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Geographical Variation in Growth Patterns of Douglas-fir

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Introduction

The great diversity in environmental conditions under which Douglas-fir (*Pseudotsuga menziesii* [MIRB.] FRANCO) occurs naturally makes it an ideal species for studies of ecotypic differentiation. The present paper reports on differences in growth patterns among young Douglas-fir from three widely different areas when grown under controlled environment conditions and under field conditions near Corvallis, Oregon. Seedlings from northern Rocky Mountains and southern Rocky Mountains (var. *glauca* [BEISSN.] FRANCO) and from the Pacific Northwest (var. *menziesii*) were used. The main objective is to relate the observed differences in growth behaviour under a number of controlled environment conditions and under field conditions at Corvallis to the differences in environmental conditions at the native habitats. No attempt is made to describe or classify the pattern of variation within the species.

Methods and Results

Experiment 1

Seed from near Flagstaff, Arizona (9000 ft elevation), southern Vancouver Island (0—1000 ft) and Kamloops, interior British Columbia (1000—1500 ft) were germinated in April out-of-doors near Corvallis, Oregon. The seed represented mass collections (commercial) from a large but unspecified number of trees. The seed was germinated in petri-dishes in large enough quantities to permit the planting of each replication with seed germinated at the same date. Each source was represented by two replications of 25 plants

each. The seedlings were kept well watered throughout the experiment. Growth and dormancy behaviour was determined by observations at five-day intervals.

Seedlings from Kamloops when grown out-of-doors began to go dormant at 40 days of age as opposed to 100—130 days for the Vancouver Island seedlings. The seedlings from Flagstaff, Arizona grew intermittently, with the majority of the seedlings going into a short period of dormancy at age 70—90 days after which more than half of them resumed growth and then went into winter dormancy. The short period of dormancy was characterized by a small, green bud, which, after breaking, left two or three thin, papery bud scales on the stem.

If seedlings from the same three sources were grown from the time of germination under a constant temperature of 20°C and 16-hour photoperiods in growth chamber (5 replications of 5 seedlings per treatment and source), the Arizona seedlings showed a characteristic intermittent growth. At about 50 days they went dormant but were active again between roughly 60—80 days of age after which they again went dormant. This last period of dormancy was also very short and a new period of active growth had just started when the experiment had to be terminated at 90 days. Some of the Vancouver Island seedlings went dormant earlier in the growth chamber than out-of-doors but they may have resumed growth again if left for a longer period in the chamber. The majority of the seedlings from Kamloops resumed growth after the first period of dormancy but they did not show as distinct intermittent growth as the Arizona seedlings.

When grown under eight-hour photoperiods and 20°C the intermittent growth disappeared and seedlings from

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the two continental sources began dormancy at about 40 days of age and those from Vancouver Island slightly later.

If grown under continuous light and constant 20° C as above the intermittent growth reappeared in the Arizona seedlings although at no time were all seedlings dormant. The majority of the seedlings from Kamloops remained active during the 90-day experimental period. The same was true for the Vancouver Island seedlings. The differences in response to the three different photoperiodic regimes were greater in the seedlings from Kamloops and Arizona than in the Vancouver Island seedlings. This is in accordance with earlier findings that continental seedlings are more sensitive to changes in photoperiod than are seedlings of coastal origin (IRGENS-MOLLER, 1962). Under continuous light the Arizona seedlings could be kept actively growing for at least 150 days with less than half of them having short periods of dormancy. The same was true of the Vancouver Island seedlings. The Kamloops seedlings, on the other hand, went dormant after 130–140 days, probably indicating a requirement for a chilling period.

Experiment II

To determine if the intermittent growth was characteristic of only Arizona seedlings, seed from single tree collections from a number of localities in the Rocky Mountains were germinated and the seedlings grown at 20° C under either eight or sixteen-hour photoperiods (Fig. 1). Seedlings from New Mexico, Utah (one female parent only) and Arizona all showed a very distinct intermittent growth under sixteen-hour photoperiods with a very short period of dormancy at around 50 days of age followed by a period of active growth similar to the seedlings from Flagstaff, Arizona used in the previous experiment. This intermittent growth was much less pronounced or almost absent in the seedlings from Montana.

Under eight-hour photoperiods (dotted line, Fig. 1) all intermittent growth disappeared as in the previous experiment. In the southern types dormancy occurred earlier under long photoperiods than under short ones, although under the former dormancy was quickly broken again while under the latter the plants remained dormant.

The distinct intermittent growth in the southern seedlings and the lack thereof in the northern seedlings may be related to the differences between the two areas in the seasonal distribution of precipitation. Only 29 percent of the annual precipitation occurs during the summer in the northern Rocky Mountains as opposed to 64 percent in New Mexico and Arizona (BAKER, 1944). The intermittent growth of the southern seedlings may permit them to go into dormancy in spite of long photoperiods during periods of soil moisture stress, and to resume growth quickly when soil moisture is abundant. In the northern Rocky Mountains where soil moisture always becomes critical in the growing season selection has favored early cessation of growth. Under conditions of the nursery at Corvallis with ample soil moisture these differences in growth habits resulted in very large differences in height at the end of the third year. Some of the southern sources were 4–5 times as tall as the northern types. SQUILLACE and SILEN (1962) found a similar association between the summer precipitation in the southwest and growth phenomena in ponderosa pine (*Pinus ponderosa* Laws.).

Experiment III

As described in an early publication (IRGENS-MOLLER, 1962) continental seedlings are generally more sensitive to photo-

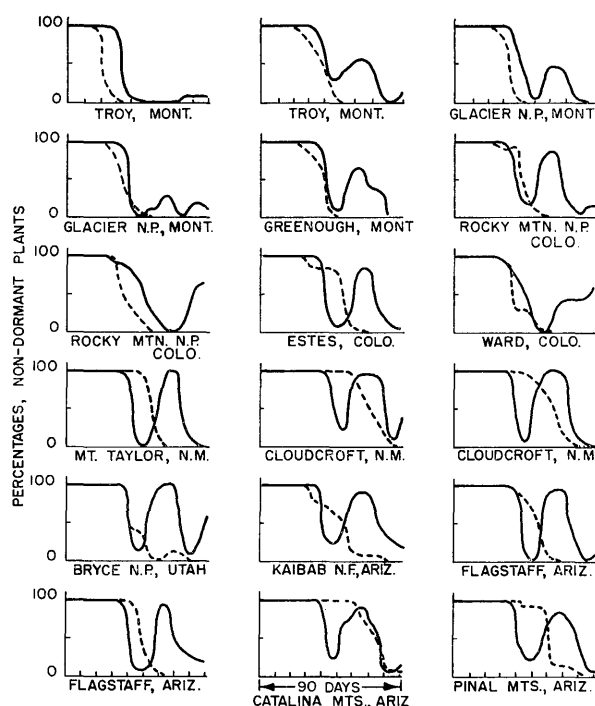


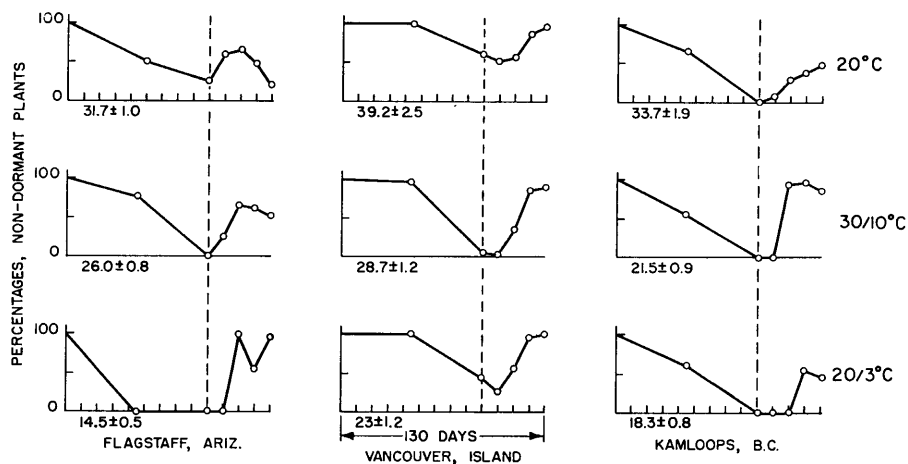
Fig. 1. — Onset and break of dormancy in young Douglas-fir seedlings from various localities in the Rocky Mountains when grown at 20° C under sixteen-hour (full lines) and eight-hour (dotted lines) photoperiods from the time of germination to 90 days of age. Based on 5 replications each of 5 plants per source and treatment. N.P. = National Park; N.F. = National Forest.

periodic changes than are coastal seedlings as far as onset or break of dormancy are concerned. The following experiment was designed to determine to what degree temperature affects the response to changes in photoperiod.

Seed from the same three sources used in Experiment I were germinated and grown under eight-hour photoperiods for 90 days under the following temperature regimes: constant 20° C; 30° C during the day and 10° C during the night (30/10); and 20° C during the day and 3° C during the night (20/3). Both day and night temperature, when different, lasted eight hours, with the remaining eight hours used in the gradual change from day to night temperature and vice versa, each taking four hours. Approximately 50 seedlings grown in plastic pots (5 per pot) in gravel and watered daily with nutrient solution were used per treatment and source. After 90 days under these conditions from the time of germination all plants exposed to sixteen-hour photoperiods at 20° C to determine any effects of the previous temperature regimes upon the response to the change in photoperiods. The percentages of non-dormant plants (i. e., without any terminal bud) were determined at ages 45, 90, 100, 110, 120 and 130 days.

As was the case in the earlier experiments the seedlings from Vancouver Island remained active for a longer period than did those from the two continental sources, irrespective of the temperature regimes (Fig. 2). The two regimes with fluctuating temperatures had a greater dormancy inducing effect than constant 20° C except in the seedlings from Kamloops which responded almost identically to the three temperature regimes. The response to the change from short to long photoperiods at age 90 days differed between the coastal and continental seedlings. The former responded slowly as evidenced from the continued decrease in percentages of non-dormant seedlings even after

Fig. 2. — Onset and break of dormancy in young Douglas-fir seedlings from three different areas when grown under three different temperature regimes from the time of germination. Dotted vertical lines indicate the time at 90 days of age when photoperiod was changed from eight to sixteen hours and the temperature held constant at 20° C. Numbers below each graph indicate average dry weight of seedlings (mg) and the standard error of the means. Based on 50 plants per source and treatment.



the change to long photoperiods. The response to this change in photoperiod also appeared to depend on the previous temperature regime. Fluctuating temperatures caused a quicker and more uniform break of dormancy (steeper curves) in response to the long photoperiod than constant 20° C. Since constant temperature caused less dormancy than the fluctuating ones the dry weight of these seedlings were also greatest. Those exposed to 20/3° C had the lowest dry weight as might perhaps be expected.

Experiment IV

To clarify further the effects of temperature upon the response to change in photoperiod, the following experiment was made.

Seedlings from the same three sources used in Experiment I were grown for 90 days from the time of germination under eight-hour photoperiods at either constant 20 or

20/3° C. They were then removed to the greenhouse at temperatures fluctuating between 18 and 25° C and exposed to sixteen-hour photoperiods. Observations on dormancy were made every 15th day in the greenhouse for the following 75 days.

Almost all plants grown under 20/3° C were dormant when moved to the greenhouse (Fig. 3) as opposed to those grown under 20° C. Some of the Arizona seedlings grown under 20° C were in the second period of dormancy. During the subsequent 75 days the changes from active growth to dormancy and vice versa occurred more rapidly and uniformly in plants initially exposed to 20/3° C than in those exposed to 20° C. The low night temperature had a synchronizing effect. This was particularly true of the Arizona seedlings. The slow response of the Vancouver Island seedlings was again evident. At the termination of the experiment the average epicotyl length of the seedlings initially treated with 20/3° C was 25, 11, and 19 mm for the Vancouver Island, Arizona, and Kamloops seedlings, respectively. The corresponding figures for those treated initially with 20° C were 68, 22, and 14 mm (standard errors of means less than 2 mm). Thus, as far as height growth is concerned the Vancouver Island seedlings showed the greatest difference in response to the two temperature regimes with a drastic reduction in height growth after exposure to 20/3° C. The opposite was the case in the seedlings from Kamloops which at 165 days had grown more after exposure to 20/3° C than after 20° C although the difference was relatively small but statistically significant. This no doubt reflects a larger chilling requirement of this northern, interior type. The cold nights have permitted a larger percentage of plants to resume growth after the change to long photoperiods than in the plants not exposed to cold nights.

The effects of the cold nights thus lasted at least 75 days in this experiment. To determine if shorter exposures to cold nights also have such delayed effects the following experiment was made.

Experiment V

Seedlings from the same three sources used in Experiment I were exposed to 25 or 40 days of either 20/3 or 20° C from the time of germination and then to 15 or 25 days of 30/10° C at eight-hour photoperiods. All plants were then removed to the greenhouse under sixteen-hour photoperiods and observed after 25 days there. At the end of the experiment more than half of the seedlings from Arizona exposed to 40 or 25 cold nights from the time of germination had broken the first period of dormancy as opposed to none of the seedlings exposed to 20° C constant. This was true

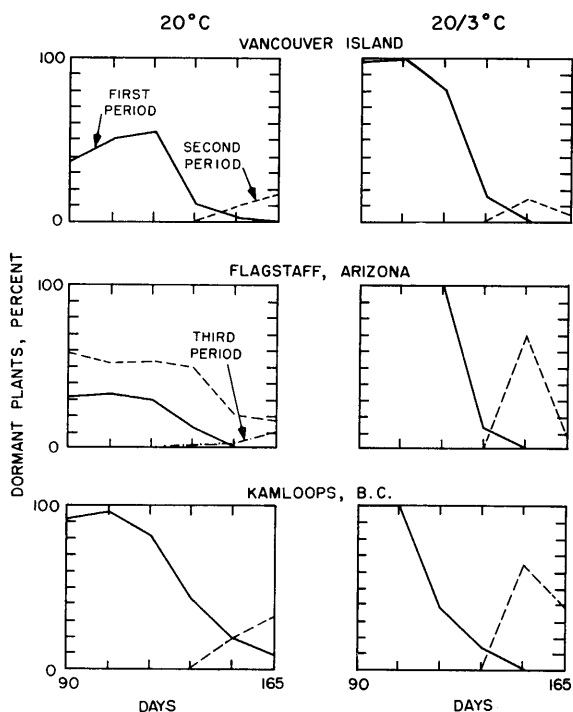


Fig. 3. — Effects of exposure to 20 or 20/3° C and eight-hour photoperiods for 90 days from time of germination upon subsequent response to sixteen-hour photoperiods under greenhouse conditions (see text). The response is expressed as changes in percentages of plants in first, second, or third period of dormancy during the 165 days following the exposure to either 20 or 20/3° C. Based on 100 plants per source and treatment.

regardless of the length of the period of 30/10° C (i. e., 15 or 25 days). The seedlings from Kamloops, B. C. showed the same pattern, although the percentages of seedlings which had broken dormancy was smaller (from 5–25 percent). The Vancouver Island seedlings were again characterized by a slow response. Cold nights had the effect of hastening onset of dormancy while without the cold nights practically all the seedlings remained actively growing.

From this may be concluded that even as short a period as 25 cold nights from the time of germination have a profound effect upon the onset and break of dormancy and that this effect was carried through 15 or 25 days of 30/10° C and clearly expressed after exposure to 25 sixteen-hour photoperiods.

Experiment VI

The above described differences among the three types of seedlings no doubt reflect the different selective pressures at their native habitats. Since the seedlings were derived from seed collected in the respective habitats, the differences in growth patterns during their early development may also reflect the differences in environmental conditions under which the seed developed and matured, i. e., be the result of a preconditioning effect as pointed out by Rowe (1964). For that reason phenological observations were also made on six to seven-year old plants from the same general areas growing in a plantation near Corvallis, Oregon. The trees in this plantation were planted in a completely randomized manner. The dates of height growth initiation were observed during the spring of 1966 and by way of weekly measurements of leader growth the dates of 90 percent completion of height growth were determined for each tree by interpolation. The number of trees measured from each source are given in Fig. 4. It should be pointed out that the origins of the plants in the plantation are only in a very broad sense the same as the origins of the plants used in the previously described experiments. That is, measurements were made in the plantations of trees originating from coastal areas (southern Vancouver Island, Forks, western Washington) northern interior (eastern Washington, northern Idaho, and western Montana) and southern Rocky Mountains (New Mexico and Arizona). The validity of comparing growth patterns of plants from these areas with those from the three sources used in the growth chamber studies may, of course, be questioned. However, it appears justified until more intensive studies are available with regard to the variation within these three broad areas (northern coastal, northern interior, and southern Rocky Mountains), which differ so greatly from each other in environmental conditions.

The earliest to start growth were the plants from Waterville, eastern Washington and the latest those from Forks, western Washington on the west side of the Olympic Peninsula (Fig. 4). The Waterville, eastern Washington plants were also the earliest to complete 90 percent of height growth (hereafter called growth cessation) and those from Forks, western Washington were the latest. There was an average of 13 days difference between these two groups of plants in the time of growth initiation and no less than 37 days in the time of growth cessation. As would be expected the amount of leader growth in the seedlings from Forks, western Washington was more than twice those from Waterville, eastern Washington. There was considerable difference between seedlings from southern Vancouver Island and those from Forks, western Washington with regard to the times of growth initiation (15 days) and cessa-

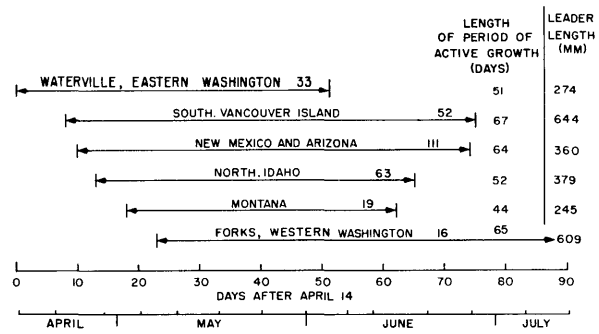


Fig. 4. — Times of height growth initiation and 90 percent completion of height growth in six to seven-year old Douglas-fir when grown near Corvallis, Oregon. Standard errors of mean length of period of growth do not exceed two days. Waterville, eastern Washington, is located in Douglas County, at 47° 39' n. lat., 120° 5' w. long., at 2600 ft. elev.; Forks, western Washington, is located in Clallam County, at 47° 57' n. lat., 124° 22' at 350 ft. elevation. The plants from Montana originated from the vicinity of Hebgen Dam, Gallatin County, at 44° 52' n. lat., 111° 20' w. long at 6400 ft. elevation. The plants from northern Idaho originated at various localities in Kootenai and Boundary Counties; those from New Mexico and Arizona from 10 different localities in the two states from Tucson, Arizona to Grants, New Mexico. Numbers immediately after the origins indicate number of trees measured.

tion (14 days) though the total length of period of active growth were about the same (67 and 65 days, respectively) as was the amount of leader growth. The seedlings from New Mexico and Arizona were very similar to those from southern Vancouver Island as far as the times of growth initiation and cessation are concerned, but total growth was only slightly more than half of that of the Vancouver Island plants. The seedlings from Montana had the shortest period of growth of all seedlings and also grew the least. They were almost as late as those from Forks, western Washington.

It should be pointed out that at the age of five years the initial differences in height between plants from Montana and from Vancouver Island, for example, were very great; in some cases the latter were 4–5 times as tall as the former. Therefore, the differences discussed here in leader growth must certainly also be a function of the initial differences in plant height.

Discussion

The differences among the seedlings and young trees from the various areas in their responses to the environmental conditions must somehow be related to the environmental conditions at their native habitats.

Some of these relationships are fairly obvious. It is clear that the late onset of dormancy in the seedlings from Vancouver Island even when grown under a variety of photoperiodic and thermoperiodic conditions is related to the relatively long period favorable for growth in their native habitat. Similarly, the low summer precipitation and short frost-free season in the northern Rocky Mountains are no doubt responsible for the early onset of dormancy in seedlings from this area. This characteristic has become genetically fixed in the population so that dormancy occurs early even when soil moisture is kept in ample supply. It appears that photoperiod plays an important role in this early dormancy, since only long photoperiods or continuous light could keep the plants actively growing. This is also evident from the quick response to change in photoperiod of the northern interior type as compared to the coastal seedlings (Figs. 2 and 3).

It is of significance that height growth was greatly affected in the Vancouver Island seedlings by the various temperature regimes as opposed to the continental seedlings. This relates well to the differences in their native habitats. A significant factor for survival in the northern Rocky Mountains is no doubt the ability to respond quickly to changes in environmental conditions by break or onset of dormancy to take advantage of the relatively short season favorable for growth. In the coastal areas, on the other hand, one of the critical factors may be the ability to maintain rapid and sustained growth in competition for light. Since the seasonal changes in coastal areas are gradual and relatively small no selection for rapid response with regard to onset or break of dormancy has occurred, but rather responses in growth rate with changing temperatures.

The intermittent early growth in the New Mexico and Arizona seedlings clearly reflects the relatively high proportion of summer precipitation in that area. This intermittent growth may conceivably permit seedlings to remain dormant even early in the season if for some reason the conditions become unfavorable, particularly with respect to soil moisture, and yet to resume growth quickly as the conditions remain favorable.

The delayed effects of cold nights emphasize the importance of temperature preconditioning effects. It is difficult at the present stage to relate these effects to conditions at the native habitats. Considerably more information is needed on microclimatic conditions at the habitats and the behaviour of seedlings in their native habitats before such relationships can be established.

The phenological observations in the field at Corvallis supports to some degree the findings obtained under controlled environment. Coastal plants (Forks, western Washington and Vancouver Island) had the longest period of active growth and those from Waterville, eastern Washington, Montana and northern Idaho the shortest. The difference in time of growth initiation between the plants from Montana and those from Waterville, eastern Washington clearly reflects the environmental conditions at their native habitats. Thus, at Hebgen Dam, Montana, in the vicinity of which most of the plants originated, the frost-free period averages only 88 days with the average late killing frost occurring on June 15 as opposed to 136 days and May 16 at Waterville, eastern Washington (U. S. D. A., 1941).

The lateness of the plants from Forks, Washington are difficult to interpret on the basis of frost-free season since

the average late killing frost occurs on April 25 in that area. However, it is possible that this lateness reflects the greater unpredictability of the date of latest spring frost in coastal as opposed to continental climates as pointed out by SWEET (1965). Another possibility may be selection for lateness caused by fungi attacking new foliage, particularly *Botrytis* spp., in early spring when air-humidity is high.

The fact that the plants from Waterville, eastern Washington initiated growth considerably earlier at Corvallis (April 14) than might be expected on the basis of their native habitat (average last killing frost on May 16) merely confirms the findings from the controlled environment studies in that they, like the seedlings from Kamloops, B. C., respond quickly to favorable conditions which at Corvallis occur considerably earlier (average last killing frost on April 15) than at their native habitat. However, this line of reasoning does not explain why the plants from Montana failed to respond earlier to the conditions at Corvallis. One possible explanation is differences in chilling requirements. The average period in which frosts may occur at Waterville, eastern Washington, is only 219 days compared with 277 days at Hebgen Dam, Montana and 154 days at Corvallis, Oregon (U. S. D. A., 1941). The possible lack of sufficient chilling of the Montana plants at Corvallis may have delayed break of dormancy. However, this remains to be tested.

Plants from Forks, western Washington continued growth into July, in spite of the apparent very high soil moisture tensions at that time in the plantations. The average annual precipitation at Forks is 117 inches compared to only 40 at Corvallis.

The intermittent growth found in young seedlings from New Mexico and Arizona was not present in the field. But plants from this area were almost all characterized by a short, second flush of growth. The intermittent growth is apparently only characteristic of very young seedlings.

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Newsletter

Contributions on tree breeding and genetics at the Ninth Commonwealth Forestry Conference

By J. BURLEY¹⁾

This conference was held at New Delhi, India, during January, 1968, and included field trips to the Forest Research Institute, Dehra Dun, to neighbouring forests of Uttar Pradesh, and to forests and utilisation operations in south and east India. The conference was attended by 65 delegates representing 19 Commonwealth countries and international organisations, in addition to about 100 Indian

Forestry Service officers. Contributed papers were discussed by separate committees in the following categories: -- Policy; Silviculture, management and economics; Harvesting, utilisation and marketing; Protection; Recreation and amenity. In addition each attending country and all Australian states presented progress reports for the period 1960-65 in a uniform format.

Readers of this journal may find interest in those progress reports which include sections on the introduction of fast-growing exotic species, particularly tropical pines and eucalypts, and with teak (*Tectona grandis*). Those species

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