stages. First, in some of the apical meristems induction of the generative state occurs leading to differentiation into vegetative and generative meristems. In the second stage male and female initials form and differentiate. This suggestion finds confirmation in some reports. OWENS and MOLDER (1976) have observed in Picea sitchensis differences in apical domes before initiation of bud scales, that is before the onset of formation of lateral organs. They found that in pith cells of future domes of vegetative buds there accumulated more phenolic and ergastic compounds than in pith cells of future domes of generative buds. These authors also report that apical domes of generative buds show greater mitotic activity during fornation of the initials.

In 1978 I collected from Norway spruce grafts both male flowers and shoots with needles from analogous sites on the branches. It turned out that the number of stamens was twice as large as the number of needles. This observation confirms the greater mitotic activity of apical domes leading to male strobiles, which also agrees with the suggestions about the causal relation between rate of growth of the apical meristem and the type of bud that will develop from it (ROMBERGER and GREGORY 1974, TOMPSETT 1978). One suspects therefore that a difference in mitotic activity in favour of generative apices is caused by earlier induction of the generative state of these meristems.

Interpreting these results on the basis of this hypothesis one can say that GA, together with CCC favoured induction of the generative state in meristems, while the fact that male and not female initials were laid down was the result of other factors. This would explain why PHARIS et al. (1975) were able to induce female flowering iii Pinus contorta DOUGL. when the GA,,, application was made during differentiation of male flower initials. The reports in the literature on the possibility of changing sex of initials under the influence of growth regulators (SAITO 1957) represents indirect confirmation of the explanation suggested above concerning sequential induction of the generative state in apical meristems.

In any case it appears that there already are distinct differences between vegetative and generative meristems at the initial stage of flower induction that is during initiation of bud scales. These differences are much greater and more difficult to alter than those occuring later between female and male flower initials.

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Comparison of a Eucalyptus tereticornis X E. grandis controlled hybrid with a E. grandis X E.tereticornis putative natural hybrid

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Summary

Species hybrids of a E. tereticornis X E. grandis controlled cross FRI-6 and a E. grandis X E. tereticornis putative natural cross FRI-10, are compared with the parental species. In more than half the total number of contrasting characters studied, the hybrids were intermediate between the parental species; in the rest, including lignotuber development, flowering precocity etc. they were more like one or the other parent, inheritance apparently being dominant for such characters. Hybrids of the putative natural hybrid FRI-10, where E. grandis was involved as the maternal parent, were conspicuously heterotic in height and diameter growth as compared to their pure E. grandis half-sibs and non-sibs. The potential practical value of such species hybrids in Indian Forestry, is discussed.

Key words: Eucalyptus *tereticornis*, E. grandis, Interspecific hybridization.

Zusammenfassung

Arthybriden von Eucalyptus tereticornis X E. grandis aus einer kontrollierten Kreuzung (FRI-6) und einer wahr-

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scheinlich natürlichen Kreuzung *E. grandis* × *E. tereticornis* (FRI-10) wurden mit den Elternarten verglichen. In mehr als der Hälfte unterschiedlicher Elterneigenschaften nehmen die Hybriden eine Mittelstellung zwischen den Elternarten ein. In den restlichen Eigenschaften, wie z. B. frühes Blühen ähneln sie einem Elter. Anscheinend handelt es sich dabei um dominant vererbte Eigenschaften. Hybriden, die aus der wahrscheinlich natürlichen Kreuzung FRI-1 mit *E. grandis* als Mutter hervorgegangen sind, zeigen im Vergleich mit *E. grandis*-Halbgeschwistern oder nicht verwandten in Höhe und Durchmesser Heterosiseffekt. Die mögliche Bedeutung solcher Arthybriden für die Forstwirtschaft Indiens wird diskutiert

Introduction

Interspecific hybrids between *Eucalyptus tereticornis* Sm. (Forest Red Gum) and *E. grandis* Hill ex Maiden (Flooded Gum) have previously been reported from certain South African countries (FAO, 1976). According to Shelbourne (1962), *E. grandis* — *E. tereticornis* F_1 hybrids, and even their F_2 offsprings, showed definite hybrid vigour, producing some of the biggest trees for their age in Northern Rhodesia (now Zambia), where therefore, matrix planting of *E. grandis* mother trees amidst *E. tereticornis* father trees was reportedly done for F_1 hybrid seed production. Hans (1974) reporting from the same country, but more recently, stated that artificial *E. grandis* × *E. tereticornis* hybrids grew better than either parent, and their form was as good as that of *E. grandis.* In drought resistance and wood properties, however, the hybrids were intermediate between the parental species.

In this article, for the first time in India, interspecific hybrids between *E. tereticornis* and *E. grandis* are described, and their potential practical value to Indian forestry is indicated.

Material and Methods

Beginning with the autumn of 1971, four different *E. tereticornis* (Et.) × *E. grandis* (Eg.) one-way species crosses were progressively attempted at the Forest Research Institute, Dehra Dun. The crosses were: 1) FRI-6-1971 (Et. 14 × Eg. 6); 2) FRI-7-1973 (Et. 19 × Eg. 6); 3) FRI-8-1973 (Et. 17 × Eg. 6) and 4) FRI-9-1974 (Et. 16 × Eg. 3). While one cross viz. FRI-8 failed to produce any seed, the three remaining yielded only limited quantity of seed. Out of this seed, a small 12-tree block planting had been done in 1973, of only the first cross viz. FRI-6, using the parental progenies as the controls, in the Kaulagarh experimental area at Dehra Dun.

Corresponding *E. grandis* × *E. tereticornis* controlled reciprocal crosses were not possible because all the *E. grandis* trees available were too tall to work upon even with ladders. However, when first flowering occurred in 1977, of the 4 year old FRI-6 controlled cross progenies, it was possible to identify using diagnostic floral characters, fifteen putative *E. grandis* × *E. tereticornis* natural hybrids which had also concurrently flowered for the first time that very year, in a 13-family one-parent progeny trial of *E. grandis* planted in 1974, in an adjoining block of the same Kaulagarh experimental area. Presumably, there were flowering *E. tereticornis* trees in the vicinity of the particular *E. grandis* tree whose open-pollinated progeny contained such hybrids. Designated as FRI-10, these were deemed to represent a hypothetical *E. grandis* × *E. tereticornis* species reciprocal of FRI-6.

As already indicated, for the controlled cross FRI-6, progenies of both parents had been planted to serve as controls. In case of the natural cross FRI-10 however, the even-aged half-sib and non-sib pure *E. grandis* progenies growing in the same or adjoining family plots, were deemed as the single parental controls for evaluating heterosis.

External Morphology

Stem form:

As a species, *E. grandis* is well known for its excellent stem form; it develops thick, clean, straight, shaft-like boles when mature. *E. tereticornis* is comparatively poorer in all these respects. While hybrid progeny of the controlled cross FRI-6 was more or less intermediate in stem form, those of the natural hybrid FRI-10 resembled more their *E. grandis* mother parent in this respect *(Fig. 1).*

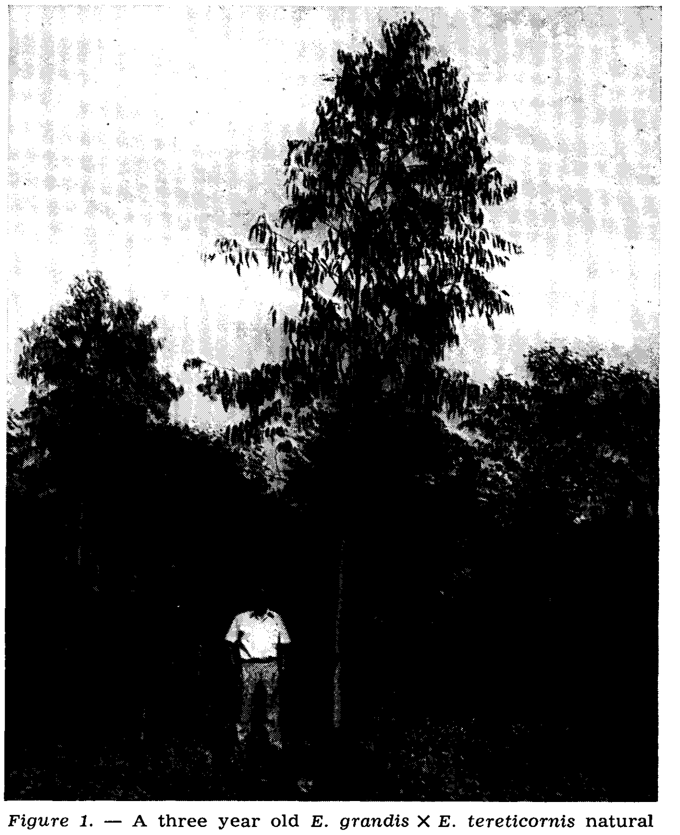

Figure 1. — A three year old *E. grandis* × *E. tereticornis* natural hybrid FRI-10 (X) with an even-aged pure *E. grandis* half-sib on the left (G). Note other similar hybrids in the background overtopping the general canopy level.

Leaf Character:

Adult leaves of *E. tereticornis,* like those of most other eucalypts, are isobilateral and concolorous. Due to an early twisting of their petioles, the leaf blades come to be disposed vertically, with their edges facing upwards or downwards. The two laterally placed surfaces are equally exposed to natural sunlight and are of much the same colour and appearance. *E. grandis* however is atypical of eucalypts in that its leaves are dorsiventrally disposed as in most other broadleaved plants. Correspondingly, its leaves are bicolorous; the upper surface which is dark green is readily distinguishable from the pale green of the undersurface. Hybrids of both FRI-6 and FRI-10 were more or less intermediate in leaf disposition and colour characters.

Figure 2 illustrates typical single leaves of the pure species and their hybrids. As can be seen, *E. tereticornis* has long, lanceolate leaves with non-wavy margins whereas in *E. grandis* the leaves are comparatively much shorter in length oblong-lanceolate in shape, and with wavy margins. Both hybrids showed broad-lanceolate intermediate length

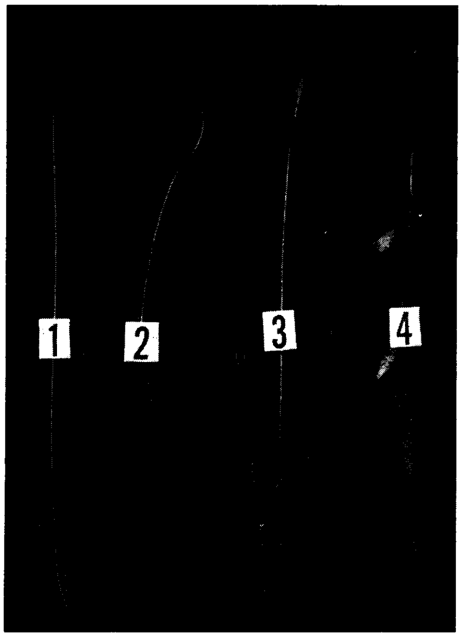

Figure 2. — Typical leaves of: 1) *E. tereticornis;* 2) FRI-6; 3) FRI-10 and 4) *E. grandis.*

leaves. In general appearance, leaves of the controlled hybrid FRI-6 tended to be more like those of its *E. tereticornis* mother parent and were often falcate. In the natural hybrid FRI-10, the leaves were much broader and had larger leaf surfaces than any of the three others but in their wavy margin, they recalled more their *E. grandis* mother parent. There is a suggestion of heterosis in leaf size in this hybrid which was also true in regard to its fruit size and growth rate, as will be described later.

Stomatal distribution:

As generally true of isobilateral leaves, stomatal frequency on the morphologically upper and lower leaf surfaces is nearly the same in *E. tereticornis.* The dorsiventral leaves of *E. grandis* on the other hand are strictly hypostomatous, that is, the stomata are confined to the undersurfaces only, as is true of most broadleaved plants. The hybrids were intermediate in this respect, having relatively many more (approximately five times more in FRI-6) stomata on the morphological undersurface than on the upper.

Floral characters:

Important floral morphological characters of the parental species and of the two sets of hybrids are illustrated in *Figure 3. E. tereticornis* has very long floral buds characterised by an elongate operculum, long style and long erect stamen filaments. In *E. grandis,* on the contrary, the flower bud is by comparison very short with sub-hemispherical operculum, short style and short inflexed stamen filaments.

In the hybrids, the flower buds were of more or less intermediate length and correspondingly this was also true of the operculum and style. In shape, the operculum is more or less conical; rather acutely so in FRI-6 and obtusely so in FRI-10. The stamen filaments in both hybrids were kinked or zig-zag in bud.

Fruit characters:

Ripe but undehisced fruit capsules of the parental species and hybrids are illustrated in *Figure 4.* As can be seen,

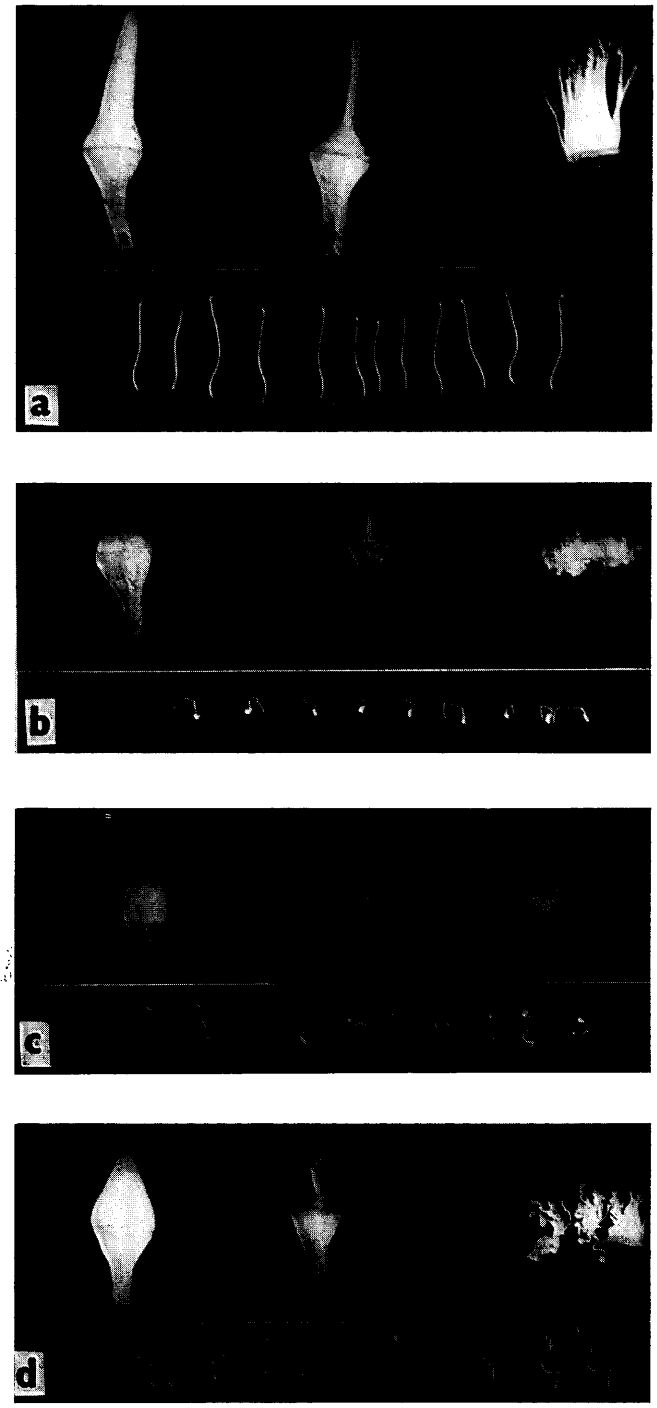

Figure 3. — Flower bud, pistil, stamen cluster and separated filaments of: a) *E. tereticornis;* b) *E. grandis;* c) FRI-6 and d) FRI-10

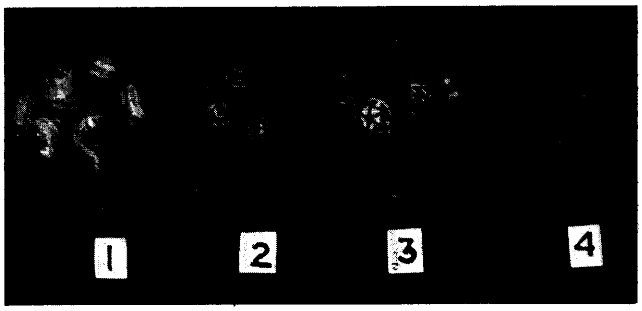

Figure 4. — Ripe fruit clusters of: 1) *E. tereticornis;* 2) FRI-6; 3) FRI-10 and 4) *E. grandis.*

fruits of *E. tereticornis* are large, hemispherical in shape with a wide and convex disc. The capsule valves are clearly exserted in this species. *E. grandis* has smaller fruits which are broadly campanulate in shape with a narrow and depressed disc. The valves in this species are more or less at rim level and not prominently exserted as in *E. tereticornis*. Both hybrids were characterised by intermediate-size fruits which were however relatively larger in FRI-10 than in FRI-6.

In their overall appearance and shape, the hybrid fruits in both cases resembled more those of *E. tereticornis* than of *E. grandis*. Also their valves were exserted though not to the same extent as in *E. tereticornis*.

Inheritance of Lignotuber

E. grandis is one of the few species of the genus which is characterised by a total absence of lignotubers in the root-shoot region of the seedling, *E. tereticornis* being typical in their presence. Seedlings of the controlled cross FRI-6 F_1s developed lignotubers, apparently having dominantly inherited the capacity to form these structures from the *E. tereticornis* mother parent. This must have been true also of the natural cross FRI-10 but the same could not be ascertained since hybridity in their case was confirmed only after first flowering at age 3 when they had past the seedling age. Dominant inheritance of lignotuber trait in eucalypt species hybrids has previously been reported in other cases also.

Flowering precocity

Under Dehra Dun conditions, *E. tereticornis* attains flowering maturity comparatively early in life — sometimes as early as 18 months from seed. On the other hand, trees of *E. grandis* (as also *E. camaldulensis)* take longer to attain flowering maturity. In the 12-tree block planting of FRI-6 hybrids and controls, *E. tereticornis* and the hybrids initiated flower buds for the first time in June 1977 at age 4. *E. grandis* progenies in this trial failed to do so even the following year.

In the *E. grandis* half-sib trials, first flowering occurred even earlier, at age 3 itself, but mainly of the natural hybrids FRI-10; very few parental *E. grandis* progenies in this trial initiated flowers although they were all of the same age. Also, compared to the hybrids they produced but few flowers and fruits. Similar heterosis in flowering precocity was earlier reported by the present authors in the case of another species hybrid FRI-4 involving a *E. tereticornis* × *E. camaldulensis* cross (Venkatesh and Sharma, 1976).

Table 1. — Comparison of the hybrids with parental species for different morphological characters.

Character	*tereticornis*	*tereticornis* × *grandis* (FRI-6)	*grandis* × *tereticornis* (FRI-10)	*grandis*
Cotyledon	Reniform	Bilobed	—	Bilobed
Lignotuber	Present	Present	—	Absent
Stem form	Poor	Intermediate	Excellent	Excellent
Leaf:				
Disposition	Isobilateral	Intermediate	Intermediate	Dorsiventral
Shape	Linear-lanceolate	Broad-lanceolate	Broad-lanceolate	Oblong-lanceolate
Length	Very Long	Intermediate	Intermediate	Short
Colour	Concolorous	Intermediate	Intermediate	Bicolorous
Stomatal frequency	Equally distributed on both surfaces	Intermediate; some on upper, more on undersurface	Intermediate; some on upper, more on undersurface	Confined to undersurface only
Peduncle	Terete	Flattened	Flattened	Flattened
Early or late flowering	Early	Early	Early	Late
Flower bud	Long	Intermediate	Intermediate	Short
Operculum shape	Elongate	Conical	Conical	Sub-hemispherical
Staminal filaments in bud	Erect	Kinked	Kinked	Inflexed
Style length	Very Long	Intermediate	Intermediate	Very short
Fruit:				
Size	Large	Intermediate	Large	Small
Shape	Hemispherical	Hemispherical	Hemispherical	Broadly campanulate
Disc	Wide and convex	Narrow and convex	Narrow and convex	Narrow and depressed
Valves	Exserted	Exserted	Exserted	More or less at rim level

Growth comparisons and heterosis

Hybrids of the controlled cross FRI-6 were, to start with, intermediate in growth rate between the superior *E. grandis* and inferior *E. tereticornis* parental progenies. But subsequently they lost this initial promise and came to occupy only third place in this small trial, falling behind even *E. tereticornis,* especially in mean diameter.

Natural hybrids of FRI-10 behaved differently. They started outgrowing their *E. grandis* half-sibs and non-sibs in the same or adjoining family plots, from about the second year onwards. At age $3^1/_2$, nine of the fifteen hybrids identified, had grown 9—10.50 m tall and ten of them ranged from 8—9.50 cm in diameter. Comparable values for the non-hybrids at the same age were only 4—6.50 m for height and 4—5.50 cm for diameter. Thus, in both height and diameter, the two principal wood and timber-yield components of forest trees, hybrids of FRI-10 appeared promisingly heterotic like those reported recently by HANS (1974) from Zambia.

The various morphological traits described in the preceding paragraphs are summarised in *Table 1*. It will be seen that in more than half the total number of contrasting characters studied, the hybrids are intermediate between the parental species; in the remaining, they are more like one or the other parent. In their kinked stamen filaments, however, the hybrids differed from either parental species and recall hybrids of two earlier described *E. tereticornis* — *E. camaldulensis* reciprocal species crosses FRI-4 and FRI-5 (VENKATESH and SHARMA, 1978).

Discussion

E. grandis is one of the best eucalypts for pulpwood. It has fast growth rate, excellent stem form and low-density wood. It is, however, a rather demanding species as regards its site requirements, needing as it does, good soils, high rainfall and in particular cannot stand a long dry period between the monsoons, a condition prevalent over large tracts of India where eucalypt planting is appropriate. As such, its plantation in this country is limited at present to high ranges of Kerala, Tamil Nadu and to some extent of Madhya Pradesh in Central India. *E. tereticornis* in contrast is very widely adaptable and drought resistant. Hence it is currently the most widely planted eucalypt in the country being grown even on poor sites, shallow soils and under dry conditions. A hybrid combining in itself the high adaptability and drought resistance of *E. tereticornis* with the excellent stem form and technological qualities of the wood of *E. grandis* would be of obvious economic value for extended cultivation in intermediate zones (hybrid habitats) where *E. grandis* by itself cannot be grown, i.e. at lower elevations, low rainfall areas and on poorer sites. Additionally, there also exists the possibility of exploiting hybrid growth vigour for quicker and higher wood production in shorter rotations much as in two other recently described heterotic reciprocal species crosses between *E. tereticornis* and *E. camaldulensis* (VENKATESH and SHARMA, 1977).

E. grandis does not develop lignotubers at the seedling stage; it is correspondingly a poor coppicer unlike *E. tereticornis* which is excellent in this respect and develops lignotubers like most other species of the genus. Since the lignotuber character is dominantly inherited in the F_1 hybrids they may be expected to be good coppicers also, like their *E. tereticornis* parent.

Lignotubers can be more directly valuable in another way too. It has recently been shown in *E. citriodora* (ANEJA and ATAL, 1969), that tissues from these structures can be cultured *in vitro* to give plantlets. This can therefore be a new and novel way of clonally mass producing, without genetic segregation, highly uniform commercial growing stock from selected best individual hybrid seedlings and seedling families.

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