ROOT GROWTH POTENTIAL:
ITS DEVELOPMENT AND EXPRESSION IN FOREST TREE SEEDLINGS

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ABSTRACT

This review presents a synthesis of current knowledge on Root Growth Potential (RGP) of nursery-grown forest seedlings. RGP, the measure of a transplanted seedling's ability to rapidly produce new roots, is a key indicator of seedling vigour and survival after planting.

Physiologically, RGP appears to be closely linked to bud dormancy. It peaks when the chilling requirement for dormancy release is fulfilled, then declines, presumably reflecting the internal allocation of current photo-assimilate to shoot growth. RGP can be manipulated in the nursery through practices that induce dormancy, increase root fibrosity, and enhance carbohydrate reserves. Autumn and winter nursery temperatures influence RGP through their effect on dormancy release. Date of lifting establishes the dormancy status of seedlings when they enter storage, and temperature and duration of storage further influence the dormancy status at the time of planting. Improper handling and misplanting can reduce RGP expression, as can low soil temperature, low soil water potential and soil compaction on the planting site.

INTRODUCTION

Initial survival of planted trees depends in large measure on their physiological readiness to rapidly produce new roots and thereby re-establish intimate contact with the soil (Smith, 1962). This ability is sometimes referred to as the "Root Growth Potential," or RGP, and many authors have stressed its importance as a critical ingredient of seedling quality and subsequent reforestation success (e.g., Gilmore, 1962; Zaerr, 1967; Larson, 1970; Larson and Whitmore, 1970; Lathrop and Mecklenberg, 1971; Etter and Carlson, 1973; Farmer, 1975; Day and MacGillivray, 1975; W. Webb, 1975a, b, 1977; von Lüpke, 1976; Day *et al.*, 1976).

While it has been difficult to establish a clear cause-effect relationship between RGP and seedling survival after planting, a compelling body of evidence (summarised in Table 1) indicates that the two are often very closely correlated.

Thirty years ago Wakeley (1948) emphasised that seedling morphological grades were inadequate indicators of seedling performance, and that seedlings that survived and performed well apparently did so due to their superior physiological grade. He concluded, however, "How to recognize physiological grades before planting the seedlings and observing their success or failure remains to be discovered."

Some twenty years later, E. C. Stone and co-workers demonstrated that a seedling's ability to grow roots in a test environment could be used as a measure of seedling physiological grade or overall seedling vigour (Stone, 1955; Stone and Schubert, 1959b, c; Stone and Jenkinson, 1971). Furthermore, the period during which seedlings exhibit high RGP coincides very closely with the period during which they are most tolerant to desiccation and physical damage (Hermann, 1962, 1964, 1967; Mullin, 1978; Lavender and Wareing, 1972) and therefore are more able to survive the rigours of lifting, handling, storing and outplanting. The RGP level can thus be used, in effect, as an index of seedling resilience (Stone, 1955; Stone *et al.*, 1963; Stone and Jenkinson, 1971; Day *et al.*, 1976).

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TABLE 1. Relationship between Root Growth Potential and field survival. (Correlation ratings are authors' interpretations.)

Species	RGP vs. SURVIVAL	Author
Lodgepole pine *(Pinus contorta)*	†††	Burdett (1979)
Loblolly pine *(P. taeda)*	†††	Rhea (1977)
Ponderosa pine *(P. ponderosa)*	†††	Stone (1955)
Ponderosa pine (January planting)	†††	Jenkinson (1976b)
Ponderosa pine (March planting)	††	Jenkinson (1976b)
Jeffrey pine *(P. jeffreyi)*	†††	Stone (1955)
Douglas fir *(Pseudotsuga menziesii)*	†††	Jenkinson and Nelson (1978)
Douglas fir	††	Jenkinson (1976c)
Douglas fir	†††	Jenkinson (1977)
Douglas fir	†††	Stone *et al.* (1961)
Douglas fir	†††	Stone (1955)
Douglas fir	†	Stone *et al.* (1962)
Douglas fir	††	Todd (1964)
Douglas fir	††	Winjum (1963)
White fir *(Abies concolor)*	†††	Jenkinson (unpubl.)
Red fir *(A. magnifica)*	†††	Jenkinson (unpubl.)
White fir	†††	Stone (1955)
Red fir	†††	Stone (1955)
Noble fir *(A. procera)*	††	Winjum (1963)
Sycamore *(Platanus occidentalis)*	—	Rhea (1977)
Sweetgum *(Liquidambar styraciflua)*	0	Rhea (1977)
Yellow poplar *(Liriodendron tulipifera)*	0	Rhea (1977)
Silver maple *(Acer saccharinum)*	††	D. P. Webb (1977)
Sugar maple *(A. saccharum)*	††	D. P. Webb (1977)
Sugar maple	†††	von Althen and Webb (1978)
White ash *(Fraxinus americana)*	††	D. P. Webb (1977)

††† Strong correlation
†† Good correlation
† Poor correlation
0 No correlation
— Inverse correlation

SCOPE

This review is divided into five parts. Part I deals with measurement and terminology. Part II examines the physiological mechanisms that regulate RGP. Part III outlines the effects of various cultural practices on the development of RGP. Part IV examines the effects of planting quality and planting site environment on the seedling's ability to express the root growth potential developed prior to planting, and Part V suggests some areas for future research. Throughout the paper we have attempted to present unpublished information (including our own), as well as to review the published literature on root growth potential. No attempt was made to review root anatomy, form, or morphogenesis as these subjects have been admirably addressed by Sutton (this volume).

PART I: TERMINOLOGY AND MEASUREMENT

Terminology and methodology in this field generally have been inconsistent and undisciplined. The terms Root Growth Capacity (Stone, 1970; Jenkinson, 1975; Burdett, 1979), Root Regeneration (Abod, 1978; Dykstra, 1974; Day and MacGillivray, 1975), Root Regeneration Potential (Day *et al.*, 1976) and Root-Regenerating Potential (Krugman and

Stone, 1966) are used commonly and more or less interchangeably throughout the literature.

Likewise, this parameter (whatever it may be called) is not always quantified in the same manner. Some authors express RGP as total length of new roots (Krugman and Stone, 1966; Stone and Norberg, unpubl.); others use the total number of new roots (Larson, 1970; von Lüpke, 1976; D. P. Webb, 1976b); others use volume or weight of new roots (Burdett, 1979); still others use growth rate of an average root (Thompson and Timmis, 1978). In addition, there are several variations on the above, such as the percent of seedlings having any new root growth at all, or the total length or number of new roots above a certain minimum length.

Thus it is difficult to make comparisons between species and studies due to the lack of a consistent basis for such comparison and because the above parameters often represent different physiological processes. For instance, number of roots per seedling is a measure of root initiation; growth rate of an average root is an estimate of the rate of root elongation; total length of new roots produced combines initiation and elongation, as do volume and weight increase. This is important because these processes — initiation and elongation — are under different endogenous and exogenous control (Krugman and Stone, 1966). Additionally, new root production can include initiation and extension of new lateral roots, regrowth of inactive roots, or development of adventitious roots, as reviewed by Sutton (this volume).

Therefore, when Thompson and Timmis (1978) compared RGP of containerised Douglas fir *(Pseudotsuga menziesii)* (Mirb.) Franco seedlings calculated on the basis of number, length, or rate of growth of the new roots, they found that the peaks of these activities were substantially out of phase with one another. RGP expressed as root length peaked in August and November. RGP as number of roots showed a plateau extending through the winter, while RGP as growth rate underwent a gradual decline, with a low point in mid-winter.

We prefer, and will use in this review, the general term "Root Growth Potential" to represent the total quantity of new roots produced in a standard test (described below). This seems more appropriate than the more common term "Root Regeneration Potential," which implies a regrowth of roots previously lost. Such root loss, while often occuring during lifting, does not seem to be prerequisite to the RGP response, as we will show later (see Part II). Additionally, the term "root regeneration" is commonly used in the rooting and tissue culture literature with an entirely different meaning. While the term "potential" might lead to some confusion with water relations terminology, as suggested by E.K.S. Nambiar (pers. comm.), the concept of a potential for growth is germane to this field, since it describes a maximum rate of growth when all external conditions are favourable. If "initiation" or "elongation" rate is measured, in contrast to length, weight, or volume, these words might be substituted for "growth" for clarity.

The standard method of measuring RGP is relatively straightforward. Seedlings are lifted, and any new white tips removed. The seedlings are then potted and held in a test environment under ideal conditions for root growth as determined for the species in question. After 28 days, they are excavated and new root production is quantified.

Conditions in the test environment can have a substantial influence on the test results. It is well recognised that soil temperature and moisture can strongly affect the expression of RGP (see Part III), and these variables are adequately controlled in most studies. However, recent work has shown that air temperature, photoperiod and potting medium also can be very important, causing up to a 40% difference in test results in Douglas fir seedlings under some conditions (Thompson and Timmis, 1978). This underscores the importance of maintaining rigorous control over all aspects of the test environment and cautions us to be wary of the results of studies in which such control was not carefully maintained and reported.

Finally, Riedacker (1976, 1978, pers. comm.) has expressed scepticism as to the value of this measurement procedure. He argues that, while a measurement of RGP made in the manner described above may have certain value as a practical index for seedling production and planting purposes, its utility in physiological work is limited. In order to gain fundamental understanding of the physiology of RGP, he recommends frequent and concurrent measurements of many aspects of root growth. This can be accomplished with tree seedlings using "minirhizotrons" (Riedacker, 1974).

PART II: PHYSIOLOGICAL MECHANISMS

There is general agreement in the literature that initiation of new root primordia, whether occurring at the base of a cutting or on an existing root system, must follow a stimulus originating somewhere in the shoot (Richardson, 1953b; Hess, 1969; Eliasson, 1971; Hermann *et al.*, 1972; Zaerr and Lavender, 1974; Farmer, 1975; Lee and Hackett, 1976; Carlson, 1977; Webb and Dumbroff, 1978), and that this stimulus is apparently transported through the phloem (Gilmore, 1962; Hess, 1969; Lavender *et al.*, 1970).

Sites of origin of the root growth stimulus

Likely sites for origin of a rooting stimulus within the shoot are the buds, the leaves, and the terminal and lateral (cambial) meristems.

Sites of origin in conifers are different from those in woody angiosperms (hardwoods). Studies with Douglas fir seedlings suggest that, at least in this species, the source of root growth stimulus is the leaves (Lavender *et al.*, 1970; Lavender and Hermann, 1970; Lavender and Wareing, 1972). Ritchie (unpubl.) found that bud removal had only a modest effect on RGP of November-, December-, and January-lifted Douglas fir seedlings, while girdling and needle removal completely prevented initiation of new roots. Similar results have been reported in red pine *(Pinus resinosa* Ait.) by van den Driessche (1978). Likewise, disbudding ponderosa pine *(P. ponderosa* Laws.)seedlings had no effect on root elongation (Zaerr, 1967). Bhella and Roberts (1975) found no relationship between rootability of Douglas fir cuttings and the presence of buds, while the opposite effect was reported by Roberts and Fuchigami (1973). Rootability of conifer cuttings and RGP may not be comparable phenomena, however, because they may respond differently to bud dormancy (Roberts and Fuchigami, 1973).

The sites of origin may vary seasonally (Riedacker, 1976). Lavender *et al.* (1975) showed that Douglas fir buds do export an essential factor for root growth in *autumn*, but not in winter or spring. Gilmore (1962) speculated that a stimulus from the buds is needed for new root growth in loblolly pine *(Pinus taeda L.).* It is also possible that buds are stimulated by material exported from leaves in Douglas fir (Hermann *et al.*, 1972).

The picture is further complicated in hardwoods by the annual loss of leaves. Observing that root growth ceased in silver maple *(Acer saccharinum* L.) seedlings within days after defoliation and resumed as soon as new leaves appeared, and that girdling produced a similar effect, Richardson (1953b) concluded that a growth promoter or precursor in the leaves was necessary for root growth in this species. However, root growth occurs during winter in the absence of leaves; therefore, he concluded (1958) that this stimulus is apparently transferred to the buds in the autumn. He also showed that buds must be in a non-dormant state to produce this effect.

Pecan *(Carya illinoensis* (Wang.) K. Koch) stem cuttings required leaves to produce roots (Taylor and Odom, 1970). When leaves were removed from rooted aspen *(Populus tremula* L.) cuttings, root growth ceased within 24 hours. This effect has been noted in numerous species (Hartman and Kester, 1975). Selim (1956, cited by Hess, 1969) demonstrated that leaves accounted for 78% of the rooting response in *Perilla* cuttings, while buds accounted for 15% and the stems 7%.

New root growth in tung *(Aleurites fordii* Hamsl.) trees was inhibited by removal of either buds or stems (Neff and O'Rourke, 1951). Trees with disbudded stems grew more roots than decapitated trees, suggesting either manufacture or storage of stimulus in the stem. Work of Farmer (1975) and Webb (1977) also suggests the presence of root promoters in angiosperm stems. Removal of buds from *Pistacia chinensis* Bunge. reduced RGP only in non-dormant seedlings (Lee and Hackett, 1976). The presence of non-dormant buds also stimulated root regeneration in red oak *(Quercus rubra* L.) seedlings (Larson, 1970). Leaf removal from red oak in autumn reduced RGP the following spring (Larson, 1975), suggesting again that leaves and buds play different roles during different seasons.

Two very closely related oak species displayed a markedly different response to disbudding just prior to the RGP test (Lee *et al.*, 1974). Complete disbudding of scarlet oak *(Quercus coccinea* Muenschh.) had no effect on RGP, while similar treatment resulted in a substantial reduction of RGP in pin oak *(Q. palustris* Muenschh.). The influence of buds could be imitated by indolebutyric acid (IBA) applied directly to the roots.

Lavender and Wareing (1972) postulated the existence of a substance produced in the root that moves to the leaves and stimulates them to produce rooting promoters. Since cytokinins, when applied externally, did not produce these results, the authors suggested a possible gibberellin (GA) effect. Later work (Lavender *et al.*, 1973) indicated that GA exported from Douglas fir roots promotes the breaking of fully chilled buds in spring when soil temperatures increase. There is also evidence that roots produce factors that, in turn, stimulate shoots to send assimilates to the root system (Kandiah and Wilmaladharma, 1978; Carmi and Koller, 1978; Wareing, 1970).

Work with rooting of cuttings suggests that the cambium may also be implicated in the manufacture or transfer of a root growth stimulus. New root primordia in Douglas fir cuttings arise from callus tissue, which, in turn, is produced by the cambium, suggesting a link between factors regulating cambial and root activity (Bhella and Roberts, 1975). Douglas fir cambium has neither an endogenous dormant period (Worrall, 1971; Bhella and Roberts, 1975) nor a chilling requirement (Lavender *et al.*, 1970), and its activity in spring is stimulated by swelling buds (Worrall, 1971) and leaves (Lavender *et al.*, 1970).

Control of cambial growth by bud activity is even more pronounced in hardwoods. Lateral roots of *Pistacia chinensis* are initiated in the cambium, leading Lee and Hackett (1976) to postulate that non-dormant buds stimulate new root growth by providing auxin and another substance to the cambium, which becomes active and initiates new root primordia. It is well known that lateral roots of both angiosperms and gymnosperms arise most commonly in the pericycle adjacent to the primary phloem tissue that transports material from buds and leaves (Esau, 1965; McCully, 1975).

Nature of the root growth stimulus

Many studies have shown that root initiation and root elongation are different processes mediated by different factors (Richardson, 1953b, 1958; Street, 1969; Lavender and Hermann, 1970; Larson, 1975; Torrey, 1976; Carlson, 1976). The growth-regulating hormones that trigger root initiation have been the subject of considerable study (Hartman and Kester, 1975; Torrey, 1976) and it is well-established that the auxins are of primary importance in this connection (Burstrom, 1957; Åberg, 1957; Hess, 1969; Street, 1969; Leopold and Kriedemann, 1975). It is not clear, however, whether auxins alone are capable of producing the rooting response (Greenwood *et al.*, 1974) or whether they must act in concert with certain so-called co-factors (Street, 1969) that might originate in the leaves (van Overbeek *et al.*, 1946) or stems (Kawase, 1964). Hess (1969) discusses the evidence for such rooting co-factors and proposes several possible modes of action.

Auxin concentration is also important, with higher concentrations tending to stimulate the initiation of lateral-root primordia and lower concentrations stimulating elongation (Zaerr, 1967).

It is also probable that auxins affect root growth indirectly through their effect on other hormones, or *vice versa* (Farmer, 1975). Street (1969) cites evidence that implicates a phytochrome system in auxin-induced lateral-root initiation; this might involve shoot-to-root translocation of a phytochrome-mediated substance. Root initiation in lodgepole pine *(Pinus contorta* Dougl.) and white spruce *(Picea glauca* (Moench.) Voss) seedlings may be a light-activated hormone response (Carlson, 1976). Root growth of Douglas fir in January (Ritchie, unpubl.) and red pine throughout autumn and winter (van den Driessche, 1978) was completely blocked when shoots were kept in darkness, while darkness had no effect on root growth in red oak seedlings (Larson, 1970).

While some workers (Zaerr, 1967; Lavender and Hermann, 1970) were unable to show an effect of exogenous auxin on new root growth in conifers, Lee *et al.* (1974) noted a marked increase in RGP of *Pistachia chinensis* following a 20-second, 200 ppm IBA dip. Zaerr (1967) monitored endogenous indoleacetic acid (IAA) levels in ponderosa pine seedling roots and stemwood and found no correlation between the IAA peak and RGP. Several workers have reported that rootability or root production is enhanced by auxin treatments only when buds are not physiologically dormant (Neff and O'Rourke, 1951; Hermann *et al.*, 1972; Bhella and Roberts, 1975), suggesting that an auxin/inhibitor balance (Lavender *et al.*, 1970; Roberts and Fuchigami, 1973) or an auxin/co-factor interaction may be involved.

The role of other hormones in new root production has received far less attention than that of the auxins. Gibberellins apparently have no direct effect on root growth in conifers (Lavender and Hermann, 1970; Pharis and Kuo, 1977), but may have an indirect effect through their influence on the distribution of photosynthate. In angiosperms, the effect of GA on root growth may be inhibitory, promotive, or neutral, depending upon species, GA concentration, and timing of application (Low, 1975; Shininger, 1975). These effects are often mediated by light (Shininger, 1975; Hansen 1975, 1976). The facts that GA levels are sensitive to red light and under photoperiodic control, that chilling can increase GA levels in buds of many angiosperms (Leopold and Kriedemann, 1975), and that delay of bud break occasioned by cold soil can be eliminated by GA (Hermann *et al.*, 1973) provide indirect evidence that GA may influence root regeneration through its role in dormancy release. GA levels apparently do increase concomitantly with dormancy release in some species (Bachelard and Wightman, 1974).

Cytokinins also are involved in bud burst and therefore may indirectly influence RGP. Cytokinin levels in sugar maple *(Acer saccharum)* increased in the spring when bud and root activity increased (Taylor and Dumbroff, 1975); however, a subsequent study (Dumbroff and Brown, 1976) indicated that the increase occurred slightly after dormancy release. Cytokinin-like factors necessary for spring root growth of red oak may have been exported from the leaves and stored in an inactive form (Larson, 1978). Support for this idea comes from Alvim *et al.* (1976), who observed an increase in zeatin riboside, a readily transported form of cytokinin (Skene, 1975), in the xylem sap of willow *(Salix)* just prior to spring growth, and from Hewett and Wareing (1973), who reported an early spring peak in cytokinin activity in the buds and sap of *Populus* × *robusta.*

Ethylene also may affect root growth indirectly through its influence on shoot growth (Farmer, 1975), or it may affect root growth directly. Leopold and Kreidemann (1975) cite earlier work demonstrating a direct stimulation of root initiation by ethylene; however, ethylene is generally considered to be a strong inhibitor of root elongation.

Abscisic acid (ABA) is synthesised in the root cap and appears to strongly inhibit root initiation and elongation (Pilet, 1972, 1975; Böttger, 1978). Furthermore, it has been positively implicated in the induction and release of bud dormancy in Douglas fir (Webber *et al.*, 1979) and root dormancy in Sitka spruce *(Picea sitchensis* (Bong.) Carr) (Philipson and Coutts, 1979). Thus ABA may exert either direct or indirect influence over RGP.

Bud dormancy and RGP

Much of the evidence cited above indicates that RGP periodicity is linked to the bud dormancy cycle. Dormancy in trees and woody plants has been adequately reviewed elsewhere (e.g., Samish, 1954; Vegis, 1964; Romberger, 1963; Perry, 1971; Wareing and Saunders, 1971; Noodén and Weber, 1978) and will only be summarised here. The dormancy cycle in Douglas fir will be used as an example because it is well documented and relevant to forestry (Lavender *et al.*, 1968; Lavender and Hermann, 1970; Lavender *et al.*, 1970; Roberts and Fuchigami, 1973; van den Driessche, 1975). The cycle can be divided into four distinct but continuous phases (Fig. 1): (1) dormancy induction, (2) dormancy deepening, (3) true dormancy, and (4) quiescence. Following the period of active shoot elongation, the over-wintering buds are formed and dormancy induction begins, primarily as a result of moisture stress. [1] During this period, a return of favourable moisture relations can trigger a second flush of growth. Dormancy gradually deepens in response to shortening photoperiod and decreasing temperature. Finally, a physiological state is reached during which a return of favourable conditions will not result in a resumption of growth. This state is known as true dormancy or "rest" (Romberger, 1963).

Before growth can resume, buds must be exposed to chilling temperatures for a certain number of hours. In Douglas fir this so-called "chilling requirement" is approximately 1200 hours within a temperature range of 0° to 10°C according to Lavender and Hermann (1970) and van den Driessche (1975, 1977) or 1400 hours below 5°C according to Ritchie and Stevens (unpubl.).

The precise chilling requirement varies with the geographic origin of the seed and may be further influenced by climatic conditions during the dormancy deepening period (D. Lavender, pers. comm.). Fulfillment of this requirement renders the seedling quiescent, or capable of rapidly initiating growth if exposed to favourable conditions.

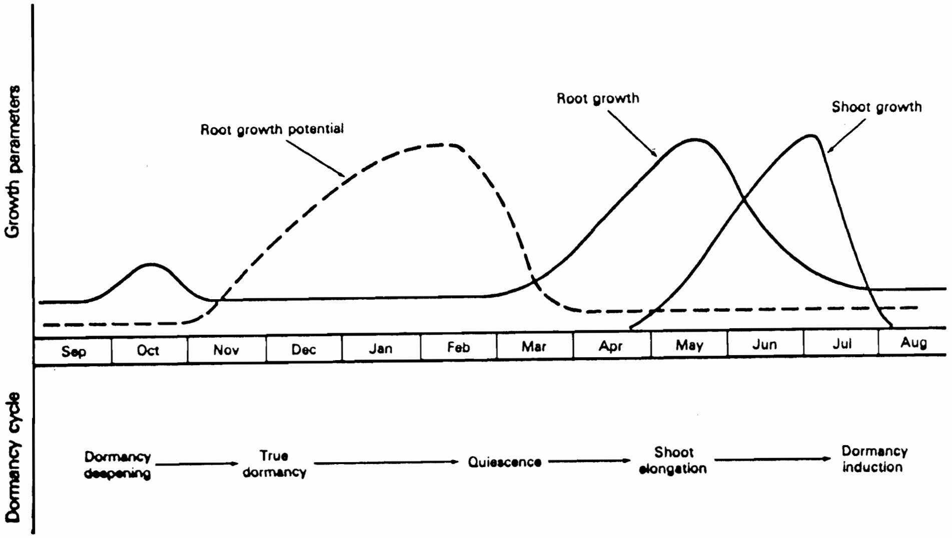

FIG. 1 — Annual cycle of bud dormancy in Douglas fir in relation to the periodicity of root and shoot growth of undisturbed seedlings and Root Growth Potential of transplanted seedlings.

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[1] Although dormancy induction in many conifers native to western North America is a function of moisture stress, European and eastern North American conifers seem to respond more to photoperiod (Hermann *et al.*, 1972).

Various aspects of growth of Douglas fir seedlings as they relate to dormancy also are depicted in Fig. 1. Root growth may occur all year in undisturbed Douglas fir seedlings (Krueger and Trappe, 1967) and many other conifers (except *Taxus* — Lathrop and Mecklenberg, 1971), and in certain hardwoods (Webb and Dumbroff, 1978; Webb, 1977) but not others (Richardson, 1958). However, there is clearly a seasonal peak of activity in early spring, just before bud break. When bud break and shoot elongation are occurring in spring and early summer, root activity declines dramatically, with an occasional autumn surge in response to rain and renewed soil moisture.

If seedlings are excavated and placed under conditions favourable for root growth, their ability to respond (RGP) varies seasonally, tending to be greatest in mid-winter. This response is, however, a reaction to highly artificial circumstances and in this sense is analogous to the seasonal changes in rootability of cuttings (see Riedacker, 1976, fig. 7).

It should be pointed out here that there is much interspecific variability with respect to these seasonal growth rhythms. The reader is referred to Riedacker (1976) for a review and synthesis.

The most compelling evidence linking RGP periodicity to the dormancy cycle is that which suggests that the RGP buildup in winter coincides with the accumulation of chilling hours and culminates with the fulfillment of the chilling requirement.

Taylor and Dumbroff (1975) found a high correlation between chilling hours received (at 5°C) and number of days to bud break — a commonly used indicator of dormancy intensity — in sugar maple. Similar correlations have been established for loblolly pine by M.P. Garber (pers. comm.). In another study with sugar maple, RGP in unchilled seedlings was far lower than that in chilled seedlings (Dumbroff and Brown, 1976).

D. P. Webb (1976b, 1977) demonstrated strong correlations among RGP, bud dormancy and chilling in sugar maple, silver maple and white ash (*Fraxinus americana* L.). Seedlings from the nursery were lifted in November, before an appreciable accumulation of chilling had occurred, and placed into 5°C storage. Sample seedlings were then retrieved at monthly intervals and maintained under favourable growing conditions. Days to bud break and RGP were measured and correlated with chilling hours. Dormancy was broken after exposure to 5°C for 2500 hours. Regressions of chilling hours V̲ dormancy intensity, chilling hours v. RGP, and dormancy intensity v. RGP gave r^2 values between 0.92 and 0.96. Similar results were reported for red oak (Farmer, 1975).

Several studies have been conducted on bud dormancy and RGP in conifers. The RGP peak in ponderosa pine occurs just prior to renewed bud growth (Stone *et al.*, 1963; Stone and Schubert, 1959a). Krugman and Stone (1966) exposed ponderosa pine seedlings to various numbers of cold (6°C) nights before assessing their RGP. RGP was very low (less than 10 cm per seedling) until the seedlings had experienced 90 cold nights. It then increased linearly to nearly 100 cm per seedling after exposure to 150 cold nights. This response may explain why the RGP peak varies from year to year in a given nursery. For instance, timing of the RGP peak in ponderosa pine at the Ben Lomond Nursery (coastal California) between 1961 and 1965 was closely related to the respective annual temperature patterns, which controlled the rate of chilling (Stone and Jenkinson, 1971; Stone, 1970).

Similar effects of chilling on RGP development have been reported in other coniferous species, including white fir (*Abies concolor* (Gord.) Engelm.) (Stone and Norberg, unpubl.,) western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)(G.H. Edwards, pers. comm.), loblolly pine (Rhea, 1977; J.R. Dunlap and J.G. Mexal, unpubl.), and Douglas fir (Lavender and Wareing, 1972).

Evidence has been offered for a direct link between RGP and dormancy intensity in Douglas fir (Ritchie and Stevens, unpubl.). Seedlings were lifted throughout the winter and placed into cold (+2°C) or freezer (−1°C) storage for various time intervals. When removed, their RGP was measured and plotted as a function of a dormancy release index (DRI):

$$\text{DRI} = \frac{10}{\text{mean days to terminal budbreak}}$$

where 10 represents the number of days required for terminal budbreak in fully chilled Douglas fir seedlings upon exposure to a favourable environment (Fig. 2). The data indicate that RGP increased as seedlings progressed through deep dormancy, then decreased following chilling fulfillment, presumably as roots entered into competition with elongating shoots for substrate. (see below)

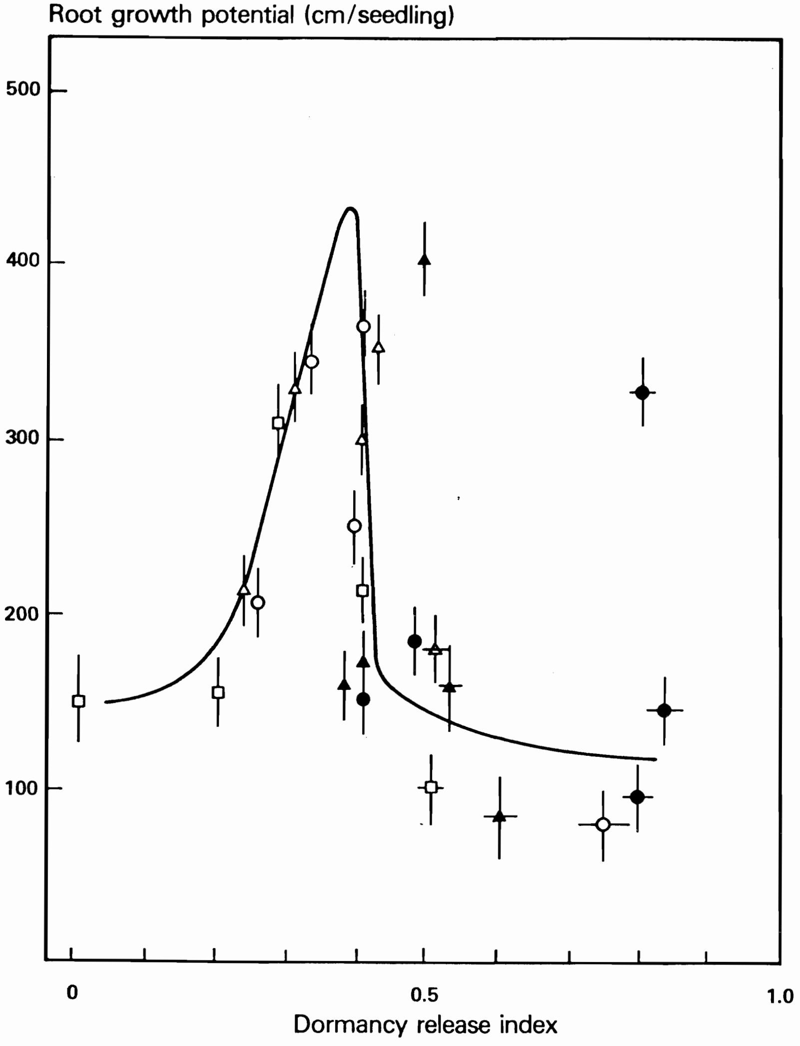

FIG. 2 — Relationship between Root Growth Potential and dormancy release index (calculated as: 10/days to terminal budbreak) of 2+0 Douglas fir seedlings that were either unstored (□), cold-stored for 2 (0) or 6 (●) months, or frozen for 2 (△) or 6 (▲) months. Horizontal and vertical lines are ± 1 S.E. Each point is the mean of 15 seedlings.

While it may be tempting to use a simple chilling sum to estimate dormancy intensity, it has been shown that temperature interruptions outside of the effective chilling range may actually negate all or part of the accumulated chilling response (Nienstaedt, 1967; Taylor and Dumbroff, 1975; Erez *et al.*, 1979). Warm days reduced the chilling effect of cold nights in western hemlock (E.G. Edwards, pers. comm.) and ponderosa pine (Krugman and Stone, 1966) seedlings, so that the number of cold hours needed to produce the RGP peak was increased in the presence of warm temperature intervals (Stone, 1967). Stone and Norberg (unpubl.) contend, based on the above evidence and later work with white fir, that nurseries located in areas whose winters are subject to interruption by unseasonably warm spells may be unable to consistently produce seedlings with a high RGP. It is also probable that intermittent chilling hours received in early autumn are ineffectual because of their juxtaposition with warm days.

Conversely, very low temperatures also may retard or even halt the physiological processes associated with chilling fulfillment (Samish, 1954; Taylor and Dumbroff, 1975). Seedlings grown in nurseries located in very cold regions therefore may tend to develop low RGP.

It is likely that the interaction between warm and cold intervals and its effect on dormancy release in forest tree seedlings changes throughout the winter, as the chilling requirement approaches fulfillment. Ideally, in order to maximise stock quality, nursery lifting schedules and handling guidelines for stock lifted at different times should be based on chilling sum rather than on calendar date. Before such schedules are entirely dependable, however, the warm/cold interation must be better understood.

Carbohydrates and RGP

Since root growth is an energy-consuming process, it can only occur at the expense of available metabolic substrates, which are principally carbohydrates. The most abundant translocatable carbohydrate in trees is sucrose. Reserve carbohydrates, on the other hand, are held primarily as starch in both conifers and hardwoods. Because starch is immobile, it must be synthesised and broken down in place. Since roots are non-photosynthetic organs, carbohydrates must be imported from leaves and stems. Roots are able to accumulate and store carbohydrates for subsequent metabolism within the roots themselves or for export to growing tissues in the shoots.Hence the question arises: Does new root growth proceed at the expense of stored carbohydrates, currently photoassimilated carbohydrates, or both?

Richardson (1953a, b) observed root growth of undisturbed silver maple seedlings growing under conditions either favourable or unfavourable for photosynthesis. His results led him to speculate that over short time periods root growth proceeded at the expense of currently produced photosynthates. Only when conditions unfavourable to photosynthesis were imposed for longer than one week did root growth proceed by apparently using stored carbohydrates. Webb (1976a) reported similar results with sugar maple. In fact, for most species studied, new root production seems to require currently photoassimilated carbohydrates (Eliasson, 1971; Ursino *et al.*, 1968; Ursino and Paul, 1973; Webb and Dumbroff, 1978; van den Driessche, 1978; Lavender *et al.*, 1975; Carlson, 1976). Much of the evidence to support this theory comes from girdling experiments (van den Driessche, 1975; Lavender *et al.*, 1970) or experiments in which shoots were held in a dark environment and root production observed (Carlson, 1976; van den Driessche, 1978). Generally, girdling completely prevents new root formation, while reducing the intensity of photosynthetically active light results in a proportional decrease in root production. Szaniawski and Adams (1974) reported that the rate of respiration, hence metabolism, in eastern hemlock *(Tsuga canadensis* (L.) Carr.) roots depends directly on the current rate of photosynthesis.

Shoots and roots compete within the plant for carbohydrates (Riedacker, 1976; Brouwer, 1977; D.P. Webb, 1976a; Webb and Dumbroff, 1978; Eliasson, 1971). The often-reported spring reduction in root growth coincident with renewed shoot activity (Fig. 1) has been ascribed to this root/shoot competition. Girdling below, or excising, terminal buds resulted in enhanced root growth in sugar maple (Webb and Dumbroff, 1978). When growth of *Populus tremula* cuttings (Eliasson, 1971) or sugar maple seedlings (D.P. Webb, 1976a) was limited by a low photosynthetic rate, increased shoot growth was attended by reduced root growth.

It is also worth mentioning that the time of maximum demand for photosynthate in conifers, especially for new shoot growth, corresponds with the time of minimum production, before new foliage has become efficient and after old foliage has declined in efficiency (Loach and Little, 1973).

The comparative sink strength of roots and shoots is essentially determined by their level of metabolic activity. This has been demonstrated with white pine *(Pinus strobus* L.) and red pine (Shiroya *et al.*, 1962, 1966; Schier, 1970), lodgepole pine (Etter and Carlson, 1973), Douglas fir (W. Webb, 1975a, b), Sitka spruce *(Picea sitchensis)* (Stahel, 1972), balsam fir *(Abies balsamea* (L.) Mill) (Loach and Little, 1973) and other species.

Sink strength is also affected by vitamins, certain nitrogenous compounds, and hormones (Eliasson, 1971; Webb and Dumbroff, 1978; Eliasson, 1978; Altman and Wareing, 1975; Hansen, 1976). It is suspected, for example, that GA modifies the normal distribution of photosynthates in conifers, sending more to the stem (Pharis and Kuo, 1977). Wallerstein and co-workers (1978) found a close relationship between GA and root starch concentration. While many reports have implicated hormones in carbohydrate allocation within plants, the exact nature of these relationships remains unclear.

Seasonal patterns of carbohydrate synthesis, storage, conversion and metabolism have been suspected as primary modulators of RGP periodicity in trees. Krueger and Trappe (1967) showed that sugar (predominantly sucrose and raffinose) concentrations in Douglas fir seedlings underwent a substantial buildup during late autumn and winter. Highest concentration occurred during January and February, coincident with the presumed RGP peak; during March, endogenous levels of sugars declined as carbohydrate metabolism shifted to favour starch synthesis. Similar results have been reported in Douglas fir by Winjum (1963) and Lavender (1964), in loblolly pine by Gilmore (1962) and in white pine by Shiroya *et al.* (1966). These data imply that low values of RGP reported in autumn-lifted stock result from a metabolic pool insufficient to sustain vigorous root production.

However, Krueger and Trappe (1967) found high root activity in undisturbed seedlings when carbohydrate levels were low (July, August, September). White pine seedlings translocated current ^{14}C-labelled photosynthate to the roots all year, but translocation was particularly high in August, September and October, a period of accelerated natural root growth but very low RGP (Ursino *et al.*, 1968); roots were apparently exporting stored assimilates in June and July. In addition, major carbohydrate metabolism may depend on dormancy release, so that natural root growth would not occur during dormancy, despite an adequate metabolic pool (Farmer, 1975).

Following girdling, food reserves in the roots of Douglas fir seedlings declined steadily but slowly, whereas root activity dropped immediately to zero. These observations led Zaerr and Lavender (1974) to conclude that, while root activity may require carbohydrates, the level of food reserves does not alone control root growth. Data of Ritchie and Stevens (unpubl.) support this view. Sugar and starch concentrations were compared with RGP of Douglas fir seedlings lifted throughout the winter and freezer-stored for 2, 6, 9 and 12 months. There was no apparent correlation between RGP and carbohydrate levels in foliage, stems, or roots (Fig. 3).

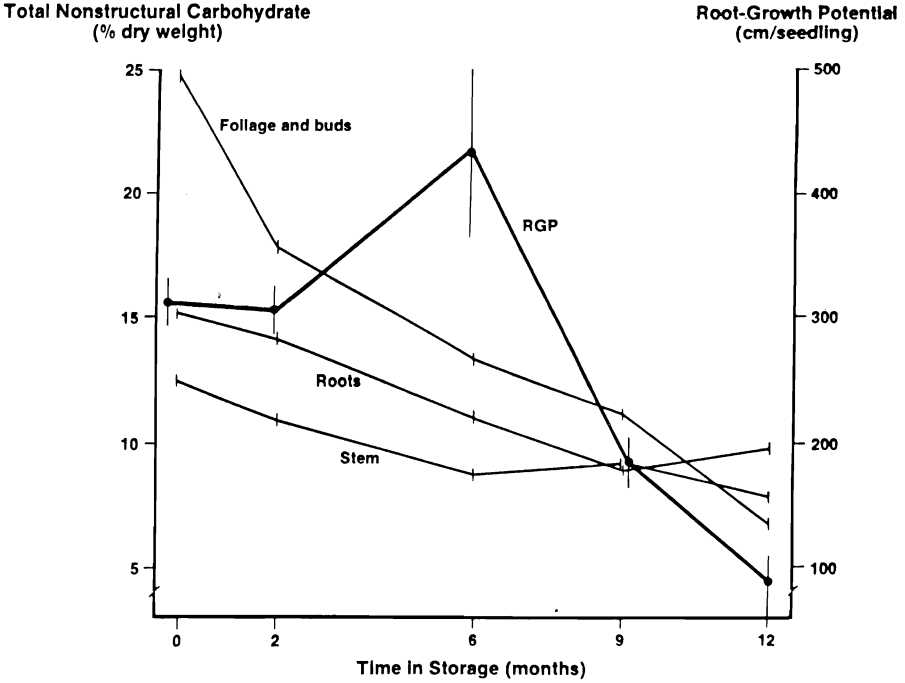

FIG. 3 — Depletion of total nonstructural carbohydrates and change in Root Growth Potential (cm/seedling, in parentheses, ± 1 S.E.) in freezer-stored (– 1°C) 2 + 0 Douglas fir seedlings. Each point is the mean of three replicates, each consisting of 3 seedlings pooled (total nine seedlings). Root Growth Potentials are means of 15 seedlings.

Summary and synthesis

Root growth potential appears to be a premature surge in spring root growth that is induced by an artificial early return to favourable growing conditions. As such, it is controlled by the same physiological mechanisms that trigger and sustain root growth in undisturbed seedlings. These are bud dormancy and, to a lesser extent, carbohydrate availability.

In summer, following the flush of new growth, moisture stress and photoperiod induce bud dormancy. As dormancy deepens, growth inhibitors (probably ABA) accumulate in the buds or bud scales until the effective promoter/inhibitor balance shifts to favour inhibitors, seedlings gradually become physiologically dormant, and RGP reaches a low level (Fig. 1). Cumulative low autumn and winter temperatures apparently result in a gradual reversal of this balance. An increase in activity of promoters such as auxins (Smith and Wareing, 1972) or gibberellins (Lavender and Wareing, 1972), or both, leads to a gradual release from true dormancy. As dormancy intensity weakens, buds apparently export increasing amounts of auxins and gibberellins, which in conifers may move to the leaves and stimulate the production or accumulation of root promoters. In deciduous species where no leaves are present, rooting promoters apparently remain in the buds or stems. In both cases, the promoter moves downward through the phloem to initiate root activity. These promoters must be continuously supplied from the shoot to the roots via the phloem, are not stored in the roots, and are essential for root activity, as is shown by the immediate cessation of root initiation following girdling. Since darkening the shoot environment also results in suspension of root growth in some species, the hormone systems involved may be light mediated, or the root promoters may move downward with products of photosynthesis.

In an undisturbed seedling growing in a natural environment, this potential for root activity is suppressed by unfavourable conditions, primarily cold soil, and is not expressed until conditions become favourable. It is doubtful that root distrubance, such as lifting or pruning, actually triggers this growth response, since several studies have demonstrated a seasonal RGP cycle in containerised seedlings where transfer from a natural to an artificial environment was not attended by root damage (Stone and Norberg, unpubl.; Thompson and Timmis, 1978; Sany, unpubl.). On the other hand, it has been suggested that RGP is, in part, an expression of the seedling's innate tendency to restore a favourable root/shoot balance following the loss of root tissue (von Lüpke, 1976). Such a tendency may strengthen the RGP response, but would not appear to control its periodicity.

Once new root growth has been triggered and is proceeding in a favourable environment, its rate seems to come under the influence of an internal carbohydrate source-sink regime. Prior to budbreak, roots are the major metabolic sink in the plant and are actively drawing upon currently assimilated (conifers) or stored (hardwoods) carbohydrate resources. Resumption of shoot elongation is accompanied by a rapid decline in root growth, suggesting a sink-strength reversal favouring the new shoot. After shoot elongation is completed, root activity may resume if environmental conditions permit.

The above summary is consistent with much of the empirical information on behavior of RGP. Transplanting in late spring gives a weak RGP response because of the reduced sink strength in roots as compared with that in active shoots. Transplanting in summer or autumn, on the other hand, gives a weak RGP response because seedlings are entering dormancy and physiologically preparing to cease, rather than to initiate, growth. Transplanting in winter gives an increasingly stronger response because, as seedlings are progressing toward complete dormancy release, the supply of rooting promoters from the shoot increases. Additionally, seedlings are highly sensitive to physical root disturbance during spring and autumn (Lavender and Wareing, 1972), so that handling shock may partially override any potential root growth response.

PART III: DEVELOPMENT OF ROOT GROWTH POTENTIAL

As outlined above, periodicity of root growth potential seems to be related to the bud dormancy cycle, while the strength of the response may reflect internal carbohydrate availability and allocation priorities. Therefore, cultural practices in the nursery (or greenhouse) that directly or indirectly affect these factors can be expected to influence the development of RGP. In this chapter we will review these factors, including (1) time of lifting, (2) root wrenching and pruning, (3) irrigation, (4) top pruning, (5) fertilisation and (6) cold storage.

Time of lifting

The factor to which RGP development seems to be linked most strongly is the time of year at which lifting occurs. In studies with a diverse range of tree species across broad geographical areas, nearly every species reported to date has followed the same general pattern. Typically, RGP increases during the autumn and winter months, peaks in late winter or early spring, and declines rapidly just prior to vegetative bud burst. Summer and autumn are normally accompanied by low RGP levels, with an occasional minor increase in mid or late summer (Table 2).

Despite some variability in exact timing of the RGP peak among species (Jenkinson, 1976c), seed sources (Jenkinson and Nelson, 1978), and nurseries (Stone *et al.*, 1963), the tendency for

TABLE 2. Season during which RRP peak occurred among several species at several locations.

		— Seasonal Pattern —		
Species	Location	Peak	Low	Author
Douglas fir	California	December-April	—	Todd (1964)
Douglas fir	Oregon	November-December	September-October	Lavender and Wright (1960)
Douglas fir	California	January-April	September	Stone *et al.* (1961)
Douglas fir	California	November-February	—	Jenkinson (1976c)
Douglas fir	California	December-January	—	Stone *et al.* (1962)
Douglas fir	Washington	February-March	October	Winjum (1963)
Douglas fir	California	November-February	—	Jenkinson (1977)
Ponderosa pine	California	December-April	—	Schubert and Baron (1965)
Ponderosa pine	California	March-May	June-August	Stone and Schubert (1959b)
Ponderosa pine	California	December-January	—	Stone (1967)
Ponderosa pine	California	January-February (depending on seed source)	—	Jenkinson (1975)
Ponderosa pine	California	January-March	—	Stone *et al.* (1963)
Ponderosa pine	California	January-February	July-September	Stone and Schubert (1959a)
Ponderosa pine	California	December	—	Jenkinson (1976c)
Jeffrey pine	California	December-March	—	Jenkinson (1976b)
Radiata pine	California	December-April	—	Krugman *et al.* (1965)
Red pine	Ontario, Canada	December-February	August	van den Driessche (1978)
Loblolly pine	S. Carolina	December-January	—	Rhea (1977)
Western hemlock	Oregon	December-March	—	Zaerr and Brown (1976)

TABLE 2. *Cont'd*

Species	Location	Seasonal Pattern — Peak	Seasonal Pattern — Low	Author
Noble-red fir	California	December-March (major peak in March)	—	Jenkinson (1976c)
Noble fir	Washington	February-March	October	Winjum (1963)
White fir	California	December-February	—	Jenkinson (unpubl.)
White fir	California	December-January	—	Jenkinson (1977)
Norway spruce	Central Europe	No peak	—	Tranquillini (1973) (cited by von Lüpke, 1976)
White spruce	Ontario	August-December	September-October	van den Driessche (1978)
White spruce	Ontario	April-May	August-September	van den Driessche (1978)
Black, spruce	Ontario	April-May	August-September	van den Driessche (1978)
Cedrus atlantica	France	December	—	Riedacker (1978)
Taxus sp.		January	June-August	Lathrop & Mecklenberg (1971)
Pin oak	N. Jersey	April	September-October	Lee *et al.* (1974)
Scarlet oak	N. Jersey	April	September-October	Lee *et al.* (1974)
Sycamore	S. Carolina	January-March	—	Rhea (1977)
Sweet gum	S. Carolina	December-June	—	Rhea (1977)
Yellow poplar	S. Carolina	January-March	—	Rhea (1977)

a summer low and a late winter peak is highly consistent. In fact, this phenomenon is becoming so widely appreciated that lifting "windows" in forest nurseries are often based on the anticipated occurrence of the RGP peak for the area and the species grown (e.g., Hermann *et al.*, 1972; Cleary *et al.*, 1978; Jenkinson and Nelson, 1978).

Root wrenching and pruning

Undercutting, wrenching and root pruning are nursery culturing practices widely used for conditioning seedlings before lifting (van Dorsser and Rook, 1972; Tanaka *et al.*, 1976). The method involves drawing a sharp blade beneath the nursery bed at a depth of from 10 to 15 cm, which severs the root systems (undercutting); then a dull blade tilted at an angle is drawn beneath the undercut seedlings at various depths and time intervals to prevent deep penetration of new roots and to promote soil aeration (wrenching). This practice causes early cessation of top growth and induces dormancy by increasing water stress. It also promotes increased root system fibrosity by stimulating lateral root formation (Carlson and Larson, 1977), and improves root/shoot balance.

Direct effects of root pruning and wrenching on RGP are dramatic. Bacon and Bachelard (1978) induced a 10-fold increase in RGP of caribbean pine *(P. caribaea)* seedlings by wrenching. Similar results have been reported for radiata pine (Rook, 1969) and Douglas fir (M. Menzies, pers. comm.). Wrenching depth and frequency are also important (van Dorsser and Rook, 1972; Dykstra, 1974; Bacon and Bachelard, 1978).

This effect probably acts through several mechanisms. Wrenching may reduce inhibitor levels in the root system. Wrenched radiata pine seedlings had higher relative growth rates and lower concentrations of inhibitors (per *Avena* coleoptile test) than unwrenched controls (Sweet and Rook, 1972). The root cap is known to be a source of ABA, and exogenous ABA has been shown to inhibit root growth and promote root dormancy in Sitka spruce (Philipson and Coutts, 1979). The continual removal of root tips by frequent wrenching may strengthen the promoter/inhibitor ratio. By increasing root metabolism, wrenching also probably improves the root system's ability to compete within the plant for carbohydrates. Rook (1971) found a tripling of the rate of ^{14}C-translocation to roots, as well as higher sugar and reserve starch concentrations in roots, following wrenching.

Root pruning increases the total length of the root system (Sutton, 1967) by stimulating lateral root development. This would promote a stronger RGP response by generating a larger basic framework for the new root network, as has been reported by Nambiar (this volume).

Wrenching or root pruning might also affect RGP by influencing the seedling's passage into physiological dormancy. This is suggested by evidence from Nikolaev (1959, cited by Sutton, 1969) and Cobb (1977), who observed that the RGP response to root pruning interacted strongly with the time of year. It has been shown that moisture relations during dormancy induction and deepening can affect the duration of the chilling requirement (Nelson, 1978), and this might also influence development of RGP. Therefore, altering seedling water balance by wrenching during late summer and autumn could result in a change in timing and perhaps strength of the RGP peak.

Irrigation

Although there is little published information on irrigation effects on RGP, it is reasonable to speculate that water stressing in late summer might influence dormancy, in a manner similar to stressing by wrenching. Alternatively, water stressing earlier in the summer could result in depressed photosynthesis, slowed translocation, and a reduction in metabolic substrate for root production.

Rook (1973) reported that seedlings which were subjected to water stressing for 6 weeks before lifting had a significantly higher RGP than unstressed controls. This increase was attributed to improved plant moisture balance, apparently resulting from greater stomatal control in the stressed seedlings. The difference disappeared after 40 days.

Very interesting data from Kandiko and Timmis (1980) suggest another possible effect. They found that 3 weeks of mild water stressing (−1000 kPa pre-dawn water potential) in western hemlock containerised seedlings resulted in an osmotic adjustment in the roots of about −200 kPa. This would presumably permit roots to maintain positive turgor and extract more soil moisture at low water potentials. Such an ability might be reflected in superior RGP under water-stress conditions (discussed later).

Top pruning

Top pruning is used to control height of nursery stock, and to facilitate lifting, packing and planting. This practice removes a portion of the physiologically important leaves and buds and often affects RGP.

Top pruning of red oak seedlings in autumn substantially reduced both shoot growth and RGP after March planting; however, moderate top pruning in spring may have been beneficial (Larson, 1975). Pruned scarlet oak seedlings had greater RGP than unpruned seedlings, while pruning pin oak had generally deleterious effects (Lee *et al.*, 1974). In white spruce *(Picea glauca)* seedlings, 25-50% removal of shoots slightly increased the number of new roots produced, while 75% removal significantly decreased new root initiation (Carlson, 1977).

Because of the rapid physiological changes that occur in buds during dormancy induction and deepening, timing of top pruning is probably critical to its effect on RGP.

Fertilisation

Since RGP is closely related to seedling vigour, it stands to reason that it should also be coupled with seedling nutritional status. Therefore, one might expect to be able to exert some measure of control over the development of RGP through fertilisation in the nursery. While this practice has not been studied in much detail, it seems apparent that fertilisation alone is not sufficient to ensure high RGP. Annual additions of sawdust and nitrogen to nursery soil in California, while they increased the organic content of the soil, did not result in improved seedling size or RGP unless annual fumigation was carried out simultaneously (Stone and Jenkinson, 1971). A. Long and S. Hee (pers. comm.) observed a decrease in RGP of Douglas fir seedlings fertilised with phosphorus in June, and speculated that some root burning might have occurred; however, spring fertilisation with nitrogen improved the RGP of seedlings lifted in February.

Cold storage

Cold-storing seedlings between lifting and planting is a valuable and widely used practice for many reasons (Hocking and Nyland, 1971), and can have profound effects on RGP in many species. These effects have been studied extensively (Stone and Schubert, 1959c; Stone and Benseler, 1962; Hellmers, 1962; Winjum, 1963; Lavender, 1964; Todd, 1964; Stone and Jenkinson, 1971; Hermann *et al.*, 1972; Etter and Carlson, 1973; van den Driessche, 1975, 1977; Jenkinson, 1976a, b; D. P. Webb, 1976b, 1977; Rhea, 1977; McCracken, 1978; Jenkinson and Nelson, 1978; Ritchie and Stevens, unpubl.).

In contrast to seedlings growing outdoors, cold-stored seedlings are isolated from the natural environmental factors necessary for normal development and physiological conditioning. As a result, RGP may decrease, increase, or remain unchanged during storage (Stone, 1970), depending upon storage temperature, lifting date, duration of storage, and other factors (see Table 3).

As with the other cultural practices discussed above, cold storage probably affects RGP through its interactions with bud dormancy and carbohydrate reserves. Storage temperatures outside the range of -2^0 to $+5^0$C are generally detrimental to seedling physiology and vigour

TABLE 3. Summary of the effects of seedling cold storage on RGP.

Species	Date Lifted/Stored	Time in Storage	Effect of RRP	Author
Loblolly pine	Oct.-Mar	Up to 8 mos.	detrimental	Rhea (1977)
Douglas fir, noble fir	Oct.-May	1 mo.	detrimental	Winjum (1963)
Douglas fir, noble fir	Jan.-Mar.	1 mo.	improved	Winjum (1963)
Douglas fir	Early autumn, spring	—	detrimental	Lavender (1964)
Douglas fir	Winter	—	improved	Lavender (1964)
Douglas fir	Early autumn, spring	—	detrimental	Hermann *et al.* (1972)
Douglas fir	Jan.-Mar.	—	extended peak	Hermann *et al.* (1972)
Douglas fir	Oct.-Dec., Apr., May	3 mos.	detrimental	Todd (1964)
Douglas fir	Jan.-Mar.	3 mos.	no effect	Todd (1964)
Douglas fir, noble fir	Nov.-Feb.	Up to 5 mos.	improved with t.i.s.*	Jenkinson (1976a)
Douglas fir, noble fir	Mar.	Up to 5 mos.	declined	Jenkinson (1976a)
Western hemlock	Oct.	1 mo.	detrimental	Zaerr and Brown (1976)
Western hemlock	Nov.-Mar.	1 mo.	no effect	Zaerr and Brown (1976)
Red fir, white fir	Oct.-Apr.	Up to 8 mos.	tended to increase with t.i.s.	Jenkinson (unpubl.)
Yellow poplar	Oct.-Mar.	Up to 8 mos.	all peaked after 3 mos.	Rhea (1977)
Sweetgum	Oct.-Mar.	Up to 8 mos.	improved, especially December	Rhea (1977)
Sycamore	Oct.-Mar.	Up to 8 mos.	all peaked after 3-5 mos.	Rhea (1977)
Sugar maple	Nov.-May	Up to 8 mos.	improved with t.i.s.	D. P. Webb (1976b, 1977)
Silver Maple	Nov.-May	Up to 8 mos.	improved with t.i.s.	D. P. Webb (1976b, 1977)
White ash	Nov.-May	Up to 8 mos.	improved with t.i.s.	D. P. Webb (1976b, 1977)

Time in storage.

(Hocking and Nyland, 1971). Prolonged sub-freezing temperatures can cause tissue desiccation and cell damage (van den Driessche, 1977; Hocking and Nyland, 1971), while temperatures above 5°C can result in respiratory depletion of carbohydrates or excessive buildup of storage fungi on the stock. Therefore, seedlings are generally stored at temperatures within their effective chilling range.

With seedlings lifted before or after the period of deep dormancy, when buds are not physiologically responsive to chilling, storage is often unsuccessful and RGP can be severely reduced (Bacon *et al.*, 1977; Todd, 1964; Hermann *et al.*, 1972; Stone and Jenkinson, 1971). These limits have been estimated at before 300 or after 1200 hours chilling sum for ponderosa pine (Stone and Jenkinson, 1971) and before 500 or after 1600 hours for Douglas fir (Ritchie and Stevens, unpubl.). On the other hand, when seedlings are placed in cold storage during deep dormancy, chilling received in storage contributes to the satisfaction of the chilling requirement (Lavender, 1964; van den Driessche, 1977). The result is that dormancy is gradually released, with a corresponding increase in RGP, until the chilling requirement is fulfilled and RGP declines.

Although most of the above data are from conifers, limited work with hardwoods suggests that they do not deviate appreciably from the above pattern. Webb (1976b) found that chilling accumulated in 5°C storage weakened bud dormancy and strengthened RGP in white ash seedlings lifted in late October. In a later study (Webb, 1977), maximum RGP in white ash, silver maple and sugar maple was attained after a storage-provided chilling sum of 3500 hours. Further chilling caused an RGP reduction in sugar maple but not in silver maple or white ash. With sycamore *(Platanus occidentalis* L.), yellow poplar *(Liriodendron tulipifera* L.), and sweet gum *(Liquidambar styraciflua* L.), RGP increased to a peak in cold storage and then declined (Rhea, 1977). The duration of the storage period required to produce the peak varied with date of lifting — the later the lifting date the less time required.

The above scheme reconciles many of the apparently conflicting results displayed in Table 3. It also suggests that cold storage might be used to release dormancy in seedlings with unusually long chilling requirements or grown in nurseries where natural chilling is not adequate.

Tree species adapted to warmer climates may have short chilling requirements, higher effective chilling temperature ranges (Noodén and Weber, 1978), or no chilling requirement at all. In these cases, effects of cold storage on RGP may not follow the above pattern. Rhea (1977), J. Dunlap and J. Mexal (unpubl.) and M. Garber (unpubl.) found this to be the case with loblolly pine.

It is also reported (Hocking and Nyland, 1971; Uhlig, 1977; M. Sandvik, pers. comm.) that seedling carbohydrate reserves are depleted during cold storage, and that this may lead to a gradual decline of RGP. Our own unpublished work with January-lifted Douglas fir seedlings (Fig. 3) confirms the carbohydrate depletion but not the RGP decline. While total nonstructural carbohydrate concentrations showed a nearly linear decline during 12 months in storage at −1°C, RGP increased gradually to a peak at 6 months, then fell.

As discussed earlier, RGP in conifers seems to depend upon currently produced assimilates transported to roots from the shoot. There is some evidence that cold storage may affect RGP indirectly by upsetting the photosynthetic mechanism. Etter and Carlson (1973) noted that, although RGP in cold-stored lodgepole pine seedlings was not positively correlated with root sugar content at planting time, sucrose contents in actively regenerating root systems were higher than in inactive roots. They postulated that the root's sucrose supply after planting was maintained by the shoot. If this were the case, then "damage during storage to either the photosynthetic or sugar transport system in the shoot . . . would result in inadequate export of sucrose to roots, which in turn affects [RGP]." Such damage was actually demonstrated by McCracken (1978) in *Pinus mugo* Turra and *P. radiata* seedlings, where cold storage reduced the rate of CO_2 uptake for 6 weeks following their removal from storage. The effect was more pronounced in spring-lifted than in winter-lifted stock, and recovery was impeded by high moisture stress after planting. Disorganisation of the photosythetic mechanism during storage was presented as a possible explanation. Deterioration of chlorophyll during storage also has been reported in Douglas fir seedlings by Lavender and Wareing (1972), who also showed that a daily period of low-intensity illumination greatly reduced the adverse effects of cold, dark storage.

Finally, Lavender and Wareing (1972) believe that vigour reduction in cold-stored seedlings is mediated through the root systems. When Douglas fir roots were maintained at 15°C during 2°C dark storage, subsequent mortality was reduced.

PART IV: EXPRESSION OF ROOT GROWTH POTENTIAL

So far, this review has examined the internal physiological conditions that must be met to maximise a seedling's potential to grow roots after transplanting. The degree to which this potential is expressed, however, depends upon two factors: (1) handling and planting quality, and (2) the nature of the planting site — specifically the temperature, moisture content and physical properties of the soil, and the air temperature.

Handling and planting quality

Although RGP can be reduced by improper handling between lifting and planting, different species respond differently at different times of the year. Douglas fir, for example, is most resistant to root abrasion and desiccation during winter, when RGP is highest (Hermann, 1962, 1964, 1967; Lavender and Wareing, 1972). This may not be true with some hardwood species, however (D.P. Webb, pers. comm.).

While planting quality has a profound impact on root system form (Tinus, 1978), its effect on RGP has not been evaluated directly. There are some indications, however, that "J" and "L" rooting can constrict phloem pathways and block carbohydrate translocation to roots. Hay and Woods (1978) analysed planted loblolly pine seedling root systems for soluble carbohydrates and found that severe planting deformities caused blockage of carbohydrate movement to taproot tips. Such blockage might result in reduced root growth, although this was not examined.

Improper planting could also result in excessive soil compaction around root systems, perhaps causing retarded root penetration due to soil impedance or root death due to anaerobiosis — especially when planting occurs on wet sites or in heavy soils. Conversely, air pockets around misplanted roots could promote root desiccation or at least retard establishment of intimate root-soil contact.

Soil temperature

Soil temperature exerts a major influence upon root growth of undisturbed seedlings (Heninger and White, 1974; Hellmers, 1963; Larson, 1970; Lyr and Hoffman, 1972), and optimum temperatures for root growth have been reported for a number of species. Generally, root development proceeds most favourably at between 18° to 25°C, depending upon species, with those species native to cooler climates tending to have lower optima (e.g., white spruce: 19°C) than those native to warmer climates (e.g., loblolly pine: 25°C).

Similarly, expression of RGP in transplanted seedlings is also highly temperature dependent (Riedacker, 1976). Stone and Schubert (1959a, b) found that root initiation and elongation in ponderosa pine seedlings lifted during different months and planted in a test enviroment varied with soil temperatures of 10°, 15°, 20° and 25°C, being greatest at about 20°C regardless of lift date, but varying somewhat with seed source and nursery.

A subsequent study with 2+1 Douglas fir seedlings (Stone *et al.*, 1962) disclosed very similar patterns. Here new root growth was more dependent upon elongation of existing lateral roots than on initiation of new laterals, but both processes were highly temperature sensitive. The result was that very little root production was observed at soil temperatures much below 15°C, even with stock lifted at the RGP peak in mid-January. The optimum soil temperature was approximately 21°C regardless of lift date. Western hemlock seedlings apparently have a slightly lower optimum of 18°C (Zaerr and Brown, 1976).

Larson (1970) studied the relationship between soil temperature and new root growth for transplanted red oak seedlings. Although he was not able to identify a single optimum temperature, seedlings always grew adequate roots at 24°C. Root growth of two tropical pines (*P. caribaea*, Morelet, *P. kesiya* Royle ex Gard.) showed a soil-temperature optimum of 25°—30°C (Abod, 1978).

From a practical standpoint, however, optimum soil temperatures for RGP expression have limited meaning in forest regeneration operations since most planting occurs during seasons when soils are cold. Even in summer, it is doubtful that optimum temperatures are attained in the rhizosphere. Information on the expression of RGP in cold soils would be far more useful. Such data are conspicuously absent from the literature.

Root sensitivity to soil temperature also varies seasonally. Transplanted ponderosa pine seedlings, for example, were able to grow roots at lower soil temperatures in spring than in autumn (Stone and Schubert, 1959a). The depressing effect of cold soil on new root growth in Douglas fir apparently acts through a delay of bud activity resulting from reduced GA export from cold roots (Lavender *et al.*, 1973).

Soil moisture

Moisture deficits exert a profound influence on nearly all aspects of plant growth, so it is not surprising that RGP expression is markedly affected by soil moisture availability. This effect has been clearly demonstrated in a number of studies.

Using polyethylene glycol solutions to impose a range of soil osmotic potentials on transplanted red oak seedling root systems, Larson and Whitmore (1970) observed excellent RGP expression at −30 kPa (field capacity) and virtually none at −600 kPa. Similarly, when Day and MacGillivray (1975) transplanted white spruce seedlings into soils at three different initial moisture contents, little or no new root growth occurred below −600 kPa. Roots of Aleppo pine (*P. halepensis* Mill) became dormant and suberised at soil matric potentials below −700 kPa (Leshem, 1970). Recent studies with loblolly pine, however, have shown that seedlings are capable of producing roots at initial soil water potentials as low as −1300 kPa (Dunlap and B. Snyder, unpubl.). In ponderosa pine seedlings lifted from October through April, there was always some new root growth at −500 kPa initial soil water potential, but only seedlings lifted in January could grow roots at −900 kPa (Stone, 1967; Stone and Jenkinson, 1970).

Similar trials were conducted by Ritchie and Stevens (unpubl.) with Douglas fir seedlings; an important difference being that in this study initial soil mositure was always at field capacity. Different watering schedules produced four separate soil moisture and plant water-potential regimes throughout the trials, with the control remaining at field capacity and the driest treatment approaching −1500 kPa soil matric potential at 30 days. In 25 trials, increasing soil and plant moisture stresses were always accompanied by decreased root growth (Fig. 4), although stock lifted in winter always had some new root growth, regardless of soil moisture. New roots that elongated under high moisture stress were short, crooked and dark in color. These roots may have elongated during the early days of the trial when soil moisture was near field capacity. Stone (1967) speculates that if new root growth is just getting under way and is potentially high when the seedling is planted, the roots may continue to elongate when planted in dry soil.

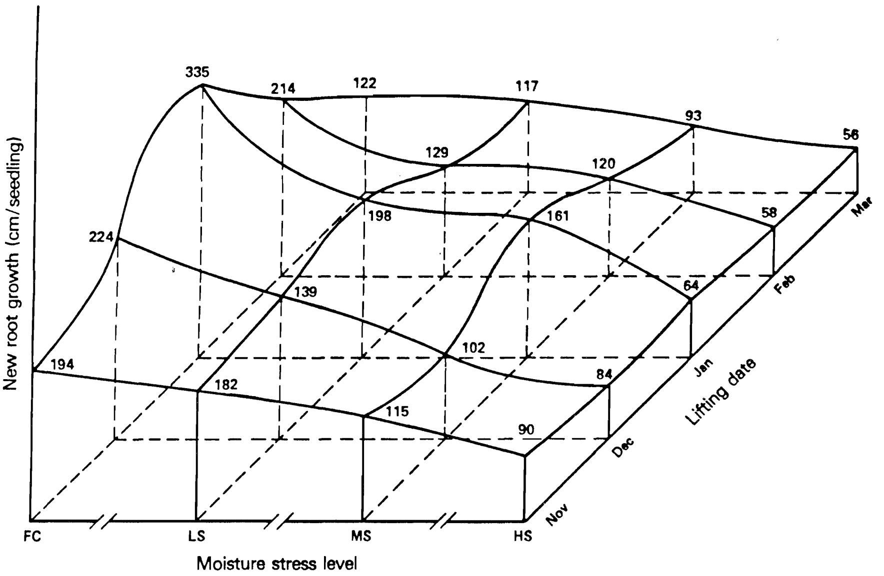

FIG. 4 — New root growth of 2+0 Douglas fir seedlings lifted on different dates and held under different conditions of soil moisture stress for 28 days. FC = soil continuously at field capacity; LS = low stress, soil began at FC and decreased to about −30 kPa; MS = moderate stress, soil began at FC and decreased to about −100 kPa; HS = high stress, soil began at FC and decreased to about −300 kPa. Each point is the mean of 75 seedling root systems. LSD (0.95) = 30 cm/seedling.

Soil characteristics

Root growth of several agricultural crop species is known to be influenced to a large extent by soil density and strength (Mirreh and Ketcheson, 1973; Goss, 1977; Marriott and Dale, 1976; Taylor *et al.*, 1966; Taylor and Gardner, 1963), with higher bulk densities tending to restrict root penetration. Also, different soil types exhibit distinct characteristics with respect to available moisture and resistance to movement (Rawlins, 1976), as well as predisposition to waterlogging. This in turn can affect root production by restricting aeration (Crawford, 1976). Death of root meristems can occur directly through anaerobiosis or indirectly through toxicity caused by products of anaerobiosis (such as ethanol and acetaldehyde) or by harmful substances produced by the waterlogged soils themselves (Coutts and Armstrong, 1976).

Forest tree species vary greatly with respect to their tolerance to waterlogging, and this is probably reflected in their ability to produce new roots under conditions of poor aeration. While flood-tolerant and intolerant species alike suffer from anoxia when the rooting medium becomes oxygen deficient, Crawford (1976) has attributed differences in tolerance to relative abilities of different species to detoxify the end-products of glycolysis through dark-fixation of carbon under anoxic conditions. Lodgepole pine is highly tolerant to anoxia and can grow roots immediately following flooding, while Sitka spruce is relatively intolerant and requires a recovery period before new root growth can proceed.

Air temperature

Although we have seen no published reports on the effect of air temperature after planting on RGP expression, it is tempting to speculate that such an effect could occur and may be important. Since bud dormancy is released by chilling, it stands to reason that chilling temperatures experienced after planting would have the same dormancy-weakening effect as chilling temperatures experienced before lifting or in cold storage. Therefore, if the relationship between RGP and dormancy intensity presented in Fig. 2 is valid, it would lead to the conclusion that RGP can change rapidly after planting if air temperatures remain within the effective chilling range.

PART V: SUGGESTIONS FOR FURTHER RESEARCH

The above synthesis has brought into focus many of the factors which affect the development and expression of RGP in forest tree seedlings. However, it has also surfaced several issues which must be addressed before RGP can be used routinely and with confidence in nursery, greenhouse and field regeneration operations. While a list of such issues is lengthy, a few items come immediately to mind:

1) A simple, rapid inexpensive test to replace the 30-day RGP assessment procedure is sorely needed.
2) The key to understanding and manipulating RGP seems to lie in its apparent dependency upon the status of bud dormancy. This relationship needs to be confirmed and clearly understood for our important forest tree species.
3) If the RGP/dormancy relationship is shown to be generally applicable and consistent, then much more must be learned about the physiology of dormancy induction and release in tree seedlings so that these processes can be manipulated or at least modelled with some degree of confidence. Some of the important unknowns are: (a) the nature of the chilling requirement (temperature, duration) for various species, provenances, and important families; (b) the effect of temperatures outside the chilling range on dormancy release (temperature thresholds, duration, etc.,); and (c) what role late summer and autumn weather conditions play in determining the nature of the chilling requirement.
4) The effect of seedling nutrition on RGP is very poorly understood. Studies should be undertaken to address nursery and greenhouse fertilisation regimes and the effects of mycorrhizas on RGP.
5) RGP expression in cold soils and the effect of cold weather after planting on RGP need to be investigated.
6) Much more must be learned about the physical and biological characteristics of planting sites and how these act and interact to influence the expression of RGP after planting.
7) Finally, while RGP is often positively correlated with survival, there are many exceptions to this rule. Such exceptions should be carefully evaluated to determine what other factors are important and under what conditions they operate. Also, it would be very useful to have a clear understanding of "how much RGP is enough" to ensure survival for various species across a range of sites and site conditions.

SUMMARY AND CONCLUSIONS

Root Growth Potential, a key indicator of planting stock quality, is affected by nursery practices and cold storage, and is expressed after outplanting (Fig. 5). Therefore, the appropriate time to assess RGP is just prior to planting.

The most important aspects of seedling physiology affecting RGP are bud dormancy and carbohydrate status. RGP increases as buds accumulate chilling and peaks with fulfillment of the chilling requirement. It then declines rapidly as the internal metabolic focus of the seedling switches to the elongation of new shoots.

In the nursery, induction and deepening of bud dormancy are affected by moisture stress, photoperiod and temperature. After dormancy is achieved, it is released by winter chilling: therefore late autumn and early winter temperatures are very important.

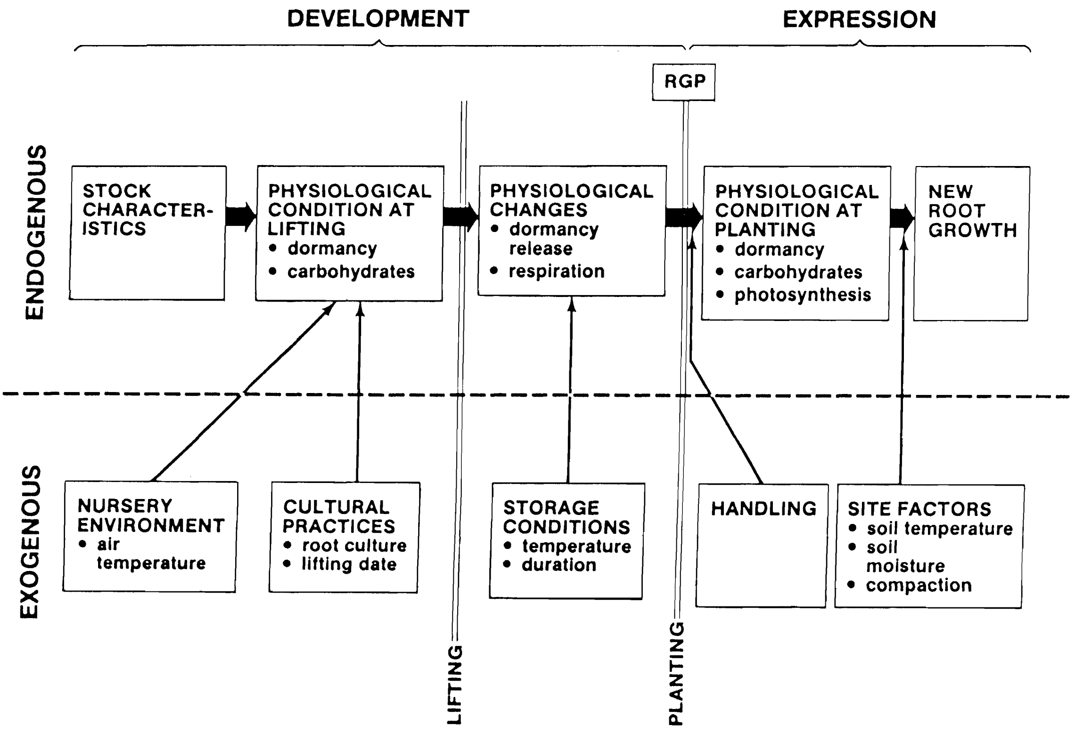

FIG. 5 — Summary of development and expression of Root Growth Potential in forest tree seedlings through nursery culture, storage and planting.

Many cultural practices can affect RGP, the most important being undercutting, wrenching, root pruning and date of lifting. The former acts by influencing induction of dormancy, enhancing root fibrosity, and improving root carbohydrate status. Date of lifting determines the status of bud dormancy that exists at the time seedlings enter storage.

The most important aspects of storage are temperature and duration. Storage temperatures just above 0°C fulfill chilling requirements; therefore, if seedlings are underchilled when lifted, cold storage can continue to release bud dormancy and improve RGP. On the other hand, if seedlings are not physiologically dormant at the time of lifting, or already have received sufficient chilling in the nursery to break dormancy, then storage has a detrimental effect upon RGP. Respiration of stored carbohydrates also occurs in cold storage and is highly sensitive to temperature — the higher the temperature the greater the respiratory losses. Carbohydrate loss through respiration may affect RGP.

RGP is fixed when the seedlings are moved from storage. Their ability to express RGP is mediated by environmental factors on the planting site. Of principal importance are soil temperature and soil moisture availability, with 18° to 24°C and field capacity being near optimum for many temperate zone species. Soil compaction or voids, as caused by misplanting, may also affect RGP expression. Additionally, if air temperatures remain low following planting and if seedlings have not fulfilled the chilling requirement in storage, RGP could change after planting due to a change in dormancy status.

Future research should focus on improving methodology, understanding the relationships between RGP and bud dormancy, determining how RGP expression is mediated by environmental conditions after planting, and building a clearer understanding of the relationship between RGP and seedling survival.

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