Target Seedling Symposium

Chapter 4
Root Growth Potential and the Target Seedling

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ABSTRACT

The review focuses on several key points regarding the conduct and interpretation of Root Growth Potential tests I n forest regeneration. Key points are 1) RGP is developed in the nursery and is expressed after planting; 2) RGP can be accurately assessed in as little as seven days in several species; 3) RGP is a very good indicator of seedling quality but only a fair predictor of survival; 4) survival prediction is only fair because RGP indicates plant quality, not site quality or planting quality; 5) RGP can indicate when seedlings possess high stress resistance or when seedlings are damaged; 6) RGP seasonal periodicity seems to be modulated internally by (a) the intensity of shoot dormancy and (b) the strength of the carbon sink in the growing shoot; and 7) despite problems associated with lack of accuracy and precision and often unrealistic expectations, RGP testing remains a valuable tool for assessing quality of planting stock.

4.1 Introduction and Objectives

The idea of a "target seedling" brings to mind morphological targets—stem diameter, height, root/shoot ratio. In practice, nearly all conifer seedlings are grown to “target” specifications based on one or more of the above variables. And for good reason, for considerable research and experience have shown that planting seedlings which fall below or above generally accepted morphological targets increases risk of failure or accelerates planting costs.

However, the modern, sophisticated forest nursery manager is now well aware that morphological targets, while important, fall short of guaranteeing high planting stock quality. It is also critical that he or she pay attention to physiological targets such as root desiccation resistance, low temperature tolerance, and the ability to endure rough handling.

One physiological target which has come into fashion during the previous decade is high Root Growth Potential (RGP = Root Growth Capacity = Root Regeneration Potential). Root Growth Potential is a seedling *performance* attribute (Ritchie 1984a) which enjoys the considerable advantage of being easily measured. However, its interpretation and use have been the subject of sometimes heated debate as researchers and practitioners have strugled to understand this novel “bioassay” concept of seedling quality testing.

The most recent comprehensive review of RGP (Ritchie and Dunlap 1980) is now a decade old. In this chapter we will attempt to update this review focusing on key aspects of testing and interpretation with a strong view toward practical application.

4.2 Brief Review of Basic Concepts

4.2.1 Historical overview

Philip Wakeley (1948) introduced the term “physiological Grade” into our lexicon of planting stock jargon. While this was a novel and powerful concept, it was not clear then how such grades were to be determined or quantified. As Wakeley himself put it: “How to recognize physiological grades before planting the seedlings . . . remains to be discovered.” Soon thereafter, Edward Stone, in a series of papers (c.f. Stone 1955, Stone and Jenkinson 1970, 1971) introduced the idea of using root growth as a measure of physiological grade. His work repeatedly showed that potentially poor performing lots of planting stock could often be identified in advance by their weak response in root growth tests.

International attention was drawn to Stone’s work and its importance in a IUFRO sponsored conference on Planting Stock Quality held in New Zealand in 1979 (Ritchie and Dunlap 1980). Since publication of those proceedings, interest in RGP has grown exponentially around the globe. Many private and public forestry organizations now routinely use RGP to screen nursery stock before planting (Sutton 1990, Landis and Skakel 1988). Private testing services have arisen throughout the United States and other countries. Even the landscape nursery industry has become interested in RGP testing of nursery transplant stock (Struve 1990).

Along with this surge of interest has come confusion, abuse, and misunderstanding of the technique and its interpretation. Some organizations rely heavily on RGP testing to verify stock quality while others have abandoned it, disappointed by its inability to predict field performance accurately and consistently. In this review we will discuss some of these issues toward developing a common sense understanding of what RGP measurements can and cannot do.

4.2.2 RGP development, expression, and measurement

RGP is defined as a seedling’s ability to grow roots when placed into an environment which is highly favorable for root growth (i.e., warm, moist, well lighted). This is a key point—RGP is distinctly different from root growth which occurs in a natural environment, as will be seen later. This ability is *developed* in a seedling while it is growing in the nursery and can be controlled by several nursery cultural factors such as time of lifting, root culturing to stimulate root fibrosity (Deans et al. 1990), fertilization, irrigation, top pruning, and (importantly) cold storage.

RGP is *expressed* after planting but this expression rarely matches the potential for root growth. RGP expression is very strongly affected by soil temperature and moisture, and also by air temperature, handling (Tabbush 1986) and planting quality. The proper time to measure RGP is immediately before the stock is to be planted. This is because RGP is constantly changing, e.g., in cold storage. So an RGP measurement carried out on seedlings before storage may or may not reflect their RGP following storage.

RGP is measured by potting seedlings in a growing medium and placing them into a warm, well lighted environment under conditions which are standardized for that nursery or testing lab. After one month in the test environment seedlings are extracted and the amount of root growth which has occurred is somehow quantified. The main problem with the test is the excessive duration of the test period. Results are often needed immediately—not after 30 days.

4.3 RGP Measurement: Do We Have a Rapid Test Yet?

4.3.1 Testing procedures and fundamentals

The first step in RGP testing is to wash the root system of sample seedlings thoroughly and clip off any white new roots to bring all the seedlings to the same starting point. Seedlings are then planted in pots, trays, or other containers. The growing media most frequently used are mixtures of peat, perlite, and vermiculite. The main consideration is that the media have good water holding capacity and at the same time adequate drainage to avoid development of a perched water table in the pot (Whitcomb 1984).

Seedlings are then placed in a spring-like warm environment conducive to "optimum" root growth. For this purpose, temperatures of air and/or media, relative humidity and daylength are often controlled. Here it is again pointed Out that RGP is to be differentiated from root growth expression in the field since the latter usually takes place under a suboptimal environment and is less than RGP.

The growing system used in evaluating RGP must provide an optimum, uniform and reasonably repeatable environment. Although most workers use a soil-less mix of some type, others have successfully used a hydroponic system (Brissette 1986, DeWald et al. 1984, Freyman et al. 1986, Johnsen and Feret 1986, Ludwig 1986, Palmer and Holden 1986, Rietveld 1989a, Ritchie 1984, Rose and Wales 1984, Williams et al. 1988) as well as aeroponic or mist systems (Brissette et al. 1988, Burr and Tinus 1988, Burr et al. 1989, Rietveld 1989a, 1989b). Each has advantages and disadvantages (Ritchie 1985, Rietveld 1989a).

Western white pine and ponderosa pine had more root growth in aerated water than in soil growing media (Ludwig 1986) while the opposite was true with loblolly pine (Brissette 1986, Freyman et al. 1986), and Douglas-fir (Ludwig 1986). Rietveld (1989a) reported that root growth of jack pine was faster and less variable in aeroponic culture than in soil or hydroponic culture. All three systems are viable alternatives and the pattern of root growth has been found to be closely related among three systems (Brissette 1986, DeWald et al. 1984, Rietveld 1989a, Ritchie 1985). The important consideration is adherence to the same method throughout a testing program with a given objective, once a system is selected.

4.3.2 Sample size

Owing to the labor intensive procedure of root counting, the following question has often been asked: how many sample seedlings does the RGP test require? There would not be one sample size that is optimum to all tests. The number depends on objectives, species, stock types, etc. The main consideration is to keep the sample as small as possible to minimize costs but yet to maintain a large enough sample to yield meaningful results. That is, to have confidence limits around means narrow enough to detect any differences among treatments, lots, lift dates, ages of trees, etc., that are being sought.

Statistically, choosing an appropriate sample size depends on: (1) the variability inherent in the population being sampled, and (2) the desired size of the differences to be detected. In general, smaller differences are more difficult to detect than large differences, especially as variability increases. A guide to determining the number of replications is offered by White (1984) in the *Forest Nursery Manual.*

Of the 32 papers we reviewed (which have been published since 1980), the sample size has ranged from 8 to 60. Six percent used fewer than 10 trees, 44 percent from 11 to 20 trees, 34 percent from 21 to 30 trees, and 16 percent over 31 trees.

4.3.3 Measurement procedures

Once the RGP test has been completed the next task is to determine how much root growth occurred. The most commonly used method is to count the number of new roots greater than a certain minimum length (0.5 cm and 1.0 cm used most frequently). Length of new roots can also be measured and summed to express total length of new roots. These two measures are generally closely correlated in many species. Index values are also used. The most notable is Burdett's Root Growth Index (RGI), which stratifies new root growth into six categories in a somewhat geometric progression (Burden 1979). RGI is widely used in some parts of Canada and found to reduce the time required to count new roots.

Change in volume or weight of roots has also been used to quantify root growth. These are measured at the beginning and end of the test and are subtracted to estimate root growth. The weight change method is used operationally in Swedish nurseries (D. Simpson, B.C. Min. For., pers. comm.). Area changes have also been successfully measured to estimate new root growth (Rietveld 1989b). Of the 32 papers we reviewed for methodology, 84 percent used number of new roots, 44 percent used root length, 16 percent used index values, 6 percent volume, and 3 percent root area (the percent values do not sum to 100 because many workers used more than one method).

4.3.4 Reporting results of RGP tests

All too often RGP test results are stated in terms of a simle mean—e.g., RGP = 100 new roots per seedling. The fallacy of this approach can be illustrated by the following hypothetical example. Suppose RGP is measured on a sample of 20 seedlings. Ten seedlings give 200 new root tips each, the other 10 die during the test. The mean RGP value is 100 new roots despite the high probability that this stock is in very poor condition.

As much information about test results should be given as possible, including: (1) sample size, (2) mortality during the test period, (3) the mean RGP value, (4) the standard deviation around the mean, (5) the highest and lowest values, and (6) a frequency distribution. This information gives the user a far better feeling for the physiological condition of the stock sample than a simple mean.

4.3.5 Opportunities for test shortening

The RGP test is considered to be one of the more reliable methods for assessing viability and vigor of planting stock. However, one major drawback of the method is a relatively long test duration. In the standard test procedure, seedlings are grown for one month before being assessed (Ritchie 1984a). One month is too long in many situations when important management decisions need to be made quickly with respect to disposition of stock in the event of suspected stock quality problems (such as frost and desiccation damage in nursery beds, mishandling during storage or transporting, etc.).

Studies conducted during the past decade have shown that shortening the test period to 14 or even 7 days is feasible for several species including Douglas-fir (Binder et al. 1988, Burr and Tinus 1988, Burr et al. 1989, Cannell et al. 1990, Simpson et al. 1988, Tabbush 1986), Engelmann spruce (Burr et al. 1989), interior spruce (Simpson et al. 1 88), Sitka spruce (Cannell et al. 1990), white spruce (Johnson-Flanagan and Owens 1985), western hemlock (Binder et al. 1988, Grossnickle et al. 1988), jack pine (Rietveld 1989a), loblolly pine (DeWald and Feret 1987, DeWald et al. 1 984, Freyman et al. 1986), lodgepole pine (Burdett et al. 1983, Simpson et al. 1988), maritime pine (Donald 1983), ponderosa pine (Burr et al. 1989), radiata pine (Donald 1983, 1988), red pine (Andersen et al. 1986), Scots pine (Mattson 1986), slash pine (Donald 1983), and western redcedar (Grossnickle et al. 1988).

4.3.6 Where are we today?

It is encouraging to find a volume of papers that report RGP results based on 7-15 day tests in many species. This clearly indicates that the test duration can be shortened to two weeks, or even one week, for a majority of tree species if tests are conducted under an optimum environment for root development.

Most of the above reports have shown that the 7-15 day RGP test can be used to detect differences in stock quality as affected by nursery treatments, storage, handling, etc. These types of comparisons are relatively straightforward as the changes in RGP can be compared with that of untreated controls. In operational application of this technology to reforestation programs, RGP of untreated controls is not often available. Since RGP exhibits distinct monthly fluctuations, additional testing would be needed to establish seasonal baseline data of each species at each nursery site over several years so that the results of any future tests could be compared at any time of year.

4.4 Interpreting RGP

4.4.1 RGP and survival

Numerous articles published on RGP concern the relationships between RGP and field performance. Ritchie and Dunlap (1980) reviewed the literature and reported that, out of 26 papers they surveyed, 85 percent showed a positive correlation. The remaining articles showed poor to inverse relationships. We've examined more recent literature since the above review and found a generally similar trend with 75 percent of 12 studies showing a positive relationship and 25 percent showing poor or no relationships.

Reasons for the lack of correlation are sometimes difficult to determine. However, there appear to be at least three. One is inadequate methods and procedures, such as use of excessively wet or dry media in pot tests, or insufficient supply of oxygen in hydroponic systems due to equipment malfunction or inadequate design. This would also include inadequate sampling procedures resulting in unrepresentative results. RGP tests can lack both accuracy and precision (Binder et al. 1 988).

The second reason relates to various steps after the seedlings have left nurseries and following the RGP tests. These include mishandling of stock during transport to

		RGP	
		Low	High
Field of Condition	Harsh	+	?
	Mild	?	+

Figure 4.1—*Failure of RGP always to predict field performance relates to the interaction of RGP with field conditions. Performance of poor stock planted on harsh sites or good stock on good sites is predictable. Performance of good stock on harsh sites or poor stock on mild sites is less so.*

planting sites or improper procedures such as planting trees in duff layers. Even the best stock with good RGP may not do well under such conditions. These problems could be overcome, however, by careful planning and design and by special effort on the part of everyone involved in the reforestation system.

The third possibility is the unpredictability of site and weather conditions in the field, factors over which we have little or no control (Burdett 1987). This may be explained using a matrix diagram of stock quality and field condition (Figure 4.1). Performance of poor stock planted on harsh sites and of good stock planted on mild sites is usually predictable. However, it is more difficult to predict performance of good stock planted on harsh sites or poor stock planted on forgiving sites. Because of these reasons, the correlation of RGP and field performance may not be high in some instances, as evidenced in our literature review.

4.4.2 The seed testing analog

Much of the current misunderstanding and dispute regarding RGP testing arises out of the misplaced expectation that RGP is designed to predict field performance (Binder et al. 1988), when, in fact, it is designed to evaluate seedling quality (Ritchie 1984). An important idea to keep in mind is that: *RGP testing is like seed testing.* Seed are tested under optimum conditions for germination. The report from the seed testing lab guarantees that the seed performed at a certain germination level *under* those test conditions. This does not guarantee the same level of germination after sowing in the greenhouse or nursery. Although one might expect a seedlot that tested out at 95 percent germination to give higher germination in the field than one which tested at, say, 30 percent, it is unrealistic to expect it to give 95 percent germination when sown in a cold wet nursery soil in April. This is common sense to nurserymen. It must also become common sense to foresters that RGP tests should be interpreted in the same manner. The test data guarantee that the stock was at some level of quality when tested. Nothing more; nothing less.

4.4.3 How much RGP is enough?

We ask this question having said that we hesitate to speculate on how much RGP is needed to ensure plantation success. However, since so much debate has surrounded this question and because it is so often asked, we would be remiss not to at least give it pause in this review.

A study conducted in British Columbia showed that the threshold value of interior spruce and lodgepole pine for good performance was 10 new roots greater than 1 cm in length (Simpson et al. 1988). Threshold values could also be determined for other species for which the positive relationship between RGP and field performance has been found (Burdett et al. 1983, Larsen et al. 1986,

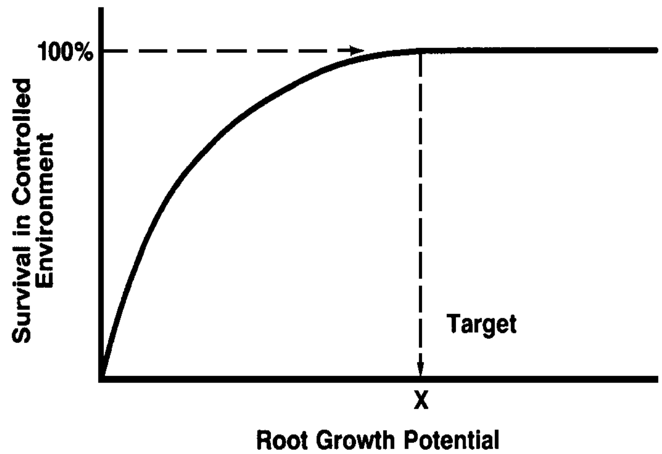


Figure 4.2 *--Illustration of an approach for determining threshold RGP values for survival in controlled environment or greenhouse tests.*

McCreary and Duryea 1987). These values would be helpful as a general guide of stock quality but would not predict survival under specific field conditions because of the reasons stated earlier.

Owing to the uncertainty of weather and site conditions, threshold values are difficult to estimate. In addition, costs of field studies are high. As a shortcut, we have conducted similar studies to determine threshold values under a more controlled environment in a greenhouse. A modified Burdett's (1979) root growth index was used to establish the relationship between RGP and four-week greenhouse pot test of seedling viability. We found that there was a curvilinear relationship between these parameters (Figure 4.2). We also found that the threshold values vary according to stock type and the duration of the test period even within the same species (Table 4.1). An appropriate RGP target could perhaps be established using the threshold value approach.

Table 4.1—*Threshold RGP values for two Douglas-fir stock types tested in a greenhouse (4-week RGP) and growth chamber (14-day RGP) environment.*

Stock type	Root Growth Index* 14-day test	28-day test
1+1	3.0	4.8
2+0	2.0	4.0

* Modified Burdett's (1979) index

4.5 RGP and Dormancy: How Are They Related?

Growth of the root system in tree seedlings is under control of both the external environment and various internal factors. Environmental factors which affect root growth are soil and air temperatures, soil matric potentials, soil aeration, soil strength, and other factors. In RGP testing these variables are held constant; nevertheless, RGP exhibits strong seasonal cycles. These cycles must be modulated by internal, rather than environmental, agents. The internal drivers of these seasonal cycles have been the subject of much research and debate.

An early theory was that these seasonal changes are modulated by changes in seedling carbohydrate reserves. This theory, however, is not well supported by experimental evidence (Ritchie 1982, Duryea and McClain 1984, Cannell et al. 1990). Another theory which enjoys considerable support is that seasonal changes in RGP are driven by the annual dormancy cycle. Ritchie and Dunlap (1980) reviewed early evidence supporting this view. Here we will examine evidence from studies reported since 1980 which bear on this hypothesis.

In many (but not all, see Phillipson 1988) species, these internal factors apparently originate in the shoot. Such factors are presumably: (1) chemical or hormonal messengers which either inhibit or promote root initiation, and (2) assimilates which sustain root elongation. This has been demonstrated in girdling, decapitation, and defoliation experiments (Lavender and Hermann 1969, Zaerr and Lavender 1974) and labeling studies with $^{14}CO_2$ (van Den Driessche 1987).

Several early investigators working with deciduous hardwoods (Richardson 1958, Webb 1 976, 1977, Farmer 1975) reported that seedlings exhibited very weak root growth when the shoots were in a state of intense dormancy, but exposure of these seedlings to chilling restored root growth. Similar studies with conifers suggested a strong relationship between chilling and RGP and dormancy intensity and RGP (reviewed by Ritchie and Dunlap 1980) indicating that RGP was in some way linked to shoot dormancy.

Other work with conifers in nurseries and in RGP environments has pointed to a distinct weakening of root growth when shoot activity is intense during spring and early summer (e.g., Winjum 1963, Stone et al. 1962).

These observations taken together suggest the following hypothesis for explaining the internal control of RGP:

Root growth tends to occur in a favorable environment unless impeded by:

(a) a *dormant* shoot (perhaps either by reducing the supply of promoters or increasing the supply of inhibitors to the root system), and

(b) a rapidly *expanding* shoot (by outcompeting the root for carbon).

Therefore, seasonal RGP peaks would be expected to occur during periods when: (1) dormancy intensity is weak, but (2) active shoot growth is not evident. This would usually be in late summer and early autumn, then again in late winter-early spring for most northern conifers.

4.5.1 Dormancy defined

Many of the problems of interpreting and communicating dormancy-related processes result from lack of a precise terminology and frame of reference. Recently Fuchigami et al. (1982) and Fuchigami and Cheng-Chu Nee (1987) have provided such a reference in their "Degree Growth Stage Model." Although developed mainly from work with hardwood species, this model appears to accommodate most dormancy-related observations reported for conifer seedlings. We feel that it has considerable merit and, when used in the context of seedling physiology and RGP, could make important contributions toward understanding and communicating dormancy related phenomena.

The degree Growth Stage (°GS) model portrays the annual developmental cycle of woody temperate plants as a sine wave cycling through 360°GS (Figure 4.3). The model contains five seasonal "point events" (indicated below the graph). These are:

<u>0°GS: Spring budbreak (SBB).</u> Defined as when bud scales part and the new leaf becomes visible. Growth rate is temperature-regulated and plants are highly susceptible to stress. This occurs around mid-March in coastal Oregon (L. Fuchigami, pers. comm.).

<u>90°GS: Maturity induction point (MI).</u> Between 90°GS and 180°GS plants will respond to shortening photoperiod and the state of rest will develop. However, this can be overcome if plants are artificially exposed to long days. In this stage, plants are not hardy to freezing temperatures. 90°GS occurs in early June in coastal Oregon.

<u>180°GS: Vegetative maturity (VM)</u>. This is the onset of rest. Before this point plants are dormant due to correlative inhibition. This stage of dormancy intensifies as chilling temperatures (roughly -3°C to 12°C) accumulate (Kobayashi et al. 1982). Cold hardiness also develops during this stage and is hastened by exposures to frost conditions. 180°GS normally occurs around September 20 in coastal Oregon.

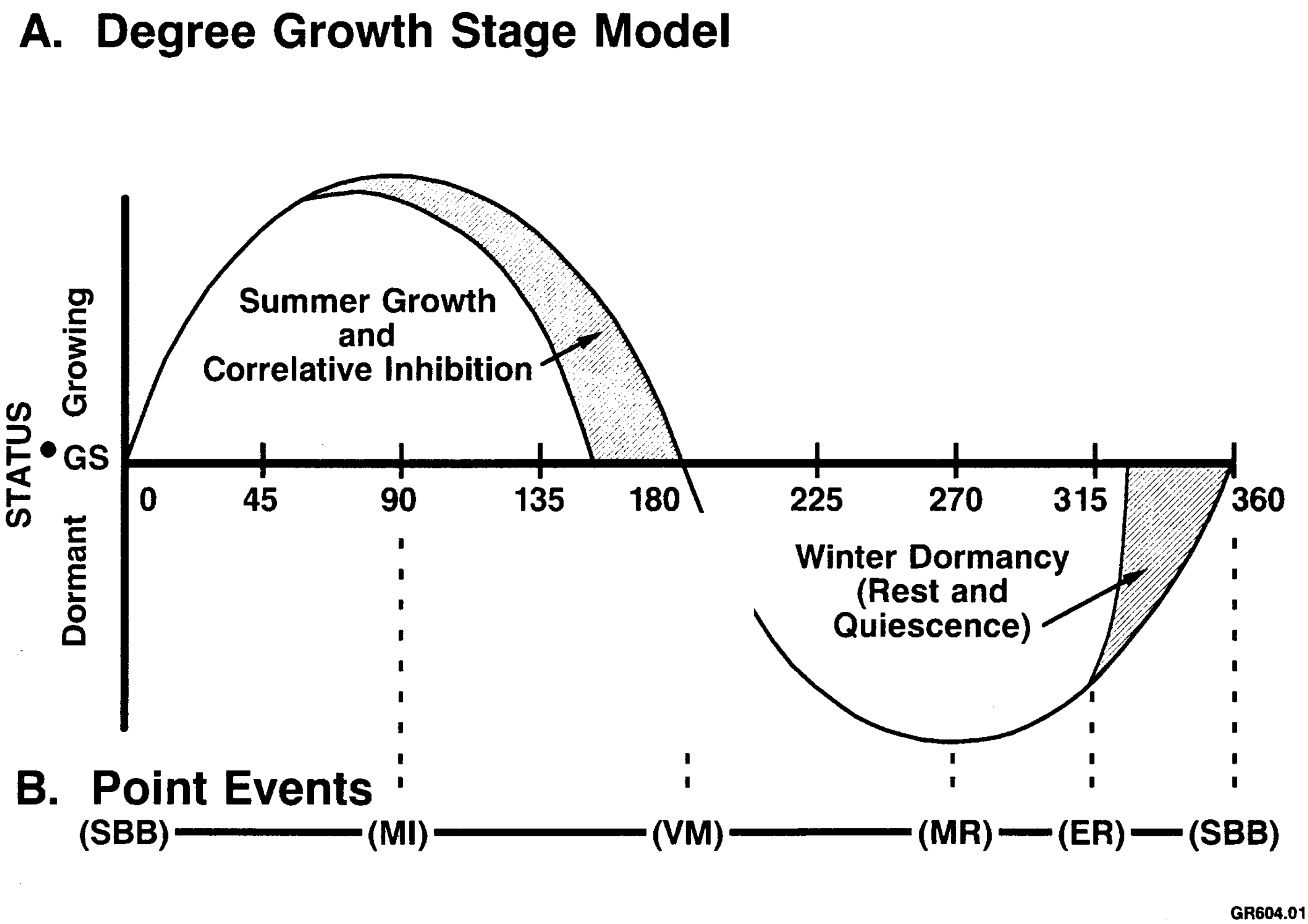


Figure 4.3—*A Degree Growth Stage (°GS) model for woody plants after Fuchigami and Cheng-Chu Nee (1987). See text for explanation. Reprinted with permission from HortScience 22:836 (1987).*

270°GS: Maximum rest. This is the point at which mitotic index (MI) reaches 0 and where plants require the maximum number of days in a warm, long day environment to force terminal budbreak. As a rule, many plants will break bud only after 200 such days. During this °GS, chilling temperatures release dormancy, rather than strengthening it, as during the previous °GS. Maximum Rest occurs around November 10 in coastal Oregon.

315°GS: End of rest. By this point, enough chilling has accumulated to complete rest but plants are held in dormancy by low temperatures. Spring budbreak (360°GS, 0°GS) is then stimulated by high temperatures, and the cycle repeats. End of Rest occurs at the end of December in coastal Oregon.

Dates provided are for the region around Corvallis, Oregon (N. at. 44° 35'). In more northerly latitudes the period from 0°GS to 180°GS would tend to be more compressed with respect to calendar dates, and from 180°GS to 360°GS would be expanded. Moving south, the opposite would occur.

4.5.1.1 RGP and degree growth stages

The above hypothesis predicts that RGP would behave in the following manner relative to the °GS Model (Figure 4.4). At 0°GS, RGP would be decreasing rapidly because expanding shoots are becoming increasingly strong carbon sinks. As shoot expansion draws to a close, between 45°GS and 90°GS roots should regain their priority for carbon allocation and RGP should begin to increase. In species which continue to exhibit shoot elongation throughout summer (e.g. loblolly pine), this RGP peak may be modest or nonexistent.

After 180°GS as dormancy intensifies, RGP would weaken considerably to a low point between 225°GS and 270°GS. Then as chilling releases dormancy, from 270°GS to 360°GS, RGP would again rise to a peak or plateau. It would then fall as shoots elongate and again outcompete roots for carbon. Seasonal peaks and valleys

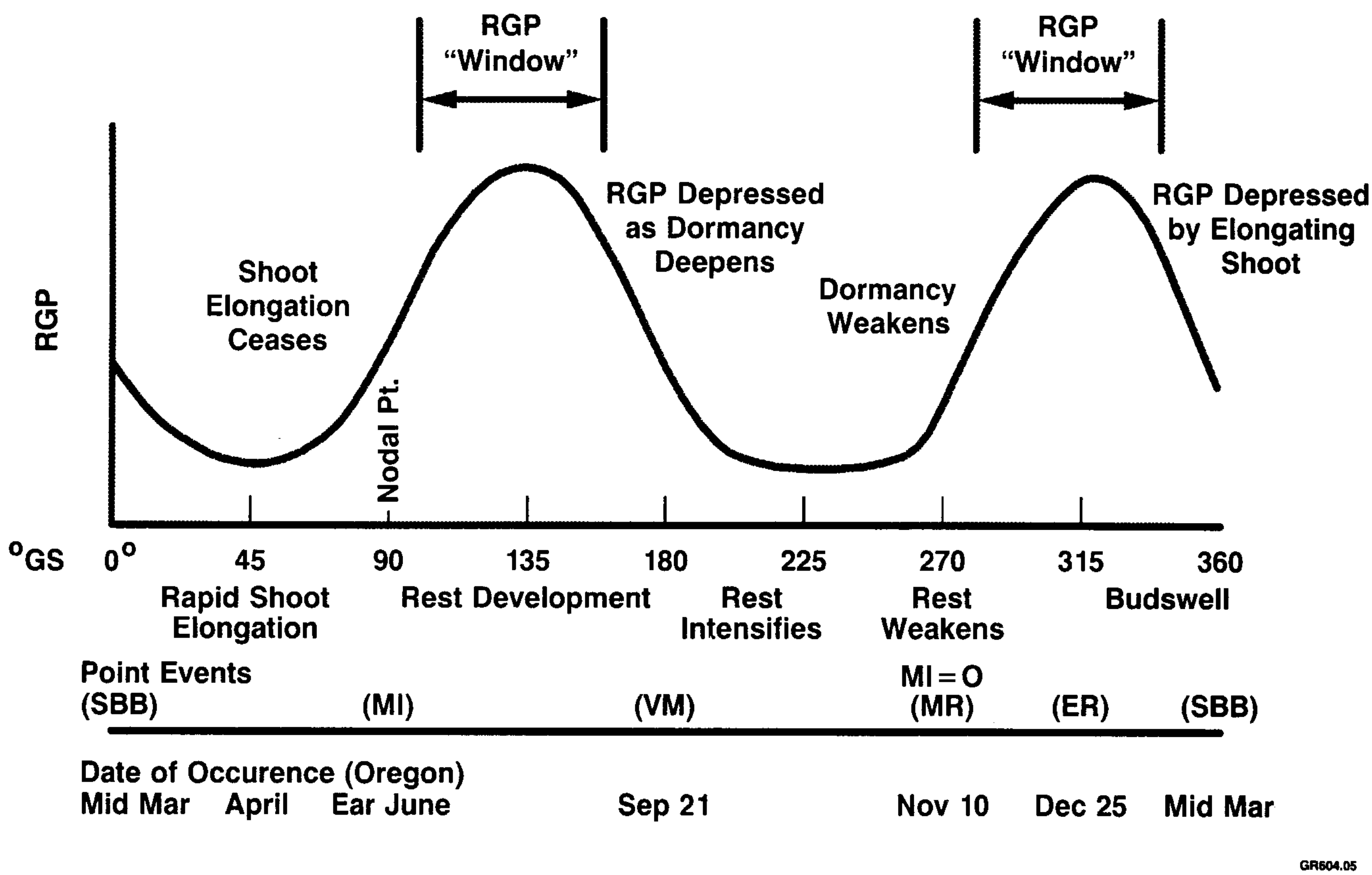


Figure 4.4—*Proposed model of seasonal changes of Root Growth Potential superimposed on Degree Growth Stages.*

of RGP, then, are modulated by changes in shoot dormancy status and sink strength.

4.5.1.2 Tests of the hypothesis

This hypothesis is suggested largely by seasonal RGP patterns reported in studies before 1980. To test the hypothesis, we will examine two case studies reported subsequent to 1980.

At least two difficulties arise in testing this hypothesis with existing data: (1) studies of RGP do not contain information on °GS, so these points must be inferred from reported calendar dates or observed phenological events, and the data calibrated accordingly, and (2) RGP studies are most often conducted during winter after the point of Maximum Rest (270°GS) Hence, only a small segment of the seasonal pattern is available for evaluation. This is understandable because most interest in RGP is during the "lifting window" which normally begins in December in Northwest nurseries.

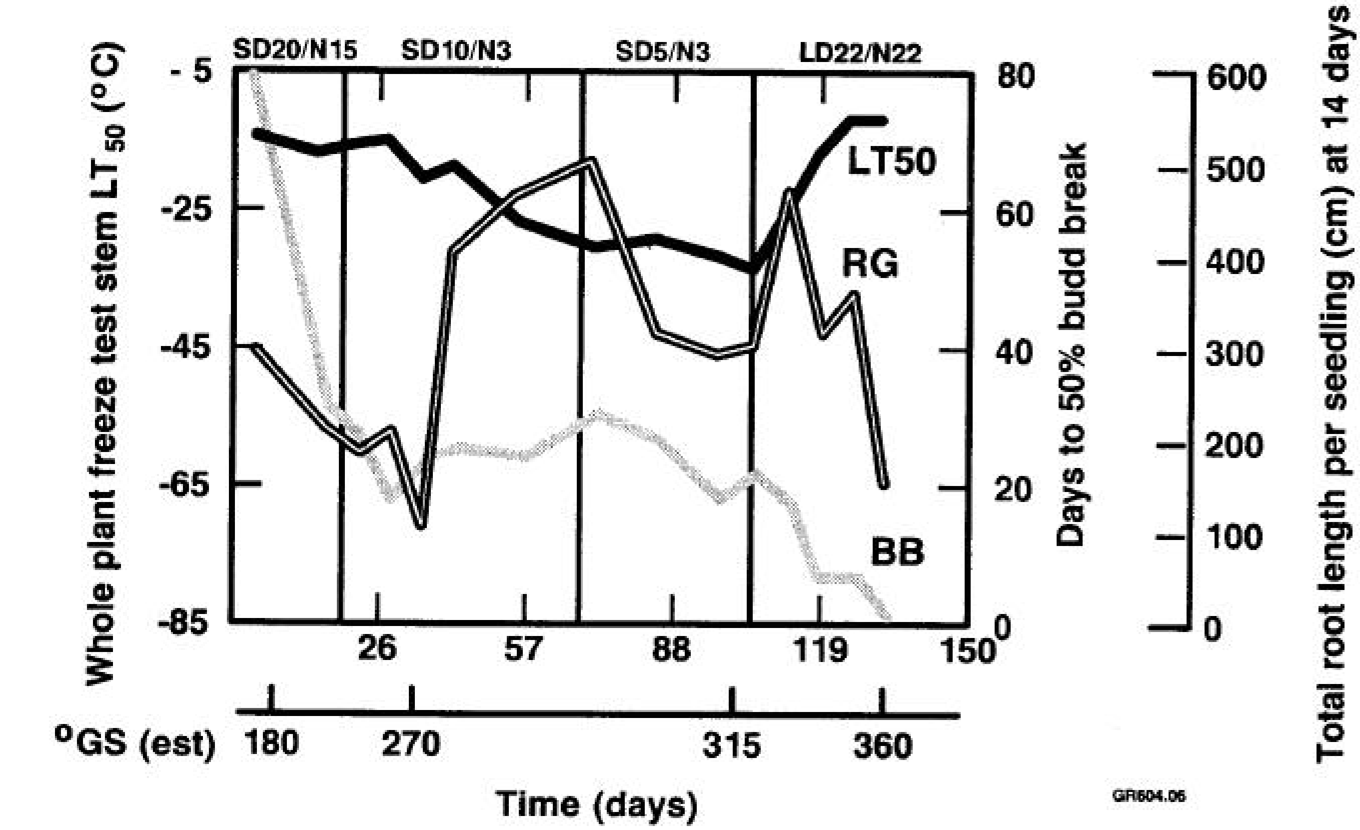
Nevertheless, two excellent recent studies have encompassed relatively broad seasonal sampling regimes and have also provided information on dormancy intensity, MI, cold hardiness, and shoot growth phenology in a range of species from diverse geographical locations. We shall now examine these studies toward gaining insight into the relationship between dormancy and RGP.

4.5.1.2.1 Ponderosa pine, Douglas-fir and Engelmann spruce in Arizona

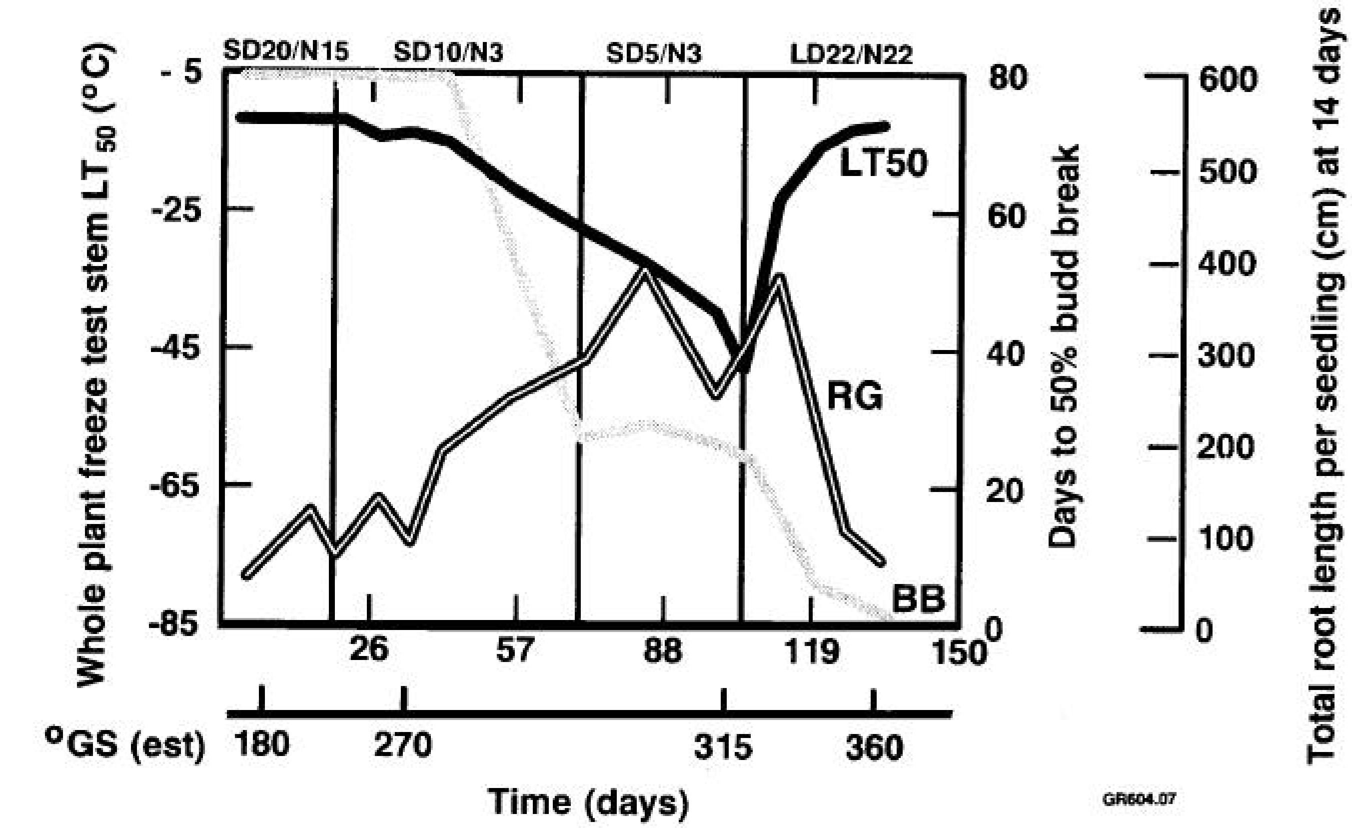
Burr et al. (1989) conducted intensive studies of RGP, dormancy intensity, and cold hardiness of ponderosa pine, interior Douglas-fir, and Engelmann spruce in controlled environment chambers. Four chamber environmental regimes were sequenced to induce dormancy and hardening, then to release dormancy and promote dehardening and budbreak. Dormancy intensity was measured with a budbreak test and hardiness was determined with whole-plant freeze tests.

Their results were calibrated against °GS from the curves of hardiness and budbreak data provided (Figures 4.5A-C). Patterns for each species were as follows. RGP was low prior to 270°GS then rose, sharply in ponderosa pine, to a peak or plateau at about 315°GS, then fell quickly as 360°GS approached. Maximum RGP coincided with maximum hardiness in all three species and this coincided

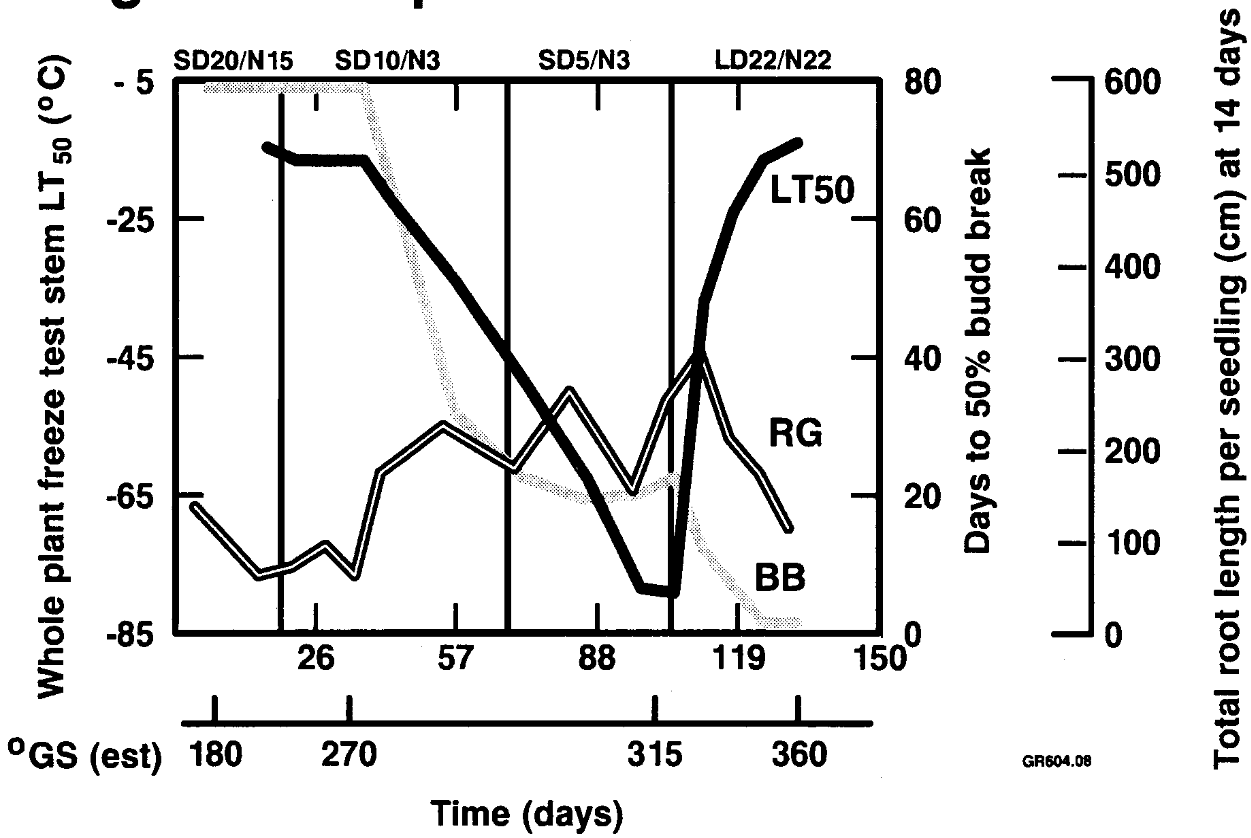
A. Ponderosa Pine



B. Douglas-fir



C. Engelmann Spruce



Figures 4.5C—*Changes in Root Growth Potential, cold hardiness and days to 50% budbreak in Engelmann spruce in Arizona (Burr et al. 1989). °GS point events are estimated from phenological data. Reprinted with permission from Tree Physiol. 5:301 (1989).*

with the period when dormancy was weakening but prior to shoot elongation. These patterns closely fit model predictions.

4.5.1.2.2 Sitka spruce in Scotland

Sitka spruce is widely planted throughout the British Isles, particularly in Scotland. Sitka spruce 2+1 transplants from the Queen Charlotte Islands (British Columbia, N. at. 53°) were lifted from a nursery in southern Scotland (N. lat. 56°) from late September through early May and measured for RGP, and several other variables (Cannell et al. 1990). This study is particularly useful because it also provides information on several aspects of seedling growth phenology enabling close calibration with the °GS model across a ten-month period.

RGP was low in September and October then increased rapidly beginning in mid-November (Figure 4.6). It remained high until late April then fell to near 0 in early May. Mitotic Index (MI) reached zero about November 20. This establishes the date of the 270°GS point. Indeed, this point coincided precisely with peak dormancy status and the beginning of the rise in RGP. MI increased again early March and shoot expansion in May, 180°GS. These results are also in good agreement with model predictions.

4.5.1.2.3 Conclusions

The hypothesis holds up well under the above independent data sets. Granted, there is some latitude for interpretation of °GS stages in these studies and other investigators might offer different interpretations. Nevertheless, results from several diverse species in two independent studies do not deviate far from model predictions.

Direct tests of this hypothesis would be more powerful than the observational tests offered above. Such tests might involve the artificial release of dormancy between 180°GS and 270°GS to induce an RGP response. This might be achieved with any number of environmental or chemical agents (Fuchigami and Cheng-Chu Nee 1987). Another simple test would be removal of elongating shoots to eliminate their influence as carbon sinks during periods of low RGP. At the least, more detailed studies of other species in which RGP and °GS are determined on a year-round basis would provide valuable additional tests.

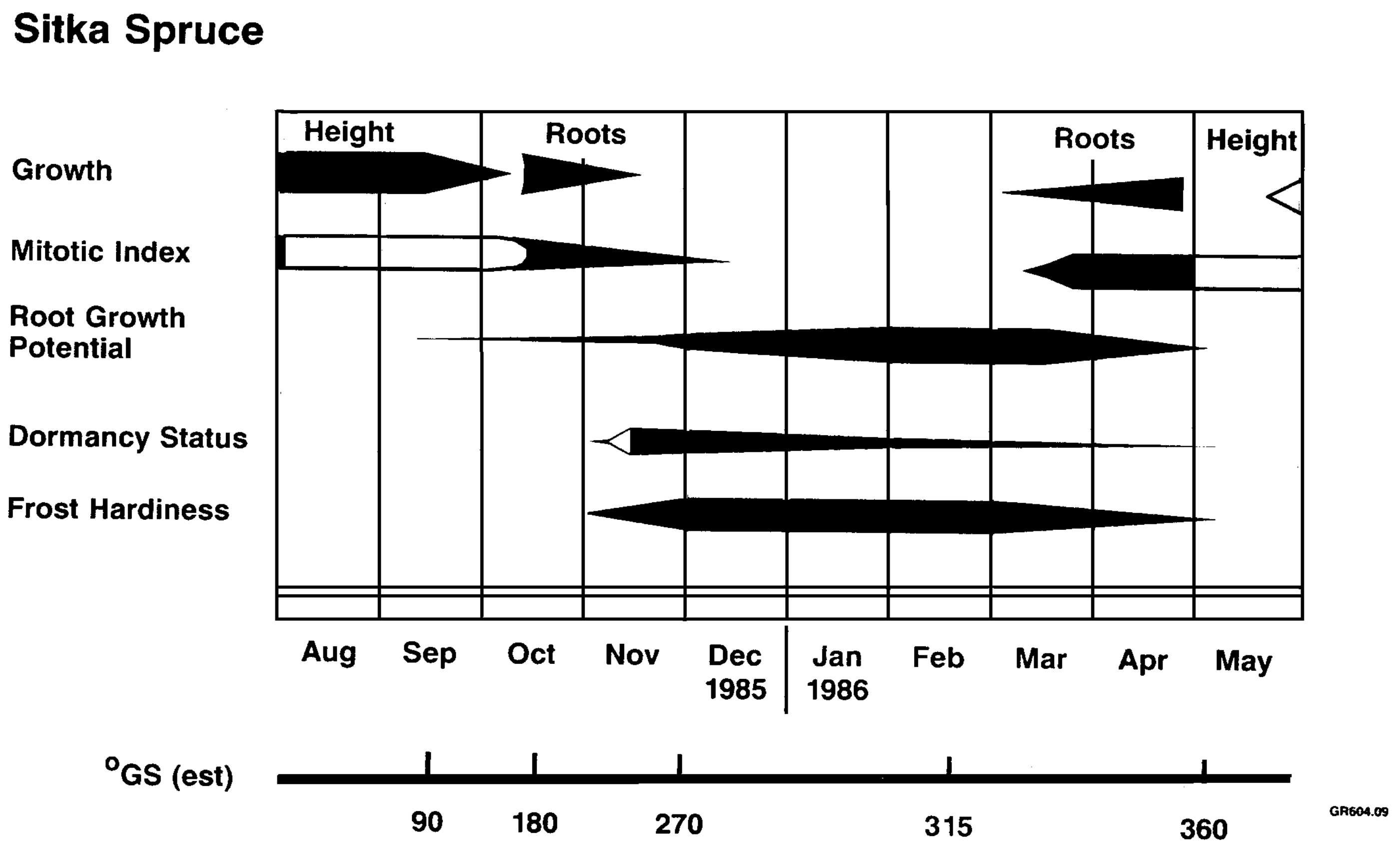


Figure 4.6—*Seasonal changes in Root Growth Potential, growth, mitotic index, dormancy status, and frost hardiness of Sitka spruce in Scotland (Cannell et al. 1990). °GS point events are estimated from phenological data. Reprinted with permission from Forestry 63:21 (1990).*

4.6 Why Does RGP Work?

When one reads the older (and even more recent) literature on RGP, one often finds statements to the effect that: "In order to become established after planting, a tree seedling must rapidly produce new roots to enable it to obtain water and minerals from the soil. Therefore seedlings with high RGP will have a better chance at survival." On the surface this logic seems sound and has pervaded the RGP literature for years. However, as pointed out by Ritchie (1985), seedlings are rarely planted into soils which are warm enough to permit roots to grow. In fact, throughout most of the Pacific Northwest, January- or February-planted seedlings must endure from two to four months before soils warm to the range in which root initiation and elongation can begin (Nambiar et al. 1979, Abod et al. 1979, Stupendick and Shepherd 1979, Ritchie 1985).

From this observation it would seem that RGP tests, conducted in 20°C soil, would have little or no bearing on what happens on the planting site (see c.f. Sutton 1983). Nevertheless, as pointed out in Section 4.4 above, RGP tests are often very good predictors of survival. One is then left with the question: Why?

There are probably two parts to the answer: the first has to do with RGP values which fall *within* normal seasonal ranges, and the second with those that fall *outside* normal seasonal ranges.

4.6.1 When RGP falls within normal seasonal ranges

As proposed in Section 4.5 above, RGP is highest when shoot dormancy is weak but when shoots are not elongating. Seasonally, this occurs during late summer into autumn, and then again in mid- to late-winter. RGP is very low in spring during shoot elongation and early winter when dormancy intensity is high.

Stress resistance and cold hardiness begin to develop at about 180°GS and peak in the range of 270°GS to 315°GS. RGP is rapidly increasing in this range. Therefore, high or rapidly increasing RGP is a signal that seedlings are at or near their seasonal peak of stress resistance and cold hardiness. Dehardening can be rapid after 315°GS and by 360°GS seedlings are completely dehardened and highly susceptible to stress. RGP is then low, denoting a seedling with low stress resistance.

By this reasoning, RGP itself does not determine survival potential, but instead indirectly indicates when seedlings have high survival potential because they have high stress resistance. This argument has been set forth earlier (Ritchie 1 985).

4.6.2 When RGP falls outside normal seasonal ranges
When RGP falls outside normal seasonal ranges it can indicate that the seedling is suffering from damage, disease, or other stresses which may portend poor performance or mortality. This logic turns on the observation (van den Driessche 1987) that short-term bursts of new root growth (hence RGP) occur at the expense of currently assimilated carbon—not stored carbon. This is a very important finding because it leads to the following line of reasoning.

If a seedling exhibits strong RGP then:

1) photosynthesis must be occurring, therefore

2) all the metabolic pathways that support photosynthesis must be functional, and

3) stomata must be open, therefore

4) transpiration, hence water uptake and transport must be occurring, therefore

5) the xylem system must be open and functional from root to shoot, and roots must be taking up water,

6) downward translocation of photoassimilate must be occurring, therefore

7) there must be an intact, functional phloem pathway from shoot to root,

8) root tips are capable of growing, therefore

9) root respiration must be occurring, therefore

10) all the metabolic pathways that support root respiration must be functional, etc.

These relationships can be demonstrated by girdling, defoliating, or holding seedlings in darkness or $C0_2$-free air (van den Driessche, pers. comm.) while testing RGP. In Douglas-fir each of these treatments effectively stops root growth.

It follows that if RGP falls within some “normal” range for a given species at a given time of year it is good evidence that there is nothing markedly wrong, structurally or metabolically, with that seedling. In contrast, if RGP values fall below what is known to be “normal” a red flag is thrown up and further testing is called for. The RGP test gives no clues to what the problem might be, but it does signal that a problem exists.

RGP testing is far more useful for sorting out bad or damaged seedling lots than for predicting survival.

4.7 Summary and Conclusions

In this review we have tried to focus on some key points bearing on the conduct and interpretation of RGP tests in reforestation. In our view these points are:

1. RGP is developed in the seedling during its tenure in the nursery and is expressed after the seedling is planted. The appropriate point at which to measure RGP is as soon before planting as possible because RGP can change rapidly.

2. The RGP measurement period need not be lengthy—ample evidence now exists that 15 or even 7-day tests can often be used successfully. However, it is important that environmental conditions remain consistent among tests because of the sensitivity of RGP to these conditions.

3. The primary value of RGP is its ability to characterize seedling physiological quality at a point in time, *not* to predict field performance. In this light RGP testing should be viewed as analogous to seed testing.

4. RGP is not a perfect predictor of field performance. This is because RGP test results are confounded by site and planting conditions which vary greatly.

5. However, RGP does have some predictive value because it indicates (a) when seedlings are physiologically resistant to stress, and (b) when seedlings are in some way damaged.

6. RGP periodicity seems to be modulated by two internal factors: (a) the depth, or intensity, of shoot dormancy, and (b) the strength of the carbon sink in the elongating shoot. When dormancy is weak but shoots are not actively expanding, RGP tends to be high, and vice versa.

7. Despite problems associated with lack of accuracy and precision and unrealistic expectations, when conducted and interpreted properly RGP testing remains a very valuable tool for assessing quality of planting stock.

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