After the Second World War the major thrust in advancing the efficiency of commercial plant propagation was to enhance the ability to initiate roots on stem cuttings. This was prompted by the need to reduce the reliance on grafting. Traditionally, grafting had been a common practice for plants such as Rhododendron because rooting stem cuttings was difficult. But grafting was only suitable for low volume production.

The advances were essentially associated with a) the use of plant growth regulators (PGRs), b) the practice of wounding the basal portion of the cutting, and c) a better understanding of the necessary functions of the rooting medium. All of these factors, and in their various combinations, had a considerable impact on advancing the efficiency of plant propagation, and this is evidenced in the literature of the time.

Experimentation
However, the practice of plant propagation and any advances in success, at that time, tended to be jealously guarded as ‘trade secrets’ by individual propagators. It was therefore difficult for less experienced propagators to put together efficient regimes. But by the late 1960s attitudes had changed dramatically, helped by the expansion of the International Plant Propagators Society, and plant propagation.

It has been known for several decades that older cultivars are usually more difficult to root than more recent ones. Philip McMillan Browse discusses the problem and how to get round it.
quickly became an open book.

At this time a large and extensive ‘experiment’ was convened by several nurseries and institutions. They conducted a comprehensive investigation to determine the importance and relative effects of PGRs, wounding, and medium composition on the rooting of particular plants. The results were inconsistent and inconclusive, especially so between sites. The investigation was repeated, as accurately as possible, the following season to determine if the results were at least consistent, on an annual basis, on any one site. Interestingly, the results were markedly at variance with the previous year – especially so for those contributors who used the same stock plants for their propagating material. They found that those repeatedly using the same stock plants were highly successful, experienced only marginal differences between the treatments, and vastly improved the overall total response. This led to the conclusion that if the plant material was ‘good’ then the effect of treatments was marginalized.

Age of stock plant
This result focused attention on the condition of the propagating material and the stock plant itself. This was seen to be a major influence on successful propagation, rather than the treatment of the propagation material after it had been isolated. In turn, this led to consideration of the age of the stock plant from which the propagating material was taken, and the management of the stock plant. This had already been widely noted as a factor affecting the success of rooting stem cuttings of × *Cuprocyparis leylandii*, Leyland cypress.

It is now known that the major influence controlling the successful propagation of woody plants from stem cuttings is the inherent level of regenerative capacity present in the material selected for propagation. By inference, this is a function of the physiological status of the plant from which propagation material is selected.

This regenerative capacity, i.e. the ability of the stem to initiate roots, does not occur as a constant function throughout the life of the plant – it declines as the plant ages. This context has particular significance for the continuous clonal propagation of a woody plant. The physiological condition of the material is not represented by the immediate age of the individual parent stock, but is a function of the chronological (and physiological) age of the original selection. This is the case however many generations it is removed from the current material. For example, a 10-year-old stock plant of *Ribes sanguineum* ‘Pulborough Scarlet’ should be regarded as 80 years old because the cultivar originated in the 1930s.

The relative capacity to regenerate between different families, genera and even species varies considerably but is normally constant. This implies that there is a spectrum of this capacity which, at the extremes, means that stem cuttings of a taxon may be ‘difficult’ (e.g. *Quercus* and *Tilia*) or ‘easy’ (e.g. *Fuchsia* and *Forsythia*) to root. Thus, the inherent capacity varies significantly and is not the same for all woody plants.

Life cycle phases
A woody plant progresses through three phases during its life cycle – juvenility, maturity and senility. The potential asexual regenerative capacity during this cycle declines in a sigmoid curve fashion. The highest level of this regenerative capacity occurs during the juvenile phase, declining only slightly as time progresses. At the onset of sexual maturity the capacity declines markedly and continues to decline steadily, until the senile phase is reached when this potential is virtually lost. At this late stage in life the normal reaction of the plant before dying is to flower profusely and produce a large quantity of seed.

The significance then of this
pattern has particular relevance in the vegetative propagation of clonal material (e.g. cultivars). The physiological age of the plant is not renewed in any way as a result of a new generation being vegetatively propagated – the physiological age is still that of (or what would have been) the original selected parent. This probably accounts for the demise of, or the extreme difficulty in rooting cuttings of, many cultivars from earlier times.

An example of this is provided by the original cultivars of Ghent azalea 

Rhododendron ‘Daviesii’ dates from the 19th century and is relatively difficult to root.

Rhododendron 

which are now 150–200 years old. They have, over the years, become progressively difficult to regenerate from stem cuttings. Subsequent deciduous azalea hybrid groups such as Mollis (dating from 1870–80), Knap Hill (mid 20th century) and Ilam (1960–70) are progressively easier to root. This pattern is true even when the presence of viruses is allowed for.

Ribes sanguineum cultivars have demonstrated a similar decline in regenerative capacity with age.

When this phenomenon was first noted in the 1960s, 

R. sanguineum ‘Pulborough Scarlet’ (raised in the 1930s) was regarded as ‘easy’ and ‘King Edward VII’ (c. 1890s) less so. Nowadays, the former is regarded as relatively ‘difficult’ and the latter as ‘more difficult’. More recent cultivars such as ‘White Icicle’ (1970s), however, are seen as easy.

The most productive rooting of stem cuttings is during the non-flowering condition (i.e. the juvenile phase). Although in practice, most cultivars are not actually selected until they enter the flowering condition (i.e. the early mature phase). Regenerative capacity then declines steadily with ageing through the mature phase, coinciding with an increased capacity to flower. Hence, it would appear that the ability to regenerate asexually declines with an increasing ability to regenerate sexually.

**Juvenile characteristics**

The definition of juvenility, in this context, is that period from the onset of germination to the point of sexual maturity. Often this phase is identifiable by differing morphological characteristics to the mature phase. This may be evident as a distinct leaf shape and structure (e.g. many conifers, Hedera, Malus, Passiflora) but may also be an alternative habit (e.g. Hedera, some Coprosma).

Typical juvenile states such as this can, however, be complicated by the fact that juvenile characters may also arise when a stem is regenerated from an adventitious bud – as from a root or from an epicormic site. Propagators once speculated that the rapid propagation of alternate generations of root cuttings and stem cuttings could push the juvenility factor back up the scale. This would hopefully ease propagation by resulting in a massive increase in regenerative capacity. The downside of this is that such practices can adversely affect the development of the desired characteristics of the mature phase.
Turning back the clock
When sexual maturity is reached there is a marked decline in regenerative capacity. The problem, noted above, is that it is not until the mature phase has been reached that the plant will be selected for its particular desirable characteristics. By this time it has lost the greater proportion of its regenerative capacity.

The propagator therefore needs to determine whether any regenerative capacity can be recovered in the mature phase by manipulation of the parent plant. This can be done by heavy pruning which causes the production of stems which do not flower, and it is these stems that recover a considerable degree of regenerative capacity. It has been shown that the greater the proportion of stem material that is removed, the faster will be the replacement growth, as the plant seeks to replace the stem tissue removed and restore the root/shoot ratio. The faster the growth achieved by this process, the higher is the level of regenerative capacity regained.

Therefore, it is the speed of growth which is the critical factor in determining regenerative capacity. This is represented morphologically by upright growth, anatomically by attenuation of the sclerenchyma sheath surrounding the conducting tissue, and physiologically by the non-flowering condition. Not surprisingly, the rate of growth of this replacement tissue is not constant, but again the pattern seems to match that of a sigmoid curve.

The basal swelling
This ‘speed of growth’ effect can be demonstrated by establishing a vigorous, relatively easily rooting plant, such as *Salix daphnoides*, and then stooling it in the late winter. The growth during the following growing season will be considerable and virtually upright shoots around 4m long will develop. In the autumn, just after leaf fall, these shoots can be severed flush with the stool (incorporating the basal swelling). Hardwood cuttings of 15cm length taken successively from base to tip should then be prepared. These can be inserted in a suitable soil bed and at the end of the following growing season they can be assessed on the basis of root and shoot production.

The results will show that the quality (size and vigour) of the new plant is greatest when derived from the basal cutting, with progressively, a declining quality with cuttings taken from the tip of the shoot. The advantage of incorporating the basal swelling into the basal cutting can similarly be demonstrated by removing it in some of the basal cuttings to make a comparison.

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The importance of incorporating the basal swelling can also be seen in other woody plants. It is particularly evident with early-season cuttings of *Syringa vulgaris*, for example.

How to succeed
For propagation of woody plants from stem cuttings, the significant factors for maximum success – especially with plants regarded as difficult to root – are that the basal swelling is incorporated into the cutting, and that only this particular cutting is likely to be successful. This basal swelling, which develops as a result of the initial surge of growth from the dormant bud, represents the fastest growth rate of the new shoot after heavy pruning – i.e. the top of the sigmoid curve. Woody plants grown from cuttings with basal swellings show the expected characteristics of the mature cultivar by the second season after propagation.

This phenomenon is not a new concept – it was demonstrated at East Malling Research in the late 1950s and 1960s. It led to recommendations for rooting hardwood cuttings of fruit tree rootstocks in a Garner bin (a container providing bottom heat to enhance rooting potential), and the phenomenon was exploited by others for rooting ornamental woody plants.

Conclusion
These findings outlined above have practical significance for the propagator in two ways. Firstly, the age of the cultivar determines its potential and relative regenerative capacity (bear in mind that date of introduction is not always a reliable guide; the plant selected as the cultivar may have germinated many years before). Secondly, the ability to recover regenerative capacity can be improved by manipulation of the parent plant.

PHILIP McMILLAN BROWSE is a retired horticulturist with a continued interest in plant propagation.