more advanced generations (Medina *et al*., 2007). Three sources of different genotypes can be considered: 1) the parent tree from which the buds are collected for grafting to establish the first generation ASO; 2) the plants from the first generation ASO seeds that will be used as the rootstock and will serve to establish the second generation ASO; and 3) the bud used as the graft. It is also possible to reduce the time required for seed generation in second and later generation ASOs by applying appropriate methods (Lott *et al*., 2003; Medina, 2005).

ASOs can potentially be used as sources of seed in reforestation programs (Byram *et al*., 2001; Jaquish, 2004). In addition, ASOs are reservoirs of forest genotypes that can be used to gain greater control over the information and genetic composition of the clones included (Jaquish, 2004; Loo, 2004). However, a wide variation in fertility has been observed in several ASOs, and in some less than 50% of the clones are seed producers (Danbury, 1972; Schmidtling, 1983a). Cone production was observed in 94% of grafted *Pinus elliottii* Engelm. trees in an ASO established in Mississippi, during the first year of establishment (Gooding *et al*., 1999).

In addition to the above, it is important to establish ASOs in high quality sites, as it has been observed that *Pinus pinaster* Ait. seed produced in ASOs established in high quality sites in Spain was more likely to germinate than seed from poorer quality sites (Cendán *et al*., 2013).

Establishing ASOs of *Pinus caribaea* var. *hondurensis* (Sénéclauze) Barret and Golfari., *Pinus oocarpa* Schiede ex Schltdl. and *Pinus patula* Schiede ex Schltdl. *et* Cham. acquired great importance in the 1980s and 1990s in countries such as Brazil, Zimbabwe, Australia and Venezuela (Valera *et al*., 1992; Pottinger, 1994; Valera *et al*., 1997). Clones of *Pinus radiata* D. Don grown in ASOs established in Spain, New Zealand and Australia have shown great potential for genetic gain, as well as substantially increased seed production (Pascual *et al*., 2000; Baltunis & Brawner, 2010). Flowering was observed to be more intense in clones produced by heteroplastic (interspecific) grafts than in those produced by homoplastic (intraspecific) grafts in an ASO in Guadalajara (Spain) (Climent *et al*., 1997). However, flowering was much lower in clones of *Pinus contorta* var. *latifolia* Dougl. in an ASO than in trees of the species in natural stands (Wheeler *et al*., 1982). It has been suggested that for some pine species, the establishment of 20 ASO clones should be considered to optimize genetic gain and decrease the risk of self-fertilization (Lindgren & Prescher, 2005).

In Turkey, pollen production was lower in a *Pinus brutia* Ten. ASO than in *Pinus nigra* J.F. Arnold and *Pinus sylvestris* L. ASOs, and age was found to be an important factor in the variable pollen production, as the *P. brutia* ASO was the youngest ASO in the country (Bilir *et al*., 2002). On the other hand, seed production was higher in a *P. sylvestris* ASO in Turkey than in orchards of the same species established in Sweden (Sivacioğlu, 2010).

In several progeny trials with seed produced in a *Pinus halepensis* Mill. ASO in Greece, significant differences in the genetic gain between the different families involved in the germplasm production were observed (Matziris, 1998; Matziris, 2000). However, in Norway, plants produced with seed from an ASO were more susceptible to cold, and the mortality rate was higher than that of the plant produced with seed from natural stands (Johnsen, 1989).

Due to the low growth yields of plants produced from seed obtained in natural stands of *Pinus armandii* Franch., a genetic improvement program was implemented in China to establish ASOs by grafting (Wang, 2004). Furthermore, *Pinus koraiensis* Siebold & Zuccarini ASOs were successfully established in the north of China, North Korea and South Korea (Wang *et al*., 2000; Wang, 2004).

In Mexico, ASOs of the main commercial species, including *Pinus douglasiana* Martínez, *P. greggii* var. *australis*, *P. patula*, *P. arizonica* Engelm., *P. pseudostrobus* Lindl., *P. teocote* Schiede ex Schltdl., *Cedrela odorata* L., *Cupressus lusitanica* Mill., *Eucalyptus camaldulensis* Dehnh., *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg., *Jatropha platyphylla* Müll. Arg. and *Swietenia macrophylla* King., have been established (López *et al*., 2011; Rodríguez, 2013). However, despite attempts to establish dense ASOs with diverse families, the planting density of these orchards is often low due to high mortality during the grafting stage (Aparicio-Rentería *et al*., 2013); likewise, in general, it has not been possible to carry out the massive reproduction of improved forest germplasm (Aparicio-Rentería *et al*., 2013; Rodríguez, 2013).

In forest genetic improvement programs that involve establishing ASOs, action plans must be designed to mitigate any damage that may be caused by natural phenomena and to minimize loss of seed production. It is also necessary to design strategies to prevent, as far as possible, economic losses such as those incurred in Mississippi in 2005, when hurricane Katrina affected 12 ASOs in the region (Byram *et al*., 2005).

Grafting in conifers: Grafts and cuttings can be used to propagate superior conifer trees (Cuevas-Cruz *et al*., 2015). However, it is difficult to propagate conifers using shoots from superior mature trees selected in the field (Medina *et al*., 2007), and it is therefore preferable to use grafting techniques in breeding programs (Holst *et al*., 1956; Barnes, 1974).

The need to establish precise protocols has been highlighted in relation to achieving successful grafting in conifer species (Mencuccini *et al*., 2007). These authors identified several variables that affect graft survival of these species in the short term (less than two years), although the influence of these variables disappeared in the medium and long term (more than two years). The following variables are most commonly considered: quality of the rootstock, environmental conditions during grafting, post-graft cultural activities, hormonal conditions of the organs to be grafted before and after grafting, and the taxonomic and anatomical affinity between the scion and the rootstock (Holst, 1956; Ahlgren & Wilderness, 1972; Jayawickrama *et al*., 1991; Valdés *et al*., 2003a).

Grafting techniques: The grafting techniques most commonly used in conifer species are terminal fissuring and lateral plating (Staubach & Fins, 1988; Muñoz *et al*., 2013). Lateral plating consists of maintaining the complete rootstock and making a longitudinal cut where the scion is inserted (Fig. 1(a)). In the scion, a long cut (3 to 5 cm) is made at the end to be inserted (Fig. 1(b)); a smaller cut (approximately 0.5 cm) is subsequently made opposite to the first cut. The length of the cut on the rootstock should coincide with the length of the long cut of the bud being grafted. To make the graft union, both cuts are joined, so that the scion is held firmly on the rootstock. Once both parts are joined (Fig. 1(c)), the graft union is tied up with a rubber band and the area is then sealed with fungicide mixed with vinyl paint. In some studies, resin-based healing wax is used to seal the graft union (Fig. 1(d)) (Staubach & Fins, 1988; Muñoz *et al*., 2013; Pérez, 2016).

The terminal fissure technique, described by Staubach & Fins (1988), Muñoz *et al*., (2013) and Pérez (2016), involves making two longitudinal cuts parallel to the cambium on the opposite side of the scion (Fig. 2(a)). For preparation of the rootstock, a transverse cut is made in the cambium, eliminating the upper part of the stem, and a longitudinal (3 to 4 cm) is then made in the in the middle of the rootstock stem (Fig. 2(b)). As in the lateral plating graft, the graft union is secured with a rubber band, and sealed with vinyl and fungicide paint, to prevent contamination and attack by fungi in the grafted area (Fig. 2(c)). In some cases, the mooring is covered with Campeche wax during the grafting.

In some species of the genera *Pinus* and *Larix*, good results have been obtained with the terminal fissure grafting (Staubach & Fins, 1988; Gallardo & Gallardo, 1991; Ávila & Pompa, 2008). However, the lateral plating technique seems to be more successful with caespitose species of the genus *Pinus* (Pérez, 2016). In an experiment carried out in Scotland the lateral plating technique was successfully applied in homoplastic grafting (see section 4) of *Pinus sylvestris* (Vanderklein *et al*., 2007). In China, in trials with *Pinus koraiensis*, lateral plating was successfully used in homoplastic grafting, whereas the terminal fissure technique yielded better results in heteroplastic grafting of *Pinus ponderosa* Douglas Ex C. Lawson buds on *Pinus tabuliformis* Carr. rootstocks (Zhang & Tang, 2005; De-li *et al*., 2007).

Fig. 1. Lateral plating grafting process. (a) Preparation of the rootstock for grafting; (b) the cut bud used for grafting; (c) lateral plating graft assembly; (d) mooring of the graft and application of fungicide. Photos: Alberto Pérez Luna (2016).

Fig. 2. Terminal fissure graft process. (a) Preparation of bud for grafting; (b) preparation of rootstock for grafting; (c) assembling, tying and sealing the terminal fissure graft. Photos: Alberto Pérez Luna (2016).

Grafting adventitious buds has recently been used in Sweden with the genera *Abies* and *Pinus*. This technique involves grafting small buds of less than two years of age onto rootstocks of smaller diameter than necessary in grafts of lateral plating and terminal fissure (Hajek, 2008; Mahunu *et al*., 2010). Grafting adventitious buds enables multiple shoots to be inserted in the same rootstock, thus reducing the time until seed production in clones established in ASOs (Khattak *et al*., 2002; Pomper *et al*., 2009).

Physiological characteristics of the grafted organs

Taxonomic affinity: Grafting can be homoplastic or heteroplastic. In homoplastic grafting, the buds and rootstock used are from the same species and variety, while in heteroplastic grafting, they are from different species or even genera. The taxonomic affinity of the species used in heteroplastic grafting is an important factor to take into consideration, as the yield from this method tends to be lower than in homoplastic grafting (Ahlgren & Wilderness, 1972; Gil *et al*., 1986; Climent *et al*., 1997). Variable results have been obtained with heteroplastic grafting, with compatibility, semi-compatibility and incompatibility observed (Ahlgren & Wilderness, 1972; Climent *et al*., 1997), as with grafting buds of the genus *Pinus* onto rootstocks of *Abies balsamea* (L.) Mill. (Ahlgren & Wilderness, 1972). In a trial of grafts of *Pinus pinea* L. rootstocks with buds of *Cedrus libani* A. Rich., carried out in winter, survival was more than 50% (Barnes, 2005).

Good results were obtained for buds of *Cedrus atlantica* (Endl.) Manetti ex Carrière grafted on *Pinus strobus* L. rootstocks, thus compensating for the difficulty in using *Cedrus* rootstocks due to the deficient formation of root systems in this genus (Barnes, 2008). In a grafting study carried out in Guadalajara (Spain), *Pinus nigra* material was used as rootstock for heteroplastic and homoplastic grafting of *Pinus nigra* and *Pinus brutia*; homoplastic grafting yielded the best results (Climent *et al*., 1997). Mutke *et al*., (2003) reported the existence of a clone bank of homoplastic grafts of *Pinus pinea* in Valladolid (Spain). Scions of *Pinus patula* were successfully grafted on *Pinus douglasiana* and *Pinus pseudostrobus* rootstocks in Mexico, with better results than the *P. patula* / *P. douglasiana* combination (Villaseñor & Carrera, 1980).

Vigour and asepsis: An important factor to consider in grafting is the sanitary state and vigour of the buds used, because the grafted plants are more likely to survive if the material used is in optimal condition (Gil *et al*., 1986; Upchurch, 2009). Similarly, it is essential to use rootstocks with healthy and robust roots (Holst *et al*., 1956; White *et al*., 1983). The characteristics of the scion and the rootstock are important for grafting success, and it is therefore necessary to use vegetative material of good phenotypic quality (White *et al*., 1983; Melchior, 1984).

Age and origin of scion and rootstock: The age of the buds and rootstock plants are important for grafting success. For *Pinus radiata* and *P. arizonica*, better sprouting and survival results were obtained with rootstocks of less than two years of age (Moncaleán *et al*., 2006; Ávila & Pompa, 2008). On the other hand, Staubach & Fins (1988) successfully grafted buds of trees of a *Larix* species of approximate age 50 years. Furthermore, no significant differences in grafting success were observed with buds obtained from *P. sylvestris* trees of ages ranging from 36 to 269 years (Vanderklein *et al*., 2007). Good results have been obtained with buds from 6 to 12-year-old *Abies fraseri* (Pursh) Poir. trees (Hinesley *et al*., 2018) and with buds from 33-year-old *Araucaria angustifolia* (Bertol.) Kuntze trees (Gaspar *et al*., 2017).

The buds used for grafting must be obtained from superior trees, so that the grafted trees inherit high genetic gain in the future production of seeds in ASOs (Lott *et al*., 2003; Venturini & Lopez, 2010). Superior conifer trees are considered to be those of dominant height, straight stem, desirable natural pruning, small crown occupying less than one third of the total height, insertion of branches at an angle close to 90°, and with no damage caused by pests and diseases (Prieto & López, 2006). These types of characteristics are detected when the trees reach maturity, once the stems and branches clearly show their definitive physiognomy (Castellanos-Bolaños *et al*., 2008; EUROPARC-Spain, 2015).

Coniferous graft yield in different environmental and protection conditions

Environmental effects: In the processes of grafting specimens of the genus *Pinus*, some environmental factors cause low rates of sprouting and survival, and some intrinsic factors in the species can lead to incompatibility between the grafted organs (Cuevas, 2014).

Grafting can be carried out in winter, when the scion is dormant; this has the advantage that the scion remains turgid for a longer time after it is extracted from the parent tree. Grafting can also be carried out in summer, when the scion has resumed its vegetative activity; however, in some species the results are usually less effective than those obtained in winter (Gil *et al*., 1986; Salvo *et al*., 2013). For grafting *Araucaria angustifolia*, the best results were obtained with dormant scions (Gaspar *et al*., 2017).

At mean temperatures below 12°C, graft survival was 35% in *Pinus patula* (Aparicio-Rentería *et al*., 2013) and less than 5% in *P. leiophylla* Schiede ex Schltdl. *et* Cham. (Cuevas, 2014) and *P. durangensis* Martínez (Pérez, 2016). It is therefore advisable to carry out grafting trials at different times, to determine the optimum climatic conditions for each species (Aparicio-Rentería *et al*., 2013; Cuevas, 2014; Pérez, 2016). In the UK, experimental grafting of *Pinus sylvestris* was carried out by maintaining controlled conditions in the greenhouse, yielding good results (Mencuccini *et al*., 2005).

Grafting when daytime temperatures are below 24°C (and preferably when the night-time temperature is around 8°C) has been recommended to avoid breaking the dormancy state in the buds (Upchurch, 2009). In an early study, it was suggested that in the northern hemisphere grafting conifers was possible at any time of the year, although it was recognised that survival rates are highest in winter and spring (Nienstaedt, 1965).

In a grafting trial with *Pinus patula* in Mexico, better sprouting results and higher survival were obtained in the nursery than in the greenhouse, because of difficulties in maintaining a constant temperature inside the greenhouse (Villaseñor & Carrera, 1980). Unfortunately, no further information regarding the environmental effects was provided.

Protection of the graft union: In a grafting trial of *Pinus resinosa* Sol. Ex Aiton, four graft protection treatments were evaluated, along with a control (no protection): microclimate induced by polyethylene bags; protection with kraft paper bags; a combination of polyethylene microclimate and kraft paper bag; and protection with cardboard cylinders (Holst, 1956). The best results for grafting and graft survival were obtained with the combination of polyethylene bag microclimate and kraft paper protection, while protection with cardboard cylinders and control (no protection) yielded the lowest percentage of sprouting and survival. In an experimental grafting trial with *Pinus taeda* L., in Alabama (US), in which the graft (scion plus graft union) was entirely covered with paraffin as the only means of protection, the graft survival rate was 90%, and the technique was reported to be very economical (White *et al*., 1983).

Due to the high temperature generated inside the polythene bags used to protect the graft, contact between water and the regenerating area of the graft should be prevented when the plants are watered. Use of fungicides is also recommended to prevent proliferation of fungi in the grafted area (Ávila & Pompa, 2008; Bioforest, 2011; Muñoz *et al*., 2013). In addition to optimizing the grafting process, acclimatization of the grafted plants should also be optimized before the planting out, to help maximise survival of the clones in the final plantation site (Salvo *et al*., 2013).

Graft compatibility-incompatibility: In several studies, the clones died two to three years after grafting and even after establishment in the field. The genetic, technical and cultivation factors that cause this apparent late incompatibility in grafts must be determined (Valera *et al*., 1997; Güçlü, 2019). Graft incompatibility can be divided into localized and translocated incompatibility (Mosse, 1962). Localized incompatibility refers to the lack of coincidence (in size or taxonomy) between the grafted organs, while translocated incompatibility depends on factors not related to the characteristics of the scion or the rootstock and that are mainly caused by inadequate application of the grafting techniques. Localized incompatibility in *Pinus radiata* grafts in New Zealand was observed, with no coincidence between the cambium of the scion and the cambium of the rootstock during grafting, thus hindering graft healing (Sweet & Thulin, 1973). On the other hand, translocated incompatibility has been observed in several trials, due to phloem damage when the grafted organs are cut, causing their degeneration and short- and long-term graft mortality (Sweet & Thulin, 1973; Hartmann *et al*., 2002).

In a study carried out on eight-year-old *Pinus taeda* L. grafts, the number of strobili, number of cones produced and the height and normal diameter of the clones were related to variables such as the collection site of the buds, tree of origin and the trees used as rootstocks, and it was found that the yield of the grafts depended to a great extent on the site and tree of origin, while the rootstock was not as important for adaptation of the grafts (Jayawickrama *et al*., 1997). Genetic incompatibility between the buds and the rootstocks used for grafting *Araucaria cunninghamii* Aiton ex D. Don. was observed as the parent trees of the seed with which the rootstocks were produced and the donor trees of the buds to be grafted had different genetic loads (Dieters & Haines, 1991).

For grafting *Pinus taeda* with rootstocks of *Abies* spp. and *P. taeda*, the rootstock condition influenced the height growth and fecundity of the clones obtained, with better sprouting and survival obtained when the first genus was used as rootstock (Schmidtling & Scarbrough, 1970; Schmidtling, 1983b).

Compatibility due to the anatomy and histology of grafts: The anatomical and histological affinity of the organs to be grafted is an important factor that determines the compatibility or incompatibility of grafts (Barnett & Miller, 1994; Kankaya *et al*., 1999; Castro-Garibay *et al*., 2017; Pérez-Luna *et al*., 2019). The effect of the resin on the graft union has been analyzed in some studies, and various authors have stated that it only functions as a means of temporary fusion, which may protect against fungal attack and moisture loss (Noel, 1968; Tiedeman, 1989; Mahunu *et al*., 2012). The meristematic activity of the cambium (between the scion and the rootstock) has been considered an important factor in the success of grafting, and it has been suggested that the graft incompatibility may be due to deficient contact between the cambium of the grafted organs (Yeoman, 1984; Tiedemann, 1989; Hartmann *et al*., 2002). Parenchymal cells are formed at the moment of contact between the cambial zones of the rootstock tissues and the grafted bud, which is important for photosynthesis, nutrient reserve and protection of the xylem and phloem (Hartmann *et al*., 2010). Likewise, during callus formation, new xylem and phloem are formed, thus enabling the formation of vascular tissue that completely connects the grafted organs (Moore & Walker, 1981a, 1981b; Pina & Errea, 2005). Unfortunately, little is known about the effect of meristematic cell activity on grafts of conifer species (Jayawickrama *et al*., 1991; Hartmann *et al*., 2010).

During the fusion of the cambial areas of the scion and the rootstock, three important stages are recognized in grafting: callus formation, cambial differentiation and cambial continuity (formation of vascular tissues) (Moore, 1984; Tekintas, 1991; Polat & Kaska, 1992; Tekintas & Dolgun, 1996). In *Prunus domestica* subsp. *insititia* (L.) C.K. Schneid., cambium cells joined 60 days after grafting, in the process of callus formation, giving rise to the process called “cambial continuity” (Dolgun *et al*., 2008). By contrast, in heteroplastic grafting of *Prunus domestica* subsp. *insititia* and *Prunus dulcis* (Mill.) D.A. Webb, the cambial zone merged within 45 to 60 days after grafting (Tekintas & Dolgun, 1996). However, some studies of woody species have shown that incompatibility can develop over several years, indicating the possible presence of vascular tissue that helps the survival and growth of incompatible grafts (Mosse, 1962; Pina & Errea, 2005).

Some theories about the activity in the cambial zone during the grafting process have been proposed. Thus, it has been suggested, on the basis of anatomical studies, that the cell walls of grafted organs are diluted during callus formation, allowing contact between plasma membranes and the subsequent secretion of proteins, generating an effect called "catalytic complex". It has also been suggested that graft compatibility depends on the formation of this complex and that incompatibility occurs in its absence (Yeoman & Brown, 1976; Yeoman *et al*., 1978; Jeffree & Yeoman, 1983). However, other authors have argued that it is impossible to determine how the catalytic complex is formed due to the poor visibility of the cell walls during callus formation (McCully, 1983; Moore, 1983).

Effect of concentration and application of hormones in grafting: For grafting in conifers, incompatibility has been found to be mainly caused by the difference in the concentration of growth hormones in the grafted organs (Coenen & Lomax, 1997; Valdés *et al*., 2003a, 2003b). The most important growth hormones in plants are auxins, gibberellins and cytokinins (Peng & Harberd, 2002; Rashotte *et al*., 2003).

Cytokinins have an important effect on the grafting and / or graft incompatibility in coniferous species, as they are of great importance in cell division and regeneration, promoting sprouting and activation of axillary buds (Kato *et al*., 2000; Valdés *et al*., 2003a; Jordán & Casaretto, 2006).

Cytokinin levels measured in *Pinus radiata* were higher in individuals younger than 30 years and the concentration was highest in 9-year-old specimens (Valdés *et al*., 2003a). Axillary buds from individuals with high concentrations of cytokinins favoured graft adaptation and survival (Valdés *et al*., 2003a).

In a later study using molecular markers to identify juvenile genotypes with a high level of maturation in *Pinus radiata* trees, the cytokinin levels decreased considerably with maturation (Valdés *et al*., 2003b). The cytokinin concentration was much higher when grafting organs originated from old trees, indicating that rejuvenation was achieved at physiological level and of the endogenous hormonal content (Valdés *et al*., 2003a, 2003b).

Several authors have pointed out that cambial differentiation between the scion and the rootstock, giving rise to cambial continuity subsequent to grafting, is due to the secretion of auxins present in the vascular tissues (Sachs, 1981; Moore, 1984).

The application of gibberellins in grafts with low production of male and female strobili promotes flowering (Ross, 1976; Chalupka, 1981; Wheeler *et al*., 1982; Hare, 1984; Ross, 1990). In a study in which gibberellins $GA_{4/7}$ and auxins were applied in the form of naphthaleneacetic acid (NAA) to grafts of *Picea engelmannii* Carr., more female strobili were produced when concentrations of 125 to 625 µg / spray of $GA_{4/7}$ and without NAA were used, with cone production reaching 48% of the individuals included in the treatment (Ross, 1990); in addition, a dose of NAA of 5 µg/spray was toxic for the female structures, but male flowering was favoured by the application of $GA_{4/7}$ and NAA at the doses indicated above (Ross, 1990).

When $GA_{4/7}$ and GA5 were applied at a dose of 100-200 µg/spray to grafts of *Pseudotsuga menziesii* (Mirb.) Franco, flowering of male strobili increased by 80 and 65%, respectively; however, production of female strobili was only significantly affected by application of $GA_{4/7}$, reaching 55% (Ross, 1976). Flowering was more intense in *Pinus taeda* and *Pinus elliottii* var. *elliotti* Engelm. when $GA_{4/7}$ was applied at a dose of 200 µg in 0.1 mL of 50% ethanol than when no NAA was applied; flowering was 69 and 62% for *P. taeda* and *P. elliottii*, respectively (Hare, 1984). Likewise, flowering in grafted *Pinus sylvestris* trees was superior when 400 mg/mL in 50% ethanol was applied without NAA, with female and male strobili produced in almost 40% of the treated grafts (Luukkanen & Johansson, 1980).

In an ASO with five- to seven-year-old grafted trees of *Pinus strobus*, only 7.5% of the individuals developed male strobili, and none of the clones produced female strobili. Gibberellins were applied, accelerating the sprouting of strobili within a year, with 38% of the clones producing female strobili, and 47% male strobili (Pijut, 2002).

Further studies are needed to determine the effect of hormonal concentrations in grafted conifers, thus helping to improve the propagation of superior forest genotypes (Coenen & Lomax, 1997; Valdés *et al*., 2003a, 2003b).

Final considerations: Advances in grafting as a means of vegetative propagation have been widely reported, mainly for fruit trees, vegetables and some hardwood forest species; however, studies of grafting in conifers are scarce. Researchers in the areas of plant physiology and forest genetic resources should give priority to vegetative propagation, by grafting economically, ecologically and socially important conifer species, thereby also helping to reduce the risk of loss of genetic diversity. Studies of graft compatibility and incompatibility in conifers due to genetic, anatomical and histological factors are also necessary. Furthermore, the characteristics of the rootstocks used for grafting diverse species of interest must be identified, considering the following aspects: seed origin for the production of rootstocks, volume and type of substrate used in root production, as well as age, height and rootstock diameter at the time of grafting. Research should focus on defining methods that guarantee grafting success, taking into account both favourable factors and the limitations of the sites where actions for the conservation and propagation of forest genetic resources are intended to be carried out, through the establishment of ASOs.

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