Acknowledgement
I am grateful to the staff of the Forestry Commission’s Genetics and Statistics (North) Branches for helpful discussion and to the staff, past and present, of Genetics and Silviculture field stations who have established, tended and assessed the experiments, providing the data on which this paper is based. In particular, I acknowledge the assistance of Colin Maclean in obtaining the volume data for the Kilhjarm experiment and that of Ian White in providing a Genstat program for covariance analysis.

References

Inbreeding and Interspecific Hybridization in Eucalyptus gunnii

By B. M. PORTS1, W. C. Potts2 and B. CAVIN3

(Received 25th April 1986)

Summary
The success and vigour of plants arising from self and close matings of Eucalyptus gunnii are compared with wide intraspecific crosses and a range of interspecific crosses. The barriers to inbreeding in E. gunnii are strong, in many cases stronger than the barriers to interspecific hybridization. The success (number of plants obtained/flower pollinated) of self-pollination and close intraspecific crosses was less than wide intraspecific crosses and most interspecific crosses investigated, as was the height and survival after 1 year's plant growth. E. gunnii females demonstrate wide crossability, with the success of most interspecific hybrid combinations tried with species from the section Maidenaria, not significantly different from that of wide intraspecific crosses. The only major barrier to interspecific hybridization found was with E. globulus. There was not a strong association between crossability and the taxonomic/genetic distance between parents, although after 1 year's plant growth, F1 hybrids from the only interspecies cross examined (E. gunnii × ovata) showed reduced vigour. The implications of these results for the development of breeding strategies as well as for gene flow and hybridization in natural populations are discussed. Strong barriers to inbreeding in Eucalyptus may result in a disparity between pollen dispersal and gene flow in natural stands, with more distant matings favoured.

Key words: Eucalyptus, breeding system, inbreeding depression, self-incompatibility, hybridization, crossability, gene flow.

Zusammenfassung

Résumé
La réussite et la vigueur des plants issus d'autofécondation et de croisements de parents génétiquement proches...
pour Eucalyptus gunnii, sont comparés avec ceux issus de croisements intra-spécifiques de parents génétiquement éloignés et toute une série de croisements inter-spécifiques. Dans E. gunnii les barrières à l'autofécondation sont puissantes, et dans beaucoup de cas plus fortes que celles des croisements inter-spécifiques. La réussite (estimée par un rapport entre le nombre de plants obtenus par rapport au nombre de fleurs pollinisées) des croisements autofécondés et intra-spécifiques de géniteurs génétiquement proches a été inférieure aux croisements intra-spécifiques faisaient appel à des géniteurs génétiquement éloignés et à la plur-part des croisements inter-spécifiques étudiés. Il en est de même pour les hautes et la survie des plants après une année de végétation en plantation. Les mâles E. gunnii ont montré une grande aptitude hybridiogène, au travers de la plupart des croisements inter-spécifiques essayés; avec les espèces de la section Maidenaria aucune différence significative n'est apparue entre ces croisements inter-spécifiques et les croisements intra-spécifiques de parents génétiquement éloignés. La seule barrière importante dans les croisements inter-spécifiques a été trouvée avec E. globulus (le croisement réciproque E. globulus X E. gunnii n'a pas été essayé). Il n'y a pas de puissants liens entre l'aptitude hybridiogène et la distance génétique taxonomique des parents; cependant, après une année de croissance en plantation, l'examen de la seule famille hybride F, issue de croisement inter-série (E. gunnii X E. uawata) a montré une réduction de vigueur. L'implication de ces résultats dans le cadre du développement d'une stratégie d'amélioration tel que la dispersion des gènes et l'hybridiogène dans les populations naturelles, est discutée. Dans le genre Eucalyptus, les puissantes barrières à l'autofécondation peuvent provoquer une disparité entre la dispersion du pollen et les gènes dans les aires naturelles, avec un appartenance en faveur des plus éloignés.

Introduction

The genetic system of Eucalyptus is a classic open recombination system (sensu Grant 1958), typical of temperate forest-tree genera such as Pinus, Populus, Cupressus and Quercus (e.g. Sierpinski 1950; Barron 1965; Sterne and Rocher 1974). Eucalypts have a mixed mating system (e.g. Pytor 1976; Eldridge 1976, 1978; Moran and Brown 1980), with relatively high outbreeding rates (0.69–0.84, Moran and Bell 1983) maintained by prunery (e.g. Pytor 1951, 1976; Hodgson 1976a; Griffith and Hand 1979) and varying degrees of self-incompatibility (e.g. Pytor 1975b, 1961, 1976; Hodgson 1976c; Eldridge and Griffith 1983) and reinforced by selection against products of self-fertilization in later stages of the life cycle (e.g. Phillips and Brown 1977; Moran and Brown 1980; Firth 1982; Eldridge and Griffith 1983; Moran and Bell 1983; Griffith et al. 1987). Barriers to interspecific hybridization are generally weak as evidenced by the prolific reports of natural and artificial hybridization (see Pytor and Johnson 1971, 1981; Pytor 1976; Potts and Reid 1983; Griffith et al. in press). However, hybridization does not occur between subgenus (e.g. Pytor and Johnson 1971, 1981; Pytor 1976; Griffith et al. in press) and, while there are general trends (e.g. Pytor 1957a, 1976; Pilenenko 1969; Pytor and Johnson 1971, 1981; Pytor and Wills 1974; Griffith et al. in press), compatibility patterns within subgenus are not well explored.

Inbreeding effects have been detailed in several Eucalyptus species (e.g. Eldridge 1970; van Wyk 1976, 1977, 1980; Hodgson 1976b, 1976c; Venkatash and Varshasya 1977; Phillips and Brown 1977; Eldridge and Griffith 1983) but studies quantifying the success of natural (e.g. Drake 1981a, 1981b; Potts 1985) or artificial (e.g. Pytor 1951, 1957a, 1957c; Pilenenko 1969; Caunin 1984) interspecific hybridization are few.

There are no studies reported which compare the relative importance of barriers to inbreeding and interspecific hybridization, although such studies are important for a full understanding of gene flow and the evolutionary consequences of hybridization in the genus (e.g. Pytor 1976; Pytor and Johnson 1981; Potts and Jackson 1980) and the development of breeding strategies.

Eucalyptus gunnii (section Maidenaria; subgenus Symphyomyrtus - sensu Pytor and Johnson 1971) is one of the most cold resistant eucalypts (Pytor 1975b; Potts and Reid 1985; Davidow and Reid 1985) and is thus one of the main species being investigated for pulpwood production in France. However, its relatively slow growth rates and poor pulping qualities when compared to more frost sensitive species from the same section. such as E. globulus, E. nitens, E. dalrympleana and E. viminalis, prompted the investigation of artificial hybridization as a means of breeding fast growing cold resistant genotypes for clonal selection (Caunin 1984). This crossing program enabled the crossability of E. gunnii to be examined by comparing the success and vigour of a wide range of intraspecific and interspecific crosses.

Methods

Crosses (self, open and controlled pollinations) were from the 1983 hybridization program undertaken by Association Forêt-Cellulose (AFOCELL) near Toulouse in the south of France. Results are presented for self, open, close and wide in intraspecific crosses and interspecific crosses using E. gunnii females and pollen from the faster growing, but more frost sensitive species — E. cordata, E. dalrympleana, E. viminalis, E. macarthurii, E. nitens, E. globulus and E. uawata.

The close in intraspecific crosses were amongst 5 descendants from 1 to 3 surviving trees in an old French plantation (Clarac-Herault). While their exact pedigree cannot be determined, they have a high probability of being related (some being at least half-sibs) and represent a narrow genetic base. Wide in intraspecific crosses involved unrelated parents from different provenances. Details of the hybridization orchard containing the 7 E. gunnii females and the methods used for artificial hybridization are given by Caunin (1984). The crossing pattern was not orthogonal due to limitations on the availability of flowers, although cross types were generally well distributed across females. For each cross type, details are given in Tab. 1 of the number of crosses and total number of plants surviving and measured after 1 season’s growth in a plantation (with one third of the progeny from each cross arranged in linear rows randomized in each of 3 blocks) established at Lamasquère, in the south of France.

The overall success of crosses was measured using the number of plants obtained per flower crossed. This integrates effects due to flower abortion (number of capsules obtained per flower crossed)- the number of germinating capsules, the survival of germinants in the nursery and the proportion of stunted weak plants (runts) in a multiplicative manner. Analyses of initial measures of the success of cross types were based on individual cross values, whereas families of each cross type were pooled for comparisons of growth and mortality. Cross types were compared using a model-1, oneway analysis of variance (ANOVA) or in the case of mortality, a contingency Chisquared test. Proportions were angular transformed prior to analysis of variance. Where the ANOVA was significant, general comparisons between means were made using the
Table 1. — The total number of crosses, different females and males used, the total number of flowers crossed and the number of plants alive after 1 season’s plantation growth.

<table>
<thead>
<tr>
<th>Type of cross</th>
<th>Number of flowers crossed</th>
<th>Number of plants crossed</th>
<th>number of females</th>
<th>number of males</th>
<th>number of flowers</th>
<th>number of plants</th>
<th>alive</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intraspecific (E. gunnii x gunnii)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>self-pollinated</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>251</td>
<td>64</td>
<td></td>
<td></td>
</tr>
<tr>
<td>open-pollinated</td>
<td>7</td>
<td>7</td>
<td>1</td>
<td>274</td>
<td>75</td>
<td></td>
<td></td>
</tr>
<tr>
<td>close</td>
<td>9</td>
<td>5</td>
<td>4</td>
<td>243</td>
<td>94</td>
<td></td>
<td></td>
</tr>
<tr>
<td>wide</td>
<td>14</td>
<td>5</td>
<td>8</td>
<td>229</td>
<td>214</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interspecific (E. gunnii x female x species)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cordata</td>
<td>7</td>
<td>7</td>
<td>1</td>
<td>239</td>
<td>79</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dalymplesana</td>
<td>23</td>
<td>6</td>
<td>6</td>
<td>496</td>
<td>224</td>
<td></td>
<td></td>
</tr>
<tr>
<td>viminalis</td>
<td>14</td>
<td>7</td>
<td>5</td>
<td>466</td>
<td>124</td>
<td></td>
<td></td>
</tr>
<tr>
<td>macarthurii</td>
<td>15</td>
<td>5</td>
<td>5</td>
<td>195</td>
<td>200</td>
<td></td>
<td></td>
</tr>
<tr>
<td>nitens</td>
<td>5</td>
<td>4</td>
<td>2</td>
<td>106</td>
<td>42</td>
<td></td>
<td></td>
</tr>
<tr>
<td>globulus</td>
<td>4</td>
<td>4</td>
<td>2</td>
<td>95</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ovata</td>
<td>4</td>
<td>4</td>
<td>2</td>
<td>94</td>
<td>70</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>110</td>
<td>2688</td>
<td>1186</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Student-Newman-Kuels multiple range test. Specific a priori comparisons between means were made using the Students t-test.

**Results**

There appear to be strong barriers to inbreeding in *E. gunnii* as the success (plants obtained/flower crossed) of both self-fertilization and close intraspecific crosses were significantly (P < 0.05) less than that of wide intraspecific and most interspecific crosses (Fig. 1). This mainly reflects the low number of plants obtained per capsule in these cross types, which no doubt reflects poor seed set. The results from self-pollination were combined from assisted (flowers emasculated and pollinated manually) and non-assisted (flowers bagged only) crosses. While not strictly comparable with the controlled crosses, the data available indicated no significant difference in the abortion rate or the number of plants/capsule between assisted and non-assisted selves. Open-pollination resulted in significantly (P < 0.01) less flower abortion than the controlled crosses. However, the number of plants obtained/flower crossed was comparable to self and close intraspecific crosses (Fig. 1) due to the low seed set in open-pollination suggesting that pollen availability may be a limiting factor in natural pollination. There was no significant difference between the cross types in the proportion of plants scored as runts, although survival in the nursery of seedlings from close intraspecific crosses was significantly (P < 0.01) less than other intraspecific crosses.

Mortality in the plantation after 1 season’s growth was significantly (X², P < 0.001) higher in seedlings from intraspecific crosses than for the interspecific hybrids (Fig. 1). This was due to significantly higher mortality in seedlings from self as compared to the wide intraspecific crosses (X², P < 0.01) and there was a trend within the intraspecific cross types for increasing mortality with an increasing degree of relatedness. Furthermore, there is strong evidence for inbreeding depression in the vigour of surviving seedlings. The difference in vigour of the intraspecific cross types was not significant in the nursery, but was highly significant (P < 0.001) after 1 season’s plantation growth (Fig. 1). This was due to the marked depression in the height of seedlings from self and close intraspecific crosses when compared to the height of seedlings from the wide intraspecific crosses. The growth of the open-pollinated progenies was on the average intermediate between that of self and wide intraspecific crosses.

The success of most interspecific crosses was not significantly different from that of wide intraspecific crosses (Fig. 1). The only major barrier to interspecific hybridization observed was with *E. globulus*. Of the species used, this was the most morphologically different from *E. gunnii*. Out of 95 *E. gunnii* flowers crossed in 1983 with *E. globulus* pollen only 1 capsule was obtained but no seedlings (1 plant was obtained from 68 flowers pollinated in the 1982 crosses but was subsequently killed by frost). This was not due to inviability of the *E. globulus* pollen as other types of
crosses using the same pollen were successful (unpublished data). The only interseries cross type examined (*Vinitodes × Ovatæ, E. gunnii × ovata*) was one of the most successful in terms of plants obtained/per flower crossed (Fig. 1). This limited study provides no evidence for an association within the section Maidensaria between taxonomic/genetic distance and genetic barriers to the artificial formation of F₁ hybrids. Most of the artificial interspecific hybrids examined were significantly more vigorous than the wide intraspecific crosses of *E. gunnii* (Fig. 1). However, the average height of F₁ hybrid seedlings from the wider interspecific crosses (*E. gunnii × nitenäs — in the nursery and particularly *E. gunnii × ovata — after 1 season's plantation growth*) was less than those of the other interspecific cross types. The height of seedlings from the interseries cross (*E. gunnii × ovata*) was also significantly less in the plantation than seedlings from wide intraspecific crosses of *E. gunnii* despite *E. ovata* generally being of greater vigour than *E. gunnii*.

**Discussion**

There are strong barriers to inbreeding in *Eucalyptus gunnii* with self and close intraspecific crosses less successful than wide intraspecific crosses and most interspecific crosses examined. This clearly supports Pwyor's (1961) observations that selfing occurs in the genus, but less readily than outcrossing and frequently less readily than interspecific hybridization. Barriers to self-fertilization have been noted in other *Eucalyptus* species (e.g. Pwyor 1957b, 1961, 1976; Eldridge 1970, 1976, 1978; van Wyk 1976, 1977, 1980; Hodgson 1976b, 1976c; Venkatesh and Vakshaya 1977; Eldridge and Griffin 1983) and Pwyor (1961, 1976) indicates there is some evidence for a gene controlled self-incompatibility system in some species. While barriers to self-fertilization are occasionally complete (Pwyor 1961, 1976), they are generally manifest as a reduction in seed set (e.g. present study; Hodgson 1976a, 1976c; Pwyor 1961; Eldridge 1970, 1976; Eldridge and Griffin 1983) and subsequent reduced vigour (e.g. present study; Hodgson 1976b; Pwyor 1976; Van Wyk 1976, 1977, 1980; Eldridge and Griffin 1983) and survival (e.g. present study; Eldridge and Griffin 1983). Reduced seed set following self-fertilization may result from incompatibility (pollen-pistil or zygote-mother) or seed inviability. Increases in estimated outcrossing rates between seed and germinants (Phillips and Brown 1977; Philip 1982) and with increasing age of the seed crop (Moran and Brown 1980) would favour the latter alternative. Furthermore Griffin et al. (1986) note successful growth of pollen tubes in self crosses but a predominance of outcrossed seed following pollination of *E. regnans* with a 1:1 (self : outcross) pollen mix.

Seedlings from open-pollination of *E. gunnii* were, on the average, intermediate in vigour and survival between self and wide intraspecific crosses (Fig. 1). A similar reduction in the vigour of open-pollinated progenies compared to those arising from controlled outcrosses has been noted previously in *Eucalyptus* (e.g. Hodgson 1976b; Van Wyk 1976; Eldridge and Griffin 1983). There is little doubt this effect is a result of inbreeding depression in the 10—30% (Moran and Bell 1983) of open-pollinated seed arising from self-fertilization and clearly, the use of open-pollinated as opposed to controlled outcross seed in plantations may result in a significant loss of productivity (e.g. Hodgson 1976b; Eldridge 1978).

An understanding of the extent to which inbreeding depression extends to other degrees of relatedness is important, although virtually unstudied in *Eucalyptus*. Van Wyk (1976) noted generally better performance of families from 'close' than from 'wide' crosses of *E. grandis*, and in a small scale study (Van Wyk 1980) found inbreeding effects to extend to full-sib matings, although half-sib matings were no different from other outcrosses. Inbreeding depression appears to be evident in seedlings from close crosses in the present study. However, while the exact pedigree of individuals involved in these close crosses is unknown, they are probably more distinctly related than full-sibs. This effect requires careful investigation using individuals of known pedigree as the implications are important to the development of breeding strategies and the understanding of the dynamics of natural populations.

Barriers to crossing of related individuals may have important consequences on gene flow in natural stands. Limited seed dispersal in *Eucalyptus* (e.g. Gilbert 1958; Kirkin-Patrick 1977; Cramer 1977) probably results in stands comprising a mosaic of individuals having full-sib or more likely half-sib relationships (Griffin 1980). Pollen dispersal is probably greater than seed dispersal due to active bird and insect vectors (e.g. Barber 1965; Hopper and Moran 1981; Griffin 1985), especially long distance dispersal. The only data on pollen dispersal curves in the genus, based on pollinator foraging observations (Barber 1965; Hopper and Moran 1981), suggest dispersal curves favouring near neighbour matings. Matings between neighbours would also be favoured by greater coincidence in flowering times (e.g. Griffin 1980). However, the present results clearly support Levins' (1981) thesis for a disparity between pollen dispersal and actual gene flow. Reduced seed set and vigour and greater mortality in selfs and related matings, likely to arise with nearest-neighbour matings in natural stands, would clearly favour matings arising from distant, even long distant, pollen dispersal. However, the genetic difference between parents in probably larger in such matings (e.g. Moran and Hopper 1983), which may lead to the disruption of local coadapted gene combinations and thus outbreeding depression (Waddington 1983). An optimum degree of divergence for seed set and heterosis has been noted in intraspecific crosses of several plant species (Price and Waser 1979; Levins 1981 and Waddington 1983) argues the optimum outcrossing distance is a balance between inbreeding and outbreeding depression. However, the amplitude of interspecific cross-compatibility demonstrated in *Eucalyptus* (present study; Pwyor 1951, 1987a; Philpens 1968; Pwyor and Wiling 1974; Calvyn 1984) suggests a degree of genetic homeostasis and that outbreeding depression, arising from genetic as opposed to ecological causes, is unlikely to be a significant factor restricting gene flow within species or between closely related species, at least up to early stages in the life cycle. In fact, the success of many interspecific cross types when compared to the wide intraspecific crosses suggests that the use of interspecific F₁ hybrids as a means of monitoring gene flow patterns (e.g. Pwyor 1976) may be just as effective as the use of intraspecific gene markers. However, in this study, cross success has been assessed in the absence of competition between pollen types, and this effect requires investigation using pollen mixes (e.g. Griffin et al. 1987).

While examination of interspecific cross types on a finer scale is warranted, this study suggests that the optimum crossability for *E. gunnii*, and probably most *Eucalyptus*
species, encompasses a broad range of genetic differentiation. At one extreme, marked inbreeding depression is evident, yet at the other extreme, outbreeding depression does not seem to be manifest until fairly wide interspecific crosses are performed where incompatibility or seed abortion (e.g. E. gunnii × globulus) and reduced F₁ vigour (e.g. E. gunnii × ovata) appear to become evident (Fig. 1). The latter result accords with the observations of Pye (1957a, 1970) and Pye and Thomas (1969). Parachute of interspecific hybrids to decrease with increasing taxonomic distance between the parents. However, the reduction in height of the interseries cross (E. gunnii × ovata, Fig. 1) may not be a true indication of vigour as these F₂ s tended to exhibit plagiotropic growth, a tendency also noted by PuiPENON (1969) for E. maidenii × ovata F₁ s. Furthermore, the height of other families of this cross type produced in 1982, were not significantly less than that of intraspecific outcrosses and several of AFOCEL’s clones are putative natural E. gunnii × ovata hybrids.

Most of the artificial interspecific hybrids examined from the series Viminiales were significantly more vigorous than the wide intraspecific crosses of E. gunnii (Fig. 1). However, rather than reflecting hybrid vigour, the few hybrids of open-pollinated progeny from the female parents were available suggested that the early growth rate of hybrids progeny was intermediate between that of E. gunnii and the faster growing, lowland species used as male parents (unpublished data). The hybridization of E. gunnii females with E. globulus is of particular interest as this cross would allow the combination of genes of one of the most vigorous, but frost sensitive, species with one of the most frost resistant species in the genus. The reciprocal cross has not been attempted as yet. However, the success of crosses using natural hybrids (unpublished data) suggests there is the possibility that the genes of these two species can be combined using another species (e.g. hybrids with E. viminalis or E. ovata) as a ‘genetic bridge’ to overcome any direct barrier to the formation of F₁ hybrids.

Cross-incompatibility may become more evident in later stages of the life cycle or in advanced generations (e.g. Pye 1956; PuiPENON 1969). Nevertheless, the broad crossability demonstrated by E. gunnii indicates the importance of pre-mating (e.g. spatial and temporal isolation) and ecological barriers (e.g. Pye 1976) in the maintenance of species integrity in the genus. The importance of ecological barriers is demonstrated by the fact that the introduction of genes from these faster growing lowland species into E. gunnii, significantly reduced the probability of surviving an extreme frost (1982 crossing program — unpublished data). Furthermore, this broad crossability emphasizes the evolutionary flexibility in the genus, allowing the potential exploitation of a wide range of genetic variability through interspecific hybridization in the adaptive response to a changing environment (e.g. Pye and JOHNSON 1981; POTTs AND JACKSON 1986).

Acknowledgements

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References


**Agreement Between Patterns of Morphological Variability and Isozyme Band Phenotypes in Pitch Pine*)**

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(Received 23rd May 1985)

**Summary**

Seventy-six isozyme bands could be consistently resolved in the peroxidase, acid phosphatase, cytochrome oxidase, and leucine aminopeptidase enzyme systems in extracts of pitch pine roots. Using band frequencies in seedlings from 15 populations, the populations were resolved into three geographic groups by multivariate techniques. Morphological characteristics, including seedling height, weight, and needle length, were also subjected to multivariate analyses. The grouping based on morphological variables was very similar to that based on the biochemical markers; only two populations shifted between groups. The results suggest that multivariate analysis of isozyme data may provide largely the same information on patterns of geographic variation obtained from morphological measurements in early tests, offering a rapid alternative to nursery or greenhouse experiments.

**Key words:** Multivariate analysis, *Pinus rigida*, electrophoresis, geographic variation.

**Zusammenfassung**

Sechsundzwanzig Isoenzymbänder der Peroxidase, Acid-Phosphatase, Cytochrom-Oxidase und Leucin-Amino-Pep-
tidase konnten in Extrakten von *Pinus rigida*-Wurzeln be-
stimmt werden. Anhand der Bandhäufigkeiten von Sämlin-
gen aus 15 Populationen wurden die Populationen mittels multivariater Verfahren in drei geographische Gruppen gruppen.

**Introduction**

No one has demonstrated whether isozymes of forest trees can be used to define regions of similar adaptation, that is, whether they correlate with patterns of variation in characters of selective value. This paper compares macrogeo-

**Key words:** Multivariate analysis, *Pinus rigida*, electrophoresis, geographic variation.

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