Further Studies on the Ortet-Ramet Relationship in Wood Characteristics of Pinus radiata

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Introduction

An initial investigation of the wood characteristics of ortets and the associated ramets (Nicholls and Brown 1971) revealed important differences between the two groups which were attributed to the effects of topophysis and cyclophysis1). On the average the ramets exhibited longer tracheids, larger spiral angles and less dense wood than the ortets. This work was followed by a comparison of the wood characteristics of grafted ramets derived from mature ortets and open-pollinated offspring of the same ortets, both of the same age and growing under the same conditions (Nicholls et al. 1974). The later findings generally supported those of the initial investigation.

The present study is a report of further evidence of the effects of topophysis and cyclophysis based on an examination of material from two lots of P. radiata ortets and their associated ramets with the following emphases:

Part 1 — South Australia. Ortets sampled both at breast height and at an upper crown position in the stem and second stage ramets (derived from first stage ramets) sampled in addition to first stage ramets (derived from first stage ramet) sampled in addition to the first stage ramets (derived from ortets).

Part 2 — Australian Capital Territory. Minimal age difference between ramets and ortets. Cuttings were collected when the ortets were 5 years old compared to 35 years for the South Australian ortets in the case of the first-stage ramets.

Part 1. Ortets and Ramets from South Australia

The upper ortet specimens should provide wood char-

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acteristic standards which are typical of the higher levels in the stem and can lead by association to speculation on topophysical effects in the ramets. The second stage ramets are expected to exhibit reduced cyclophysical and topo-
physical effects where these exist because of the young age and small height of the first stage ramets at the time of scion collection for the second stage propagules.

Material (Part 1.)

Four clones supplied material for this investigation.

The ortets are growing in the 1925 plantation at the Penna Forest Reserve of the Woods and Forests Department of South Australia. The plantation is at an elevation of 152 m and has a rainfall of 760 mm. The site is virtually level and the soil is Nanwarrab Sand comprising 1.8–2.0 m fine sand overlying related clays. Tree spacing was initially 2.5 m and after four thinnings is equivalent roughly to 6.5 m. In early life the ortets would have had to compete with nothing more than light to medium bracken fern.

In 1958 (age 32) scions were collected from first and second order laterals in the upper crown of each ortet, some 3–4.5 m from the top, and were used to establish grafted ramets (GR1) in a randomised clonal seed-orchard some 16 km from the 1925 plantation. This orchard is on low banks of Young Sand, namely, leached dune sand over an illuvial organic layer, in a swampy area carrying grass and light bracken.

In 1962 these grafts were 1.8–2.4 m tall and from their first and second order laterals scions were collected for use in establishing grafted ramets in another randomised clonal seed-orchard (GR2) 5 to 6 km from the 1925 plantation. This site also is virtually level and the soil is Kalangadoo Sand, namely a meadow-podzol with a depth to clay of 1.8–2.0 m. The vegetation here comprised grasses and other pasture plants; the ramets were given assistance by hoeing or by the application of a weedicide. Spacing in both orchards was 9 m.

The set of ramets propagated from the ortets will be referred to as GR1, and that established from material taken from GR1 will be designated GR2.

Four ramets were available from each of the four clones in each ramet set, i.e. 32 in all.

Experimental Procedure (Part 1.)

In December 1970 each tree was sampled by the method of Pawsey (1969 a) to extract 25 mm cores extending from bark to bark and including the pith. Specimens were located between branch whorls, and where necessary, at right angles to the direction of stem lean at the point of sampling, at a nominal bract-high position. Before removal from the tree, the ends of each specimen were marked to show the direction of the tree axis. Sampling heights were adjusted as far as possible so that the sixteen cores from each set would show the same number of growth rings. Nevertheless the parcel of specimens designated GR1 showed 8 and 9 complete rings and those entitled GR2 exhibited 6 and 7 complete growth rings.

For the ortets, in addition to the specimens taken at breast height, sampling was also carried out in the upper levels of each tree at a height to show 11 complete growth rings.

Determinations of spiral grain angles, average tracheid length, and the collection of densitometric data were carried out according to techniques described elsewhere (Nicholls and Phillips 1970; Nicholls 1971). The tracheid di-
mensions and densitometric data were obtained using material from the shorter of the two radii of each core to avoid compression wood. Angles of grain deviation for individual growth rings in each specimen were expressed as the mean of values from both radii. Pieces to be used in the determination of densitometric data were treated with methanol in a Soxhlet apparatus to remove extractives.

Material from the growth ring adjacent to the pith was not examined because this ring is invariably incomplete and non-representative. Resampling to check some tracheid lengths was carried out in 1974 and enabled this determination for the GR2 trees to extend to the ninth growth ring.

The data for the ortets at each level, and those for each set of ramets, were grouped separately on the basis of ring number from the pith and means were calculated for each characteristic. The variation in these means through successive growth rings from the pith for the four groups of specimens are set out in Figures 1 and 2. A detailed sta-

data that is not possible because differences between groups attributable to the method of reproduction are confounded with any differences which may arise due to the location and cultural treatment of the plants. Furthermore, the arithmetic is difficult because of the unavoidably unbalanced nature of the sampling design and the influence of ring number from the pith upon the attributes examined. A series of 't' tests was used (treating each ring separately) to give an indication of the significance of differences between the means whilst recognising that any effects shown to be
significant might owe that fact to factors of the environment or culture as well as reproduction. The 5 per cent level of significance was accepted as a real difference.

Results and Discussion (Part 1.)

Ring Width

Ring widths in the ortets (see Figure 1) steadily decreased towards the bark from a maximum at the second growth ring. Breast-high rings were invariably much wider than those from the higher level. Ring widths for the two groups of ramets show a similar increase from the second to the fifth (GR1) or sixth ring (GR2) then a decrease.

The environmental factors most likely to account for the differences in radial growth between the ramets and the ortets (breast-high values) are weed control and wider spacing for the ramets (9 m) compared with the ortets (2.5 m). Climatic and edaphic factors for the tree sites are similar and seem unlikely to be responsible. The two groups of ramets, grown under the same silvicultural conditions, show very similar ring widths.

Spiral grain

The pattern of variation is typical of P. radiata material grown in Australian plantations, viz. initial 'left hand' spiral angles which decrease with age through zero to a 'right hand' spiral (Fielding 1967). It may be seen from Figure 1 that grain angles for the ortet specimens decrease from a maximum at the third growth ring from the pith, with values for the breast-high specimens decreasing slightly more rapidly than those from the higher level, as found previously (Fielding 1967). The values for the two ramet groups are generally larger than, and also
decrease less rapidly, than those for the breast-high ortet specimens, differences being significant at rings 8 and 9.

It now seems likely that the observations by Pawsey (1965b) that grain angles in seedling trees were similar to those for trees of the same age grown from cuttings from mature ortets may not have general validity.

It is suggested that differences between the spiral grain angles for the breast-high ortet specimens and the derived GR1 ramets are not due to climatic variation between the two periods of juvenile wood formation nor to differences in other environmental factors such as tree spacing but are the result of topophysical effects. Although there is little evidence to relate the magnitude of grain angles between the trunk and the branches (Noskowiak 1960) there is some similarity between values for the ortet top specimens and those for the GR1 ramets.

Grain angles for the GR2 specimens are consistently larger than those for the GR1 specimens but differences are not significant. While this may be a manifestation of further topophysical effects resulting from the propagation of the GR2 trees from scions originating in the crowns of the GR1 ramets, the effect would not be expected to be large as the GR1 trees were less than 2.5 m high when the scions were collected for the establishment of the GR2 clones.

Average tracheid length

The typical pattern of tracheid length variation is shown in this material, that is, a rapid increase throughout the early growth rings (juvenile period) until a more or less constant value is attained (Sanio 1972), usually at 12—15 years in the butt log of Australian-grown Pinus radiata (Dadswe11 1957). From Figure 1 it may be seen that the normal pattern is evident in all cases but detailed variation is apparent between individual means in respect of initial values and duration of juvenility. The breast-high ortet specimens have an initial tracheid length of 2.24 mm and are still exhibiting the juvenile rapid increase at age 9 years, whereas the upper ortet specimens have an initial length of 2.58 mm, are longer than the former up to the eighth ring, and may be showing indications of a diminution in the rate of length increase by the ninth ring. The GR1 and GR2 ramets show initial tracheid length of 2.73 mm and 2.54 mm respectively, maintain this superiority compared to the breast-high ortet specimens for several growth rings, and appear to reach more or less constant tracheid lengths at the seventh growth ring. There are significant differences between the means for the breast-high ortets and those for the ramets, at rings 2 and 3 for GR1 and at ring 9 for GR2.

It is suggested that the difference in average tracheid length between the breast-high ortets and the ramets are due to the effects of cyclophyllis and topophysis. Differences in tree spacing seem unlikely to be important as the spacing for the two ramet groups is the same and the mean of tracheid length for the GR2 trees is consistently smaller than that for the GR1 stems. It is also unlikely that the differences are due to climatic variation between the two periods of juvenile wood formation.

The apical meristem association with the scion has undergone age changes according to the age of the tree and the position of the branch supplying the scion, and the effect of cyclophyllis is to preserve these age differences in the ramet. The expression of this greater physiological age would be expected as a decreased juvenile period in the ramet with respect to the ortets and this apparently is observed in the curves depicted in Figure 1. Furthermore,
the second stage ramets (GR2) should exhibit a shorter juvenile period than the first stage ramets (GR1) and this also is suggested by Figure 1, although the effect should be small as the GR1 trees were four years old at the time scions were collected for the propagation of the GR2 ramets. A significant correlation exists between tracheid lengths in branch material and values in the adjacent stem (Bisser et al. 1951; Jackson and Greene 1958). Therefore as the scions were taken high in the tree the effect of topophysics should yield average tracheid lengths in the GR1 ramets which are similar to those recorded for the upper ortet specimens. There would appear to be evidence of this in Figure 1. By the same argument the tracheid lengths of the second stage ramets (GR2) should be similar to values expected for specimens taken in the upper levels of the stems of the GR1 trees, although as the GR1 trees were less than 2:5 m high at the time of scion collection any variation of tracheid length with height in tree should be small.

**Maximum density**

The means for all groups of specimens show an increase from the second growth ring (Figure 2). That for the breast-high ortet specimens continues to increase throughout the period under review (values are more or less constant beyond the ninth ring) whereas the mean for the specimens from the higher level only increases to the seventh growth ring. The mean for the GR1 ramets does not exhibit any increase beyond the sixth ring and that for the GR2 group is constant after the third growth ring. The means for the ramets are less than those for the breast-high ortets and differences are significant at rings 8 and 9 for the (GR1) trees.

Maximum density in P. radiata is generally recorded in the last-formed late wood at the position where cell wall thickness is a maximum and cell radial diameter is minimal (Nicholls unpublished data). In addition, relatively large changes in wall thickness occur for small changes in radial position. Wall thickness in late wood tracheids increases from the pith outwards at a given height to a maximum that varies with growth conditions, and increases from the apex of the tree downwards (Larson 1963, 1966). These variations are clearly expressed in the present case in the curves for maximum density for the two sets of ortet specimens (Figure 2).

It is unlikely that the observed differences in maximum density between the breast-high ortet specimens and those for the ramet material are due to climatic variation between the two periods of juvenile wood formation. It is suggested that these differences are topophysical or cyclophysical effects.

**Minimum density**

Minimum density in the case of the breast-high ortet specimens (Figure 2) increases from about 250 kg m\(^{-3}\) at the pith to a more or less constant value of 315 kg m\(^{-3}\) at the seventh ring. Minimum density in the upper stem however fluctuates about a mean value of 319 kg m\(^{-3}\) and is invariably larger than at breast-height. On the other hand the data for the GR1 and GR2 ramets exhibit a slight initial decrease followed by a slight increase, but with values beyond the third growth ring increasingly less than those for the breast-high ortet specimens.

Minimum density in this species is usually recorded in the early wood at the position where tracheid radial diameter is at or near maximal and wall thickness is minimal (Nicholls unpublished data). However, because minimum density is sensitive to small changes in wall thickness, the position of minimum density is not always as clear or as constant as that for maximum density. In the early wood, radial diameter on a cross-section generally tends to increase with increasing ring number from the pith to a maximum width and then fluctuate thereafter, and up the tree usually increases from the butt to a maximum at a particular height and subsequently decreases towards the apex (Larson 1963). Wall thickness in the early wood also increases from the pith outwards to a maximum (Nicholls unpublished data). For the ortet breast-high specimens increasing cell wall thickness at the successive position of minimum density seems to largely determine the variation pattern for this feature; maximum wall thickness being reached at the seventh growth ring. On the other hand, wall thickness appears to be of little importance in the case of the two ramet groups and tracheid diameter apparently controls the expression of minimum density. Smaller radial diameters for the tracheids in the upper specimens are seemingly responsible for the greater minimum density of this material compared to the breast-high wood.

Nicholls (1971) has shown that minimum density is not affected by thinning and therefore the observed differences between results for the breast-high ortet specimens and those for the ramet material are unlikely to be due to differences in tree spacing. It is also unlikely that the differences are due to climatic variation between the two periods of juvenile wood formation. It is suggested that these differences are due to topophysical and cyclophysical effects.

In view of the fact that minimum density in the upper stem of the ortets was generally higher than at breast-height, and that the ramet values were even lower, there does not appear to be any influence on minimum density due to topophysics. However, the effects of cyclophysics may be expressed through the sparser crowns of the ramets compared to the ortets (Filling 1970), i.e. as a result of the lesser foliage of the ramets there may not be sufficient photosynthetic capacity for other than needle elongation at this time in the growing season resulting in very low minimum density.

**Late wood ratio**

Late wood ratio is the proportion of late wood in a ring, assuming a linear change from early wood to late wood and an early wood/late wood boundary at the mid-density point (Nicholls and Brown 1971). It may be expressed as the ratio of (average density — minimum density) to (maximum density — minimum density) (Hausa 1969). The means for this feature depicted in Figure 2 show a common pattern of initial decrease followed by either an increase or fluctuation about a constant value. The mean for the upper ortet specimens exhibits values which are markedly larger than those for the breast-high ortet material or the ramet specimens.

**Average density**

From Figure 2 it may be seen that average density for the ortets generally increase with increasing age. On the other hand, results from the ramets initially decrease to the fourth or fifth ring and then increase. Values for the ramets are invariably less than those for the ortets and differences are significant at rings 8 and 9.

In view of the relationship between average density and the other densitometric parameters the discussion already

76
given dealing with the effect of topophys and cyclophys on the components should serve for average density.

Therefore, it is suggested that cyclophys is the most likely cause for the observed differences in density between the wood of the orrets and ramets. The curves for average density (Figure 2) do not contradict this view.

Part 2. Orrets and Ramets from Australian Capital Territory

Cuttings were collected from five-year-old orrets planted at two sites in the Australian Capital Territory and were themselves planted at two other sites. A study of their wood characteristics was undertaken to elucidate the effects of topophys and cyclophys when the age difference between orrets and ramets was small.

Material (Part 2.)

Samples were obtained from eight clones, the orrets of which formed two groups —

Group 1 — four orrets planted in 1954 at Halls Block.
Group 2 — four orrets planted in 1954 in Compartment 60, Kowen.

From each orret, two ramets were planted in 1960 in plantation 25, Kowen, and another two ramets in 1961 in plantation 24, Blue Range.

The four orrets at Halls Block lie on a line 120 m long. The underlying soil is derived from Ordovician sediment and is probably low in P and to a lesser extent N. Mean annual rainfall is from 1000—1125 mm and tree spacing was 2.4 m. The site is 25 km WSW of Canberra.

The four orrets in compartment 60, Kowen, lie within 100 m of one another. The soil is derived from Ordovician sediment but with less evidence of N and P deficiencies than at Halls Block. Rainfall is 675 mm per year and tree spacing was 2.7 m.

From groups 1 and 2, 16 ramets of 8 clones were planted at Blue Range unrandomised along a line 240 m long. The site is 9 km north of Halls Block on material described as Middle Silurian Paddy River volcanics. No marked deficiencies of major nutrients are known and mean annual rainfall is 875—1000 mm. Tree spacing was 2.4 m.

A further 16 ramets of the same clones were planted as unrandomised 4-tree plots at a spacing of 2.4 m at Kowen. This site is 5 km SW of compartment 60 on soil derived from similar sediments to compartment 60 with a rainfall of 625 mm per year.

All ramets were propagated as rooted cuttings.

Experimental Procedure (Part 2.)

Wood specimens were collected in December 1971, January and September 1972 at a nominal breast height position according to procedures outlined in Part 1. The specimens were machine-sawn pieces measuring 25 × 25 mm. Sampling heights were adjusted to show 7 growth rings in the ramet specimens from group 1 and 8 rings for those from the group 2 trees.

Procedures for the examination of specimens were as before.

The data for the four orrets of each group and their 8 ramets at each site were grouped separately on the basis of ring number from the pit and means were calculated for each characteristic. The variation in these means through successive growth rings are shown in Figures 3 (Group 1 clones) and 3 (Group 2 clones). Average tracheid lengths were determined for the Group 1 material only and the means are shown in Table 1.

Table 1. — The means of average tracheid length through successive growth rings for four clones of Pinus radiata grown in the Australian Capital Territory.

<table>
<thead>
<tr>
<th>Growth ring no. from pith</th>
<th>Orrets from Halls Block</th>
<th>Ramets from Cpt 25 Kowen</th>
<th>Ramets from Cpt 24 Blue Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>2.85</td>
<td>2.84</td>
<td>2.91</td>
</tr>
<tr>
<td>4</td>
<td>3.39</td>
<td>3.38</td>
<td>3.39</td>
</tr>
<tr>
<td>6</td>
<td>3.81</td>
<td>3.91</td>
<td>3.83</td>
</tr>
<tr>
<td>7</td>
<td>4.05</td>
<td>4.09</td>
<td>4.19</td>
</tr>
</tbody>
</table>

Results and Discussion (Part 2.)

Ring Width

From Figure 3 it may be seen that there is little difference between the growth rate of the orrets and the two sets of ramets.

Figure 3. — The variation through successive growth rings from the pith of the mean of ring width, spiral grain, maximum and minimum density, late wood ratio and average density for the wood of group 1 orrets and their associated ramets grown in the Australian Capital Territory.

In both Figures 3 and 4, there is a well-defined decrease in ring width at growth rings 4 and 5 respectively for the ramets from Kowen plantation. This site has a relatively poor rainfall and this decrease in ring width is an expression of the water stress to which these trees were subject during the drought in the 1967/68 growing season.

Spiral grain

The means for both the group 1 and 2 trees show a decrease in grain angles from growth rings 2 or 3 with increasing ring number from the pith (Figures 3 and 4). In neither figure were there differences between the ramets and orrets.

Average tracheid length

Values for this feature set out in Table 1 show that there are no consistent differences between orrets and ramets.
There are indications in Part 1 of significant differences in wood characteristics between ortets and ramets when cuttings are obtained from mature ortets. These differences appear to be associated with the age or position of the cutting used for Propagation. These differences are not apparent in the data presented in Part 2 when cuttings are obtained from juvenile ortets. Therefore the results of the observed influence of vegetative propagation on the quality of the raw material depends not only on the end product, but also on the age of the ortets supplying cuttings.

Acknowledgements
Appreciation is recorded of Mrs. D. Dixon, J. Jurgensky and Miss S. Ward in the carrying out of the detailed measurements on which the results of this investigation have been based. The authors also thank Mr. B. A. Mitchell at the Mt Gambier Station, Division of Forest Research, CSIRO for his assistance in resampling material used for checking tracheid length.

Summary
Wood specimens from sexually propagated Pinus radiata trees (ortets) and members (ramets) of the associated vegetatively propagated clones in two Australian states were examined for such characteristics as average tracheid length, spiral grain, ring width, maximum and minimum density, late wood ratio and average density.

Observed differences in these characteristics between the ortets and ramets were attributed to the effects of topophysis and cyclophysis. Generally the ramets exhibited longer tracheids, larger spiral grain angles and less dense wood than their ortets provided the latter were mature at the time of scion collection.

Special features of the present investigation involve the sampling of one set of ortets at two heights in the tree and the use of first and second stage ramets, and ortets of young and advanced ages at the time of scion collection.

Key words: Tracheid length, Spiral grain, Ring width, Wood-density, Late wood ratio, Topophysis, Cyclophysis, Pinus radiata D. Don.

Zusammenfassung
An zwei Orten Australiens wurden an normalen, die heiß aus Samen hervorgegangenen Pinus radiata sowie an deren vegetativen Abkömmlingen die Holzzeigenschaften Tracheidenlänge, Drehwuchs, Jahrhundertbreite, maximale, minimale und durchschnittliche Holzdichte und Spaltlochanteil untersucht. Dabei konnten z. T. erhebliche Unterschiede festgestellt werden. Diese waren sowohl als Topophysys- als auch als Cyclophysysseifakte zu erkennen. Im allgemeinen hatten die vegetativen Abkömmlinge längere Tracheiden, eine geringere Holzdichte und größere Drehwuchswinkel als ihre aus Samen erwachsenen Ausgangsbäume, wenn diese im Zeitpunkt der Entnahme der vegetativen Abkömmlinge bereits alter gewesen waren.

References
Germination Value – A New Formula

By K. DIAVANSHIR and H. POURBREID

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Introduction

Many seed analysis and authors have tried to derive a formula that evaluates germination tests. The principal aim of to obtain such formula is to present a standard procedure for the viability of a seed lot, the effectiveness of various presowing treatments, and expected seedling survival from field or nursery sowings.

CZABATOR (1962) Proposed a new formula for the objective evaluation of germination tests and also demonstrated the problems which were encountered using previous methods.

He mentions that results of germination tests are too often subjective, with tables of experience, graphs of the course of germination, or statistical transformation of the data being used to qualify the expressed percentage of germination. Furthermore, CZABATOR (1962), after a review of the literature, established that with conventional methods of evaluating the results of germination tests could be different and misleading. Since CZABATOR reviewed the literature most adequately, no further review is necessary. Therefore this discussion will be limited to the validity of CZABATOR’s formula, plus the presentation of a new formula for germination evaluation.

CZABATOR’s Formula

CZABATOR mentioned that a practical formula for evaluating germination tests should meet the following specific requirements:

1. Both speed and totality of germination should be considered, but with more emphasis on germinative energy than on totality.
2. Values should be comparable regardless of the duration of the tests.
3. Differences in frequency of counting germinated seed should not render the results erratic.
4. Each seed lot should be evaluated as a single figure, to allow for direct comparisons and to simplify statistical analysis of the results.
5. A more vigorous lot of seed should be indicated by a higher value, and this value should vary directly with increased speed of germination, or higher total germination, or both.
6. The formula should be sensitive to relatively minor differences in speed or totality of germination.
7. The calculations should be simple.
8. The application of the formula should not involve drastic changes in commonly accepted methods of conducting and recording germination tests.

CZABATOR’s formula is as follows:

\[ GV = MDG \times PV \]

where GV is germination value, MDG is mean daily germination calculated as the percentage of full-seed germination at the end of the test divided by the number of days to the end of the test; PV is peak value, or the maximum quotient derived from all of the cumulative full-seed germination percentages on any day divided by the number of days to reach this percentages. The peak value is the mean daily germination of the most vigorous component of the seed lot, and is a mathematic expression of the break, or shoulder, of a sigmoid curve representing a typical course of germination. To demonstrate the formula’s use the following table cited by CZABATOR is given in Table 1.

The tables germination value will be:

\[ GV = MDG \times PV = 4.01 \times 5.08 = 20.44 \]

<table>
<thead>
<tr>
<th>Days since beginning of test</th>
<th>Cumulative germination percent (%)</th>
<th>T-value</th>
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</thead>
<tbody>
<tr>
<td>8</td>
<td>20</td>
<td>2.50</td>
</tr>
<tr>
<td>9</td>
<td>24</td>
<td>3.78</td>
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<td>10</td>
<td>42</td>
<td>4.20</td>
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<tr>
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<td>74</td>
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<tr>
<td>16</td>
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<td>4.81</td>
</tr>
</tbody>
</table>

Critical points of CZABATOR’s formula

CZABATOR’s formula seems to be adequate for the seed germination testing of pines. It has been used by many authors (See all literature cited except BATES and CZABATOR).