Development of improved Sitka spruce for Ireland

David Thompson[a]*

Abstract

Over the past 40 years a significant effort has been made to develop a variety of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) which is specifically adapted to Irish climatic conditions. This has involved selection of the best seed source or provenance, selection of plus-trees, comparative field testing and breeding. The result is an improved variety of Sitka spruce that will provide increased height growth and improved stem form (straightness), but with no loss in wood density (related to timber strength properties). This paper will summarise the work to date in Ireland, how it was carried out, document the benefits of using improved planting stock, and outline what remains to be done.

Keywords: *Plus tree selection, progeny testing, breeding, sexual propagation, vegetative propagation.*

Introduction

The term Tree Improvement refers to the selection and breeding of trees to increase the frequency of certain desired characteristics resulting in an increased economic return over the rotation of the crop. Tree improvement depends on naturally occurring heritable variations in important traits so that selected individuals with different desired traits can be brought together to interbreed to produce new individuals which combine the desired traits of both parents. These changes are permanent and can also provide the basis for further breeding work. Man has been breeding agricultural crops and animals for more than 10,000 years, but tree improvement efforts date back only to the early part of the 20th century. By its nature tree improvement is a slow and expensive process, but despite the considerable up-front investment involved, tree improvement programmes for a range of species around the world have demonstrated a positive return on investment (ROI).

The very legitimate question of "why is it necessary to improve trees?" must be addressed. Data presented in Table 1 shows that naturally occurring forests achieve only about one third of their full productive potential. At least some of this difference can be reduced by planting improved material. Most forest tree species are essentially undomesticated wild populations, with generally more than enough natural genetic variation available to the tree breeder without the need to resort to modern genetic modification (GM) methods.

a Coillte Teoranta, Tree Improvement Programme, Technical Services, Kilmacurra Park, Kilbride, Co. Wicklow.

* Corresponding author: david.thompson@coillte.ie

Table 1: *Potential and Actual Productivity (Mg equals one metric tonne) of natural forests (From Farnum et al. 1983).*

	Mg ha^{-1}
Theoretical Maximum Potential Net Primary Productivity	55.0
Actual Measured Productivity	18.0
Douglas-fir (*Pseudotsuga menziesii*)	5.7
Loblolly pine (*Pinus taeda*)	3.6

While growth is an important factor, other traits which are also under some degree of genetic control, such as stem form (straightness), branching habit, wood properties, insect and disease resistance and adaptability or survival, can also be improved by breeding. However, not all variation may be due to genetically controlled factors. Some are due to environmental influences, but this variation cannot be used to produce genetic improvements.

Tree improvement programmes consists of two distinct parts. First is breeding to produce improved material and second is propagation of the improved material in large amounts for commercial use. Breeding is necessary for the production of new, improved material whereas propagation produces enough material for it to be used commercially. A review of breeding work with Sitka spruce in Europe has recently been published (Lee at al. 2013). The objective of this paper is to explain the methods that have been used to breed and propagate Sitka spruce (*Picea sitchensis* (Bong.) Carr.), then summarise the results achieved in Ireland over the last 40 years and discuss the work that is currently underway.

Tree improvement methods

What is the source of the inherent genetic variation?

Tree improvement programmes follow a defined sequence of steps in order to take full advantage of the natural genetic variation in the species which is available at several different levels.

- **Species selection** – Different species grow at different rates and require different conditions for optimal productivity. For example, Sitka spruce grows at an average of 16.6 m^3 ha^{-1} $year^{-1}$ in the Coillte estate compared to Norway spruce (*Picea abies* (L.) Karst) which grows at an average of 15.6 m^3 ha^{-1} $year^{-1}$ on similar sites.
- **Provenance selection** – Provenance or the geographic origin of the seed source can have a large effect on subsequent growth and performance. Washington sources of Sitka spruce on average produce one full Yield Class (2 m^3 ha^{-1} $year^{-1}$) more wood than more northerly sources such as Queen Charlotte Islands (QCI) (Thompson et al. 2005).
- **Parental selection** – Selecting individual or plus-trees that display superior characteristics for the desired traits, is the first step in establishing a breeding programme. The offspring of these parents (progeny) are field tested to select only those plus-trees with the highest genetic quality for use in the breeding programme.

- **Individual selection** – This refers to the selection of the best individuals from a family resulting from the crossing of two superior parents. The progeny from crosses of the same selected parents can be very different due to unique combinations of genes in each individual. There can be as much genetic variation between individuals from the same cross as there can be between different provenances.

To achieve maximum genetic improvement it is necessary to follow the sequence outlined above. For example, selecting superior individuals without first considering the most suitable provenance or parents will not provide the maximum amount of genetic improvement that is possible. It is not always necessary to follow the sequence fully. This depends on the level of improvements required and the resources available. For example, it may only be necessary to identify the best provenance of a species and go no further for species that are of less economic importance, are more difficult to breed or where biological or other constraints exist. Following the full sequence from species to individual selection generally can only be justified for the most commercially important species.

Breeding Sitka spruce

Species testing

Differences in the growth rates of native species, as well as non-native species planted in gardens and arboreta were observed in the 19th century. Species that performed well were considered good candidates for forestry use. Sitka spruce was first planted in Ireland in the 1830s. This species performed very well in those early trials and was established in the plantations of the 1870s and 1880s, but only became a commercially important species in the 1920s (Joyce and OCarroll 2002).

Between 1958 and 1965 the Research Branch of the Forestry Division of the Department of Lands established a series of species trials on a range of suitable afforestation sites around the country. Although these trials had their limitations, Sitka spruce and lodgepole pine (*Pinus contorta* Doug.) were the most successful species both in terms of survival and growth rate across almost all sites. Although other species may have higher growth rates, Sitka spruce is best adapted to the soils and climatic conditions in Ireland and produces a versatile timber.

Provenance testing

The first formal Irish Sitka spruce provenance trial was established in 1960 using commercial seed collections from 10 sources ranging from Alaska to Oregon. This was later followed in the 1970s by a more comprehensive series of IUFRO (International Union of Forest Research Organisation) trials planted on nine different sites across the country consisting of 67 seed sources covering the entire species range from Alaska to northern California. In both provenance trials, the superiority of Washington sources over all others was clear (Thompson et al. 2005), although on low, frost-risk sites along the southern coast of Ireland, Oregon material may be suitable (Thompson 2007).

Figure 1: *An example of a Sitka spruce plus tree selected in Baunreagh property in Mountrath Forest, Co. Laois.*

Plus-tree selection

In the early 1970s, the first efforts towards a Sitka spruce improvement programme began. The original objective was to select and test 1,000 phenotypically superior plus-trees from which the best 10% would be re-selected after field testing based on the performance of the offspring. The re-selected best 100 plus trees would form the basis of the breeding programme. In hindsight this was perhaps too ambitious and it was never achieved.

Plus-trees were selected from above-average yield class stands of Sitka spruce across the country that were between 25 and 35 years-old (Figure 1). Initially the selection intensity was high with only one tree being selected in every 8.5 ha of forest, but later this was reduced to about 1 tree in every 1.7 ha surveyed. This decision was based on work in the Forest Commission in the UK which showed that highly intensive selection of plus-trees did not always result in significantly better gain and that the extra costs associated with the high selection intensity could not be justified (Lee 1999).

Each original plus-tree was assessed against a number of criteria (Table 2) in comparison with the immediately surrounding dominant trees. In later years, wood density was introduced as an additional criterion. In total, only 747 of the originally planned 1,000 plus-trees were selected. Table 3 documents the progress of the plus-tree selection programme between 1973 and 1990.

Table 2: *Criteria used to select Sitka spruce plus-trees.*

Trait	Assessment criteria	
Stem	Straightness	Spiral grain
	Forking	Circularity
	Bends	Drought cracks
	Taper	Resin weep
	Sweep	Epicormic shoots
	Buttressing	Disease (presence)
	Broken leader	
Branching	Branch size	Internodal branching
	Branch length	Branch angle
	Number of whorls	Self pruning
Other traits	Indirect assessment of wood density of plus-tree and several surrounding trees	
	DBH of plus-tree and several surrounding trees	
Overall quality	Plus-trees are rated on a 1 to 10 scale	

Progeny testing

Once the plus-trees were selected, the next step was to test them to identify the best parents, in terms of genetic quality for use in the breeding programme. Climbers were sent to each tree to collect both cones and branch material. The branch material was grafted onto seedling rootstocks to provide a copy of the original plus-tree. Seed was used to grow the offspring or progeny which were planted in field trials on typical Sitka sites. The performance of the progeny gave an indication of the genetic quality of the parent plus-trees.

Progeny tests consisted of a standard design of plots with 8 to 10 trees per row, randomised and replicated four or five times on each site, together with a standard control of imported and unimproved Washington and QCI seed sources against

Table 3: *Year of selection and number of Sitka spruce plus-trees selected for the improvement programme.*

Year selected	Number of plus-trees
1973	39
1976	65
1977	48
1984	236
1985	97
1987	105
1988	57
1989	23
1990	76
Total	747

Table 4: *Summary of Sitka spruce progeny tests.*

Test series	Number of locations	Number of plus-trees	First assessment	Second assessment
1	4	33	1986	1995
2	3	32	1986	1995
3	3	29	1990	1999
4	4	54	1993	2002
5	4	40	1993	2002
6	4	42	1993	2002
7	1	17	1994	2003
8	3	45	1994	2003
9	3	44	1994	2003
10	3	44	1994	2003
11	3	43	1998	2007
12	3	46	1998	2007
13	2	36	1998	2007
Total		505		

which improvements could be measured. The 747 plus-trees were divided into a total of 13 trial series, each of which were planted on two to four different locations around the country (Table 4). Trials were established with 3 year-old transplants and were first assessed after six growing seasons in the field (9 years-old from seed) and again after 15 growing seasons in the field. Of the original 747 plus trees selected, only 505 (68%) were progeny tested for a variety of reasons (e.g. plus tree was felled, no seed was produced, or not enough plants were available for the progeny tests).

Parental selection

After six growing seasons in the field, any plus-tree parents of progeny that were at least 15% taller than a standard Washington control in each trial went forward in the breeding programme (later confirmed in the 15-year assessment). Of the 505 progeny tested plus-trees, only 86 (17% of the original 505 plus-trees tested) were selected based on increased height growth and improved stem form (stem straightness). However, it is known that increased growth rate in Sitka spruce is inversely correlated with wood density, a trait which is well correlated with wood strength properties. As a result, fast grown trees generally tend to have a lower wood density than slower grown trees. Following a further screening of the wood density of the 86 plus-trees, the number of plus-trees that provided increased height growth, improved stem form with no significant loss in wood density, was reduced to 41 (8.1% of the 505 plus-trees tested). These 41 parents formed the basis of the Coillte Sitka improvement programme.

Table 5 provides an example of the results from a typical progeny test, which shows that of the 54 families included in this test, only five were 15% taller than the

Table 5: *Results from a typical Sitka spruce progeny trial containing (half-sibling) progeny collected from 54 plus-trees around Ireland and planted in Coolgreany forest, Co. Wicklow.*

Performance	Number of families
Below Washington control	5
Equal to Washington control	4
Above Washington control	45
10% taller than Washington control	25
15% taller than Washington control	5
20% taller than Washington control	2

Washington control. Thus only these five plus-trees went forward in the breeding programme and all other plus-trees were rejected. While this may seem wasteful, significant genetic improvements will be achieved if only the best individuals enter the breeding programme. Table 5 highlights the fact that selecting the original plus-trees in the forest was not a very precise process.

Under regulations covering the marketing of Forest Reproductive Material in the EU there are four quality grades depending on the degree to testing that has been carried out on this material (Source Identified, Selected, Qualified and Tested). To achieve the category of Tested, the material must have undergone tests in scientifically accepted statistically designed trials compared to a standard seed source. The 86 plus-tree parents discussed above have met the criteria to qualify to be described and marketed as Tested, so all material produced by crosses between them is also considered as Tested.

Breeding

Crosses between individuals are either referred to as open-pollinated or half-sibs, if only the female parent is known and the pollen source is just back-ground material, or as control-pollinated or full-sibs if the identity of both parents are known (the term sib or sibling means offspring or progeny).

As a result of meiosis and subsequent fertilisation, each new individual receives half of its genes from the female parent and half from the male. This recombination of traits from both parents results in a new unique combination of genes which has a large influence on the performance of the offspring, as illustrated in Table 6. Certain parents, such as female 140 and male 56, are known as good general combiners because they tended to produce superior progeny each time they were used in a cross, while other parents produce variable results, such as female 61 and male 125. There were also good specific combinations such as 140 crossed with 2, 140 crossed with 56 and 61 crossed with 56, which produced above average progeny only when crossed with specific parent trees.

It is important to point out that at the time these full-sib controlled crosses were made, progeny test information on the parents was not yet available. When these data became available it turned out that none of these plus-tree parents used in the

Table 6: *Height performance of full-sib crosses of Sitka spruce parents relative to the unimproved Washington control.*

Female Parent	Male Parent		
	2	**56**	**125**
48	5.7%	7.4%	8.3%
61	1.2%	16.0%	0.0%
140	21.4%	15.4%	7.4%

crosses in Table 6 were good enough to be included in the breeding programme. Nevertheless, these results show that some of the progeny resulting from crosses between unselected parents can still produce offspring that could be selected for use in a breeding programme (15% or more above control seed lot performance).

The same is true for crosses between selected parents. Table 7 shows the height growth of 34 different full-sib crosses between selected Sitka spruce plus-trees in the breeding programme. Overall, 32 out of the total of 34 crosses were taller than the Washington control, demonstrating the benefit of using selected parents.

Selecting the best individuals from the best crosses

Genetic variation also occurs between different individuals, i.e. siblings resulting from the full-sib cross of the same two parents. Each improved seed derived from a full-sib cross can be vegetatively propagated, producing many copies (clones) of the original individual. Table 8 shows the variation in height growth between 10 clones originating from the same full-sib cross (519 × 547). Two of the 10 clones were 11% taller than the average of all the clones. This demonstrates that within the progeny of each cross there are a certain few that are superior individuals. In this case (Table 8), a further 12% increase in height is possible by using only the two best clones from this full-sib cross. Other similar superior clones from full-sib crosses of other parents could be assembled to produce a clonal mixture that would provide further improvements without sacrificing genetic diversity. These individuals could either be used to establish seed orchards or they could be used to produce material for vegetative propagation.

Production of improved material

The second objective of a tree improvement programme is to ensure that enough of the improved material is available for commercial use. Breeding without large-scale

Table 7: *Field test results of 34 full-sib crosses of selected Sitka spruce parents in Ballynoe Forest, Co. Waterford.*

Performance	Number of Families
Below Washington control	2
Above Washington control	32
5% Taller than Washington control	29
10% Taller than Washington control	24
15% Taller than Washington control	11
20% Taller than Washington control	7

Table 8: *Height growth of 10 clones (A to I) of the full-sib cross 519 × 547 and percentage difference from the clonal average (118.9 cm) in a nursery trial at Kilmacurra (4 tree square plots, randomised and replicated 4 times for 16 plants per clone) after 3 growing seasons.*

Clone	Height (cm)	% above/below average
G	104	−12.5
F	107	−10.0
I	112	−5.8
C	113	−5.0
J	118	−0.7
A, D, H	123	+3.4
B, E	133	+11.8

production of the resulting improved material is of limited commercial value. Improved material can be produced either by sexual or by vegetative propagation methods.

Sexual propagation

The advantage of sexual propagation has already been demonstrated in Table 6. It results in new combinations of genes that may outperform the parents and the process is a relatively simple one. The disadvantage is that crosses between selected good parents will always result in a mixture of both good and poor genetic combinations.

Seed orchards

Seed orchards are designed and managed specifically to produce seed rather than timber and are the main method used to produce improved seed (Figure 2). Sitka

Figure 2: *A young Sitka spruce seed orchard at Ballintemple Nursery, Ardattin, Co. Carlow.*

spruce is slow to flower, and even if sexually mature branches are grafted onto seedling rootstocks, it takes about 10 years for them to produce seed in significant quantities. For a number of reasons, seed orchards typically capture only a part of the genetic improvement that they should be capable of providing. These include contamination by pollen from unselected trees outside the seed orchard, the fact that not all parents flower each year and that some seed may result from selfing (pollen from the parent tree fertilises the seeds of the same tree) which results in poor quality offspring. Some of the combinations between all the flowering parents in a seed orchard also will result in material that is only average or even below average in productivity and quality.

Seed production

Currently Coillte Nurseries produce approximately 28 million Sitka spruce plants per year, which requires the sowing of approximately 165 kilos of seed. Sitka spruce will not begin to flower normally until it is about 20 years-old from seed and good seed crops normally occur on average once every 3 to 7 years. This is due to the fact that a warm, dry period during May and June is required to initiate flower buds which will flower and produce seed the following year. These conditions do not happen very often in this country so good seed crops are infrequent. For this reason, methods have been developed to stimulate flowering of trees in orchards and make seed crops more frequent and reliable.

Flowering is basically a stress response. Studies on flower stimulation in grafted Sitka spruce has shown that a combination of warm temperatures, water stress and the presence of a plant growth regulator, gibberellic acid (GA), which occurs naturally in sexually mature trees, act together to stimulate flowering (Phillipson 1992). While these stress treatments can be applied to large trees in outdoor gene banks or seed orchards, they are more effective when applied under more controllable conditions.

This has led to the development of indoor seed orchards wherein grafts of plus-trees are grown in pots in a greenhouse or polyhouse. Environmental conditions can be modified readily. The plants can be subjected to higher than ambient temperatures, water stress and injected with hormones such as GA to induce flowering. This approach results in a regular supply of both male and female flowers each spring to allow for controlled crosses to be made (Figure 3A). Sitka spruce, like most conifers is monoecious, meaning it can produce both male and female flowers on the same tree which allows the use of selected plus-trees as both male and female parents. Table 9 shows the effect of different treatments on the production of male and female flowers in an indoor potted Sitka spruce seed orchard.

The small size of the trees in the indoor seed orchard however, means that only a limited amount of seed can be produced. While this is adequate for progeny testing of new full-sib crosses, it is not adequate for large-scale production, although this limited amount of valuable material can be multiplied by using vegetative propagation.

Table 9: *Effect of different treatments on flower production in potted grafts of Sitka spruce plus-trees.*

Treatment	Number of male flowers/graft	Number of female flowers/graft
Outdoor potted control	3.0	1.7
Indoor control	14.5	5.6
Indoor + GA 1.0 mg	12.2	16.3
Indoor + GA 1.5 mg	9.8	12.2
Indoor + GA 2.0 mg	17.9	15.4

Vegetative propagation

The advantage of vegetative propagation is that individuals with superior traits can be reproduced exactly (i.e. no genetic variation in the resulting plants). The disadvantage is that the techniques used to vegetatively propagate material results in higher per plant costs than seedlings propagated from seed.

Vegetative propagation techniques include air-layering, grafting, the rooting of cuttings and several tissue culture (micropropagation) techniques. Air-layering is used only in specific cases with certain species. Grafting, although it is widely used in the establishment of clone banks and seed orchards, is too expensive for large-scale propagation. The rooting of cuttings works well with a range of species, especially with juvenile material, and large-scale clonal propagation programmes with forest trees have been in use for many years (Table 10).

However, rooted cuttings typically cost 1.5 times or more to produce than seedlings due mainly to the extra labour required to collect, insert and root cuttings and the capital investment in facilities. Most tissue culture methods have the potential to produce a larger number of plants than is possible with rooted cuttings; however the cost of tissue culture production is still higher due to the increased amount of labour involved. The higher production costs associated with vegetative propagation require that only rare or valuable material can economically be propagated using this approach. Nevertheless, the benefits of clonal planting stock with its uniform growth rates and more uniform products keeps the idea of clonal forestry alive.

Vegetative propagation also allows for the production of the most advanced improved material years earlier than might be possible using seed orchards. As mentioned earlier, a Sitka spruce seed orchard requires at least 10 years after

Table 10: *Clonal plantations worldwide (Kellison 2004).*

Species	Area (000 ha)
Conifers	5,080
Poplars	1,567
Eucalyptus	1,217
Other broadleaves	22
Total	7,886

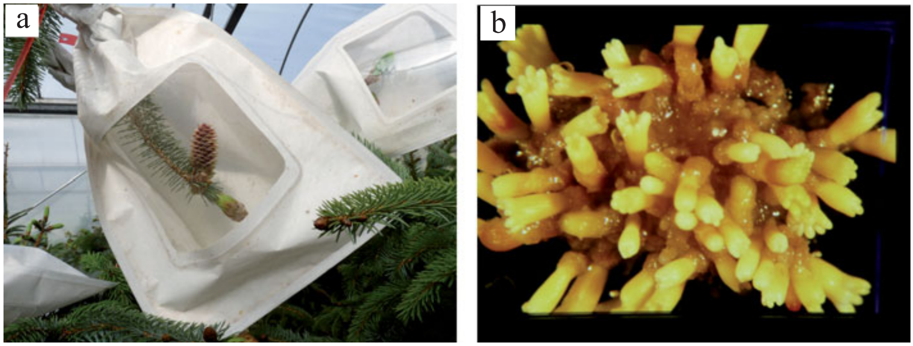

Figure 3: *Female Sitka spruce flowers in an isolation bag to produce a full-sib cross between two selected parents (a) and somatic embryos of Sitka spruce produced in the laboratory (b).*

establishment to come into full production, whereas the latest improved material from an ongoing breeding programme could be available in only 3 to 5 years. There is no delay due to a lack of flowering if vegetative propagation methods are used.

The small amount of valuable seed from the full-sib crosses in indoor seed orchards can be increased using vegetative methods to produce commercial-scale amounts of planting stock. The most effective way to do this is by a tissue culture process known as somatic embryogenesis (SE). In this process an immature seed is used to establish special cells of that individual which are then grown on in a Petri dish in the laboratory. The unorganised cells are multiplied to produce large amounts of this tissue in a relatively short time. When enough material is available, the culture conditions can be changed and the unorganised cells can be induced to mimic the process that takes place in the developing seed, to form complete embryos similar to those formed in seeds (Figure 3B). The advantage of SE over other tissue culture propagation methods is the large number of plants that can be produced very quickly with a minimal amount of handling on a year-round basis.

Due to the amount of labour required to produce plants by SE, the current cost per plant is currently about 10 times that of a seed-produced plant and as such it would not be economic to establish a plantation with SE plants, except for research purposes. Work is underway around the world to reduce production costs by automating the process or by producing artificial seeds. Nevertheless, the fact that SE can produce a larger number of copies of an individual faster than any other method has led to the use of SE to establish stock plant hedges of Sitka spruce (Figure 4A) from which cuttings can be collected, rooted (Figure 4B), transplanted into a nursery bed and eventually planted in the field. Once established, a Sitka spruce stock plant can produce up to 50 cuttings per year over a 5- to 6-year period, so the high cost of the original SE stock plant is reduced when it is spread over all of the cuttings it produces over its lifetime. The resulting two year-old Sitka spruce rooted cutting is equal in height and root collar diameter to a three year-old seedling transplant and it provides improved planting stock quickly without the delay associated with the seed orchard approach.

Parent trees from the Coillte Sitka improvement programme are currently

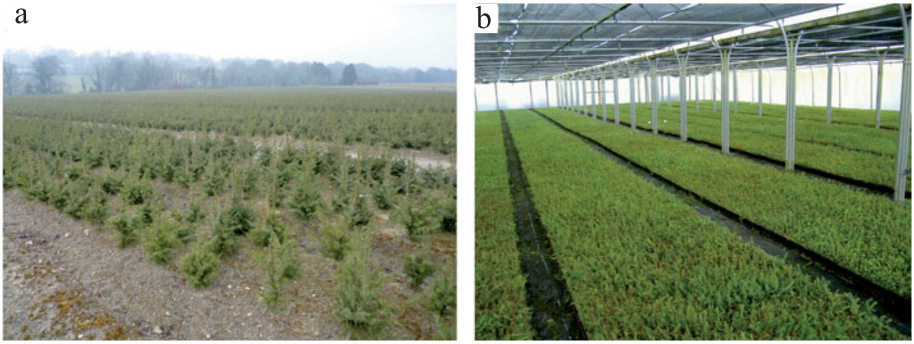

Figure 4: *A hedge or cutting orchard of Sitka spruce to provide cuttings for rooting at the Coillte Nursery at Clone near Aughrim, Co. Wicklow (a) and Sitka spruce cuttings being rooted in a tunnel at the Coillte Nursery at Clone near Aughrim. Co. Wicklow (b).*

crossed and the resulting seed used to produce SE stock plants from which cuttings are taken and rooted to provide commercial amounts of improved planting stock in Ireland. In the initial propagation stages, the genetic identity of each plant is maintained and observed for any irregularities, but once the material is established in a hedge orchard, clonal identities are no longer retained. In this way the genetic diversity of the rooted cuttings can be kept as wide as possible, and the resulting crops are likely to be more resilient over the length of the rotation. Currently Coillte produces about 2.5 to 3.0 million rooted cuttings of improved Sitka spruce per year. This material is commonly referred to as rooted cuttings, cuttings, vegetatively propagated, veg prop or VP planting stock.

Economics and performance of improved material

A series of demonstration/experimental trials comparing unimproved Washington and improved Sitka spruce produced by rooted cuttings were established in the 1990s. The results from two of the trials are presented in Table 11, which shows that the improved Sitka spruce produced about 25% more wood volume than the unimproved Washington material after 14 growing seasons in the field. The increased volume production is the result of the selection for increased growth, together with selection for lighter branching.

As discussed earlier, improved rooted cuttings cost more than unimproved Washington Sitka spruce seedlings. For this reason, combined with the fact that only limited amounts of the improved rooted cuttings are available, it is recommended to plant the rooted cuttings in mixture with unimproved seedling material. The results

Table 11: *Increased productivity of improved vegetatively propagated plants over unimproved Washington Sitka spruce seedlings after 14 growing seasons in the field.*

Source	Height (m)	DBH (cm)	Volume (m^3ha^{-1})	% volume increase
Unimproved Washington	12.3	15.7	207	--
Vegetatively propagated	13.1	17.1	262	26.5

of an economic analysis of the discounted benefit of increasing volume production of the improved rooted cuttings over the full rotation of the crop showed that a 50/50 improved rooted cuttings/unimproved Washington Sitka seedling crop would more than pay for the extra cost of the rooted cutting material (Phillips and Thompson 2010). Although the cost of the plant material (both improved rooted cuttings and unimproved seedlings) has increased since the 2010 analysis, the result is the same using current costs.

In addition, there are other benefits to planting improved rooted cuttings which are more difficult to quantify. These include faster exploitation of site resources, thus minimising or eliminating the cost of vegetation control treatment, significant improvement in stem straightness and reduction in forking, significant improvement in branching (fewer and smaller branches) while at the same time causing no significant reduction in wood density. Improved Sitka spruce will also sequester carbon more quickly than unimproved material.

Conclusions

The work discussed in this paper summarises the results achieved over the last 40 years on improving Sitka spruce in Ireland. While similar work has been done with QCI Sitka spruce in the UK, the Irish programme is based mainly on more productive Washington material which has been selected and tested under Irish climatic conditions. In retrospect, the same progress could have been achieved in a shorter period of time, but limitations in funding and manpower delayed the production of improved material.

Improved Sitka material from the Coillte tree improvement programme is currently only available as rooted cuttings, but in time (5 to 10 years) it will also be available from recently established seed orchards, which will increase the availability of improved planting stock. Nevertheless, with an active Sitka spruce breeding programme, the most advanced and best quality material will always be available first from the veg prop programme because of the delay of seed production in seed orchards.

Perhaps the greatest obstacle facing the use of the improved Sitka spruce material is the extra cost of the planting stock. While higher up-front investment costs involved in producing improved planting stock has impeded planting of improved rooted cuttings, an economic analysis has shown conclusively that the higher initial costs are more than offset by the increased timber volumes produced over the rotation (Phillips and Thompson 2010).

Tree improvement is a cumulative process in which further improvements are added to those accomplished in the past. The current programme has focussed on volume production and wood quality to produce high quality structural timber. Breeding for other traits such as branching habit, other wood properties or disease or insect resistance is also possible. Time is perhaps the greatest limiting factor in tree improvement and efforts to make tree improvement more efficient (shorten the testing period) and effective (using morphological, physiological or molecular "markers") are currently underway in the DAFM-funded ForGen research programme.

In addition, as shown in Table 8, the use of clonal material can further improve the productivity and quality as well as providing a more uniform crop to manage and a more uniform product for processing. Sitka spruce is a species that lends itself very well to clonal propagation, but there are genuine concerns about the potential risks of reduced genetic diversity in clonal plantations which can be addressed. The economics and public acceptance of clonal forestry will determine whether it has a commercial application or not.

Practical implications

- The use of improved material offers a permanent way to increase the productivity and quality of new forest plantations.
- Improved Sitka spruce has been developed specifically for Irish conditions that provide increased growth, improved stem form with no loss in wood quality.
- The improved productivity and quality of the resulting crop will more than offset the higher cost of improved planting stock.

Acknowledgements
This paper is dedicated to all the researchers and foresters who contributed to the Irish Sitka spruce tree improvement programme over the past 40 years.

References

Farnum, P., Timmis, R. and Kulp, J.L. 1983. Biotechnology of forest yield. *Science* 219(4585): 694–702.

Joyce, P.M. and OCarroll, N. 2002. *Sitka spruce in Ireland*. COFORD, Dublin.

Kellison, B. 2004. Clonal forest plantations in the world. In *2004 IUFRO Joint Conference of Division 2 Forest Genetics and Tree Breeding in the Age of Genomics: Progress and Future*. Eds. Li, B. and McKeand, S., North Carolina State University, pp 324–6.

Lee, S. 1999. Improving the timber quality of Sitka spruce through selection and breeding. *Forestry* 72: 123–33.

Lee, S., Thompson, D. and Hansen, J.K. 2013. Sitka spruce. In *Forest Tree Breeding in Europe*. Ed. Paques, L.E., Springer Dordrecht/Heidelberg/New York/London, pp 177–228.

Philips, H. and Thompson. D. 2010. Economic benefits and guidelines for planting improved Washington Sitka spruce. *COFORD Connects Reproductive Material Note No. 17.* COFORD, Dublin pp 4.

Philipson, J.J. 1992. Optimal conditions for inducing coning of container-grown Picea sitchensis: effects of applying different quantities of GA 4/7, timing and duration of heat and drought treatments, and girdling. *Forest Ecology and Management* 53: 39–52.

Thompson, D., Lally, M. and Pfeifer, A. 2005. Washington, Oregon or Queen Charlotte Islands? Which is the best provenance of Sitka spruce (*Picea sitchensis*) for Ireland? *Irish Forestry* 62: 19–34.

Thompson, D. 2007. Where should Washington and Oregon sources of Sitka spruce be planted in Ireland? *COFORD Connects Reproductive Material Note No. 11*. COFORD, Dublin, pp 4.