

DROUGHT RESISTANCE IN
SEEDLINGS OF
PINUS PINASTER AIT.

by
E. R. HOPKINS

Forests Department
Perth
Western Australia

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W. R. WALLACE
Conservator of Forests

PERTH
1971

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SUMMARY

The drought resistance of seedling of *Pinus pinaster* was determined for different provenances and seedling ages under glasshouse conditions. Three trials were conducted using *Pinus radiata* seedlings as a standard of comparison. In one trial plants of *Pinus elliottii*, *P. taeda* and *P. brutia* were included.

In all trials, provenances of *P. pinaster* proved to be more resistant to drought than *P. radiata*. The Corsican provenance was separated as the most resistant, then the Portuguese and finally provenances from the French Landes and Tunisia. The Portuguese provenance showed a wide range of resistance indicating considerable variability. Plants of this population, obtained as full sib crosses from phenotypes selected for superior form and vigour in Western Australian plantations, showed decreased variation within a high drought resistance. Breeding within the provenance is maintaining a high resistance in improved plants.

Pinus brutia was the most resistant species tested with *P. pinaster* ranking second. *Pinus radiata*, *P. taeda* and *P. elliottii* were relatively sensitive to drought. Testing procedures employed allowed resistance to be gauged for both mild and extreme drought conditions.

The significance of natural drought resistance to plantation management is briefly discussed.

DROUGHT RESISTANCE IN SEEDLINGS OF *Pinus pinaster* AIT

THE PROBLEM

INTRODUCTION*

Pinus pinaster, an important exotic in Western Australia, serves as a supplementary species to *Pinus radiata* D. Don within the State's afforestation programme. As such it is used only on sites known to be marginal or otherwise unacceptable for *P. radiata* planting. Unsuitability of site for *P. radiata* is largely associated with low soil fertility but is also attributable to soil and climatic situations in which low water availability or drought may restrict commercial production of wood.

It is generally accepted that *P. pinaster* is more resistant to drought than *P. radiata*. Factual data to prove this point are lacking since most observations, or field comparisons, are confounded by fertility gradients, variable fungal or insect damage or variable silvicultural treatment. The desire to increase the plantable area by utilizing drier sites, and recent experience with plantation mortalities during a record general drought, emphasize the need for more useful information on management of the two species under droughty conditions.

In particular, the question of drought resistance became important in planning an improvement programme for *P. pinaster*. For commercial production the Portuguese provenance has proved superior under local conditions (Hopkins, 1960) and an intensive breeding programme to improve this provenance has been in progress since 1957. Possibilities arose that selection in breeding for form and vigour could lessen any advantages (over *P. radiata* as a planting proposition) proffered by drought resistance within the natural population. If drought resistance was to be an important selection factor it is probable that other provenances of the species have characteristics to contribute towards genetical improvement.

These various uncertainties prompted studies into the drought resistance of the two species in 1966. All studies concerned seedlings and aimed to provide information on the comparative drought resistance of the Portuguese provenance. In particular, the performance of improved seed, obtained through mass selection within the breeding programme, was of interest.

DROUGHT RESISTANCE

The subject of drought resistance in plants is well reviewed by Levitt, Sullivan and Krull (1960). Drought resistance is defined on the basis of a plant's capacity to survive periods of drought. Total resistance represents a combination of drought avoidance, or the ability of a plant to exclude the drought from its tissues and drought tolerance which is the degree of drought within the plant tissues that it can survive.

For perennial species such as forest trees, drought resistance is the definition of survival value through all developmental stages—germination, seedling, pole, pile and mature tree. Such can only be determined from long-term field studies and is impracticable in absolute terms (Levitt, 1961).

* Note: Metric equivalents are given in the text but not in accompanying tables or appendices.

It is conceded, however, that in nature the seedling stage is most susceptible and competitive and knowledge of drought resistance of seedlings can usually be related to the drought resistance of the perennial. Detailed studies of drought resistance of forest trees have therefore commenced with seedling studies.

Many studies of drought resistance concern cut shoots of seedling or mature plants and have studied transpiration rates, tissue moisture content, biochemical changes under defined conditions of desiccation and tissue death (Parker, 1956; Levitt, Sullivan and Krull, 1960; Henckel, 1964; Oppenheimer, 1969). These procedures have proved necessary to understand the plant processes associated with avoidance and tolerance. Workers using these techniques acknowledge that roots may play as important a role as shoots in the expression of drought resistance. Difficulties in approaching the subject, however, often necessitate the study of fragmented plants.

Daubenmire (1943) and Bourdeau (1954) used small container-grown seedlings to study the importance of drought resistance in the ecology of species of the Rocky Mountains and oak-hickory piedmont forests, respectively. These studies were relatively successful in associating drought with species distribution and have set a basic approach for most recent studies of drought resistance in forest trees. Hopkins (1964) used potted seedlings to demonstrate significant differences in drought avoidance and drought tolerance between different eucalypt species growing in mixed species foothill forests in Victoria. It was shown that a propensity for drought avoidance was associated with variation in soil fertility and leaf area production. To compare drought hardiness, ten month old plants were reduced to a standard soil moisture potential by wilting sunflowers planted in the pots. Pots were then sealed and placed in a drought chamber for exposure periods measured as 34, 68, 102 and 136 ccs evaporation from a Livingston Atmometer. Survival, recorded as plant deaths within exposure classes and percentage of leaf damage, clearly demonstrated different capacities for resistance. Species found naturally in the drier habitats demonstrated the greatest capacity for both drought avoidance and drought tolerance. Bolotin (1967) was also able to demonstrate differences in drought resistance of seedlings for different provenances of *Euc. occidentalis* Endl. Comparative differences were based on percentage survival of plants following a standard drought period.

Pharis (1966) demonstrated differences in drought resistance of sugar pine, grand fir, Douglas fir, incense cedar and pond pine by comparing the soil moisture content and foliar moisture content for each species at the lethal level. Plants were droughted in a common soil medium until they were considered to be near the death point. Soil and leaf moisture content were then measured and compared at the lethal stage. The determination of lethal point (Brix, 1960) and its comparison between species is somewhat subjective. It was subsequently shown that both soil moisture and leaf moisture content may be a measure of drought avoidance but do not necessarily relate to drought resistance (Pharis and Ferrell 1966; Levitt 1962).

Ferrell and Woodard (1966) and Pharis and Ferrell (1966) utilized potted seedlings under glasshouse and laboratory conditions to demonstrate differences in drought resistance between provenances of Douglas fir. The inland provenances proved to be consistently more resistant than the coastal forms. Plants were reduced to a standard soil moisture potential by wilting sunflowers growing in the pots. The plants were then droughted under comparable conditions

until the lethal point was reached. Following rewatering, drought resistance was determined as the number of days' exposure until the death point was reached.

These studies demonstrate that comparative values for drought resistance can be obtained by simple, if laborious, techniques to show differences between both species and provenances within a species. Results obtained are in accordance with what may be expected from knowledge of the drought severity of the environment and the natural distribution of species or provenances. Generally however, the only useful conclusion on drought resistance was expressed by days survival under comparative drought exposures. Significant definition of resistance depends largely on the use of a large number of plants to clearly illustrate trends present in mortality values. Studies by Hopkins (1964) and Bolotin (1967) associated sensitivity to drought with the potential for growth. Testing conditions such as soil fertility may thus have a marked influence on the comparative resistance demonstrated in any one trial. Generally, information on soil moisture and leaf moisture have proved of little value in defining drought resistance.

No factual reference can be cited for previous studies of comparative drought resistance in *P. pinaster*. Work in Israel placed *P. pinaster* as less drought resistance than *Pinus halepensis*. This source could not be located for reference purposes. Current work in Israel (Oppenheimer, 1969) shows that *P. radiata* has a relatively low drought resistance; considerably less than that of *P. pinea* and *P. brutia*.

THE STUDY

Work reported in this bulletin covers three separate trials investigating the drought resistance of *P. pinaster* provenances. Techniques adopted in the trials vary to some extent but in each trial, survival of plant groups can be related to length of exposure since drought commenced. Different trials incorporate different species groups, plant ages and hardening conditions. To this extent results, or the order of ranking of degree of drought resistance, are replicated for *P. pinaster* over both age classes and different trial conditions.

Procedures are reported in detail, even if of little significance to the final result. This is considered necessary, as a major objective in the study was to establish simple practical procedures for screening progenies; if this was considered necessary to further the development of the breeding programme.

TRIAL I

INTRODUCTION

Indications of variable adaptation to drought in *Pinus pinaster* were obtained from a pot trial completed in 1966. This trial compared four provenances of *P. pinaster* with *P. radiata* under two levels of nutrition and two levels of watering. For the low level of watering, treatments were droughted and not rewatered until permanent wilting (P.W.) was evident in the foliage. It was found, that from a standard volume of soil, *P. radiata* transpired the least soil water before wilting, the Portuguese provenance of *P. pinaster* was next and

the Luccan, Landes and Corsican followed in that order. Amount of water extracted was independent of plant size. These results are indicative of significantly different plant effects both between species and between the provenances within *P. pinaster*.

The amount of water utilized to, or the time to onset of, P.W. is an expression of tendency to escape drought rather than an indication of drought resistance. In a complete evaluation, resistance to leaf water loss through desiccation following P.W. must also be considered. Ultimate survival following droughting must be a practical criterion. With this objective a further pot trial was run in the period 1966 to 1967.

Pinus radiata was employed as a control species or standard of comparison, and compared with provenances of *P. pinaster* from Portugal and Tunisia. The Tunisian provenance has a quite different appearance to the Portuguese and it was suspected that the Tunisian source would be subjected to greater drought stress under normal selection than the Portuguese. These two aspects represent extremes of variation within the provenance range and were the basis for selecting this provenance pair for comparison.

To confirm previous observations, the time taken to reach the P.W. condition was compared for the three plant groups. On attaining the P.W. condition the plants were then subjected to different degrees of desiccation prior to rewatering.

PROCEDURE OF TRIAL

Potting and Grouping

One year old seedlings of each plant group were potted in June 1966. Six plants of uniform size were potted into cans nine inches (23cms) deep and seven inches (18cms) diameter. One can contained seedlings from only one plant group and thirty cans were prepared for each plant group using a uniform soil mix of equal weight and volume per can. The mix consisted of 6:2:2:1 of coarse sand, loam, peat moss and rotted cow manure, respectively. All cans were maintained in the glasshouse with regular watering until January 1967.

The mean plant height per pot was determined in January 1967 and the pots were graded into five uniformity groups. Each uniformity group contained the six pots, per species or provenance, of most uniform height; grading from the tallest plants in Group I to the smallest in Group V. Six treatments A to F (Table 1) were randomly allocated to plant types within each uniformity group.

Treatments

An atmometer was used to provide a standard exposure during treatment. A loss of 40ccs. from the atmometer represented an average daily exposure in the glasshouse for the period of the trial. Treatments C, D, E and F hence represent P.W. plus 2, 4, 8 and 12 days exposure respectively. Following treatment plants were regularly watered for a month before survival counts were made.

Droughting

Treatments were randomised within blocks in the glasshouse. On the evenings of January 25 and 26 the pots were watered to excess and weighed, after 15 hours drainage, on the following mornings. This assured that the trial commenced with all pots at a similar and known optimum water capacity.

TABLE 1
Schedule of Treatments

Treatment	Uniformity Block (height group)				
	1	2	3	4	5
A	Maintained with optimum water				
B	P.W. + rewatering				
C	P.W. + 80 ccs. evaporation + watering				
D	P.W. + 160 ccs. evaporation + watering				
E	P.W. + 320 ccs. evaporation + watering				
F	P.W. + 480 ccs. evaporation + watering				

Following the 26th, watering was discontinued. Pots were weighed and inspected each morning, daily, until P.W. was apparent from foliage and or leading shoot symptoms. When in doubt, P.W. was verified by the daily pattern of pot water loss. At P.W. the treatments were continued as specified.

Foliar Sampling

Needle sampling to determine relative turgidity (R.T.) was carried out through all stages of the trial up to the rewatering. In sampling a can, six needle pairs, one from each plant and from a standard position and age class, were taken. R.T. determinations were made for needles cut into one inch (25 mm) sections and employed a five hour flotation period. This technique was found suitable in a preliminary trial.

It was not possible to sample all plants each day. Where practicable the sampling was distributed evenly to each plant type and treatment, concentrating on the plants which appeared to be most severely effected by drought.

RESULTS

Permanent Wilting

The trial was initiated by watering all pots to capacity. Weighings on two mornings following irrigation in the evening, to attain this capacity, revealed that all pots were wet to a constant weight and at capacity. Mean values for pot weights at capacity and P.W. are set out in Table 2.

TABLE 2
Mean Pot Weight (grams) at Watered Capacity, Permanent Wilting and Water Loss to Permanent Wilting for Each Plant Group

	P. radiata	Tunisian	Portuguese
Pot Capacity	8,182	8,379	8,325
Permanent Wilting	6,768	6,838	6,721
Water Loss	1,313	1,541	1,604

Pot weight at watering capacity varied with the plant group, the *P. radiata* group being approximately 150 grams. less than *P. pinaster* on a comparison of means. These differences may be accounted for largely by differences in plant fresh weight. This fact could not be confirmed due to the destruction and modification of plants during droughting.

At P.W. pot weight for *P. radiata* was equivalent to that of the Portuguese and slightly less than that of the Tunisian provenance (Table 2). In effect, the greatest water loss to time of P.W. was from the Portuguese, next greatest was from the Tunisian and least was from *P. radiata*. These differences are significant.

TABLE 3

Mean Rate of Daily Water Loss (ccs.) up to P.W. for Plant Groups (Watered January 26)

	Period of Measurement				
	27/1-31/1	31/1-1/2	1/2-2/2	2/2-3/2	3/2-4/2
<i>P. radiata</i>	1,113	91	68	45	40
Tunisian	1,244	85	62	31	31
Portuguese	1,188	108	73	39	37

Initially *P. pinaster* lost water at a greater rate than *P. radiata* (Table 3). This rate tended to be slower as the plants approached the P.W. condition. The nett result to time of P.W. (Figure 1) was for the Portuguese to take the longest to wilt, the Tunisian was next in order and *P. radiata* wilted with the least exposure. This result confirms findings in previous work.

Survival by Treatments.

Means for the percentage survival by treatment are recorded in Figure 2.

With the two lowest exposures since P.W. (B and C) least mortality occurred with Tunisian and most with Portuguese plants. For treatment D mortality is comparable for the three groups. With treatment E Portuguese mortality is least. Mortality is complete with the greatest exposure (F), except for a minor portion of the Tunisian provenance.

From these results one may assume (a) that 50 per cent. of the Portuguese population is less resistant to desiccation following permanent wilting than are the other groups and (b) that the remainder of the population is more resistant with prolonged exposure than are the other plant groups. In fact the treatments are not comparable. Since the *P. pinaster* population required greater exposure to attain P.W., mortality values in Figure 2 are biased against this species. Even so it is evident that survival to prolonged exposure under identical conditions is greater in *P. pinaster* than in *P. radiata*.

Drought Resistance

In this trial, resistance to droughting can only be compared satisfactorily by relating survival to the total period of droughting or exposure since watering

ceased. With the unfavourable method of gauging the start point for treatment, this comparison can only be made by means of the scatter diagram in Figure 3.

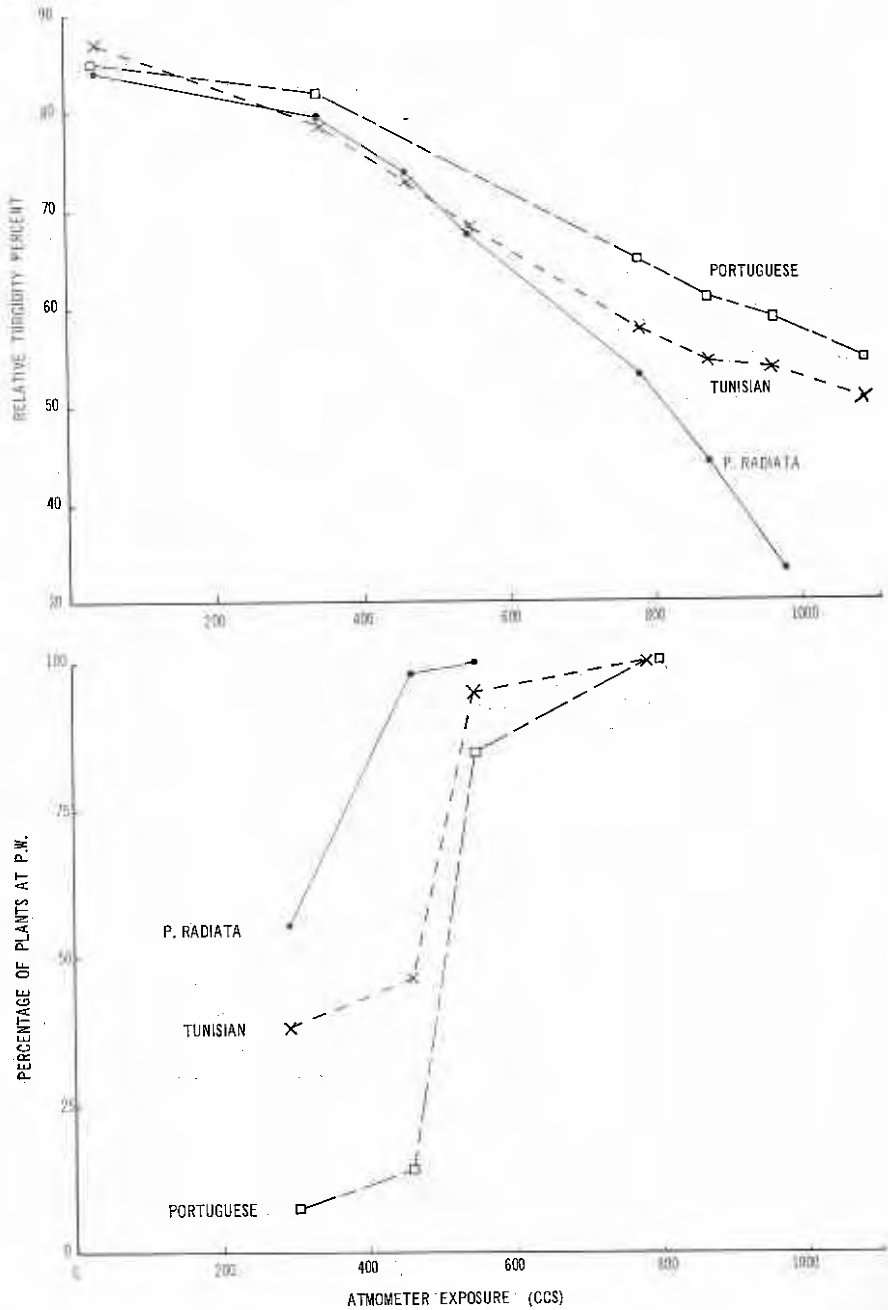


Figure 1.

Variation in relative turgidity and plant wilting with increasing exposure to drought.

Distribution data in Figure 3 leave no doubt that, under the condition of the trial, the Portuguese plant group was the most resistant and the *P. radiata* was the least resistant to drought effects. These differences are obviously highly significant. One would also assume that, on the basis of distribution in Figure 3, differences between the Portuguese and Tunisian provenances are significant, the Portuguese being superior in resistance to drought.

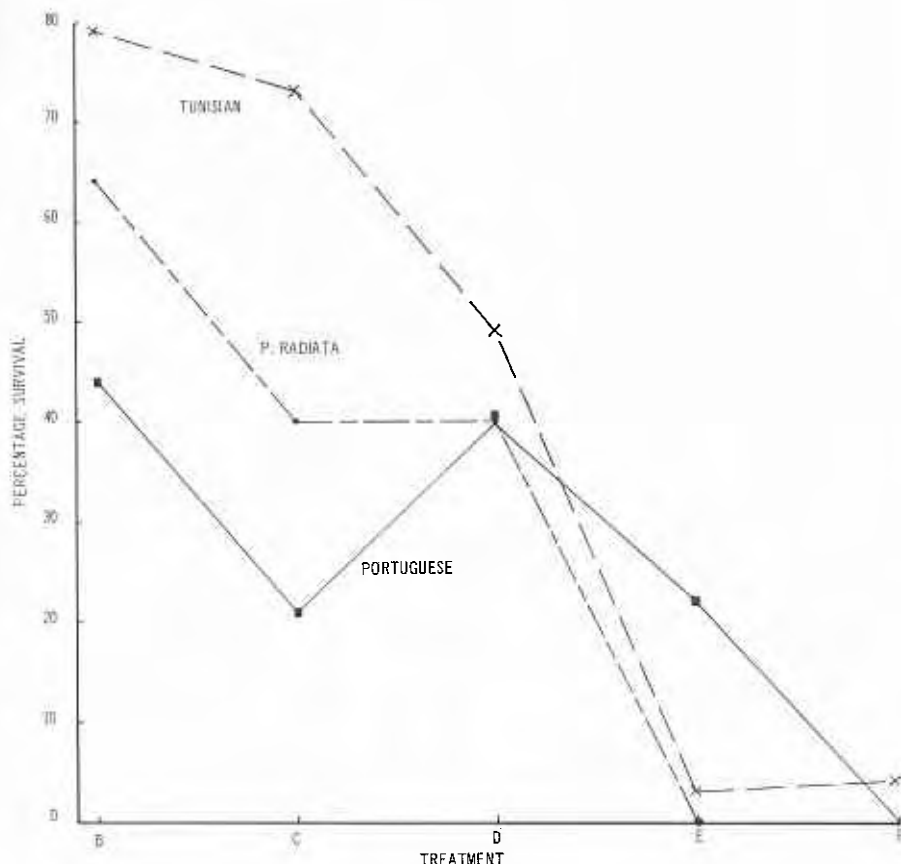


Figure 2.

Percentage of survival of plant groups for drought treatments commenced at permanent wilting of plants.

It should also be noted in Figure 3 that none of the Portuguese treatments incurred exposures of less than 550ccs. atmometer loss. It was within this range that the other two plant groups recorded 100 per cent. survival. Within the trial it was hence not possible to compare the Portuguese populations with the other two at low exposures. The data once again reveal the fact that a longer exposure to P.W. was required for the Portuguese provenance.

Leaf Water Content

Relative turgidity determinations were made at exposures of 40, 335, 455, 537, 782, 864, 958 and 1022ccs. atmometer loss since commencement of droughting. Mean values for each plant group in each sampling stage are plotted in Figure 1.

For each plant group R.T. decreased progressively as droughting period increased. Although the pattern of decline varies to some extent for each group a pattern for *P. pinaster*, distinct from that for *P. radiata*, is apparent. *Pinus pinaster* declined in R.T. at a slower rate with increasing exposure tending to level off between 50 and 60 per cent. *Pinus radiata* tended to decrease R.T. rapidly with increasing exposure and within the range studied, appears to approach zero at a rapid rate.

The trends indicate that following P.W. there is a greater resistance to water loss from *P. pinaster* needles than for those of *P. radiata* (Table 2). From the data it is evident that at R.T. values of 80 per cent. and higher, over

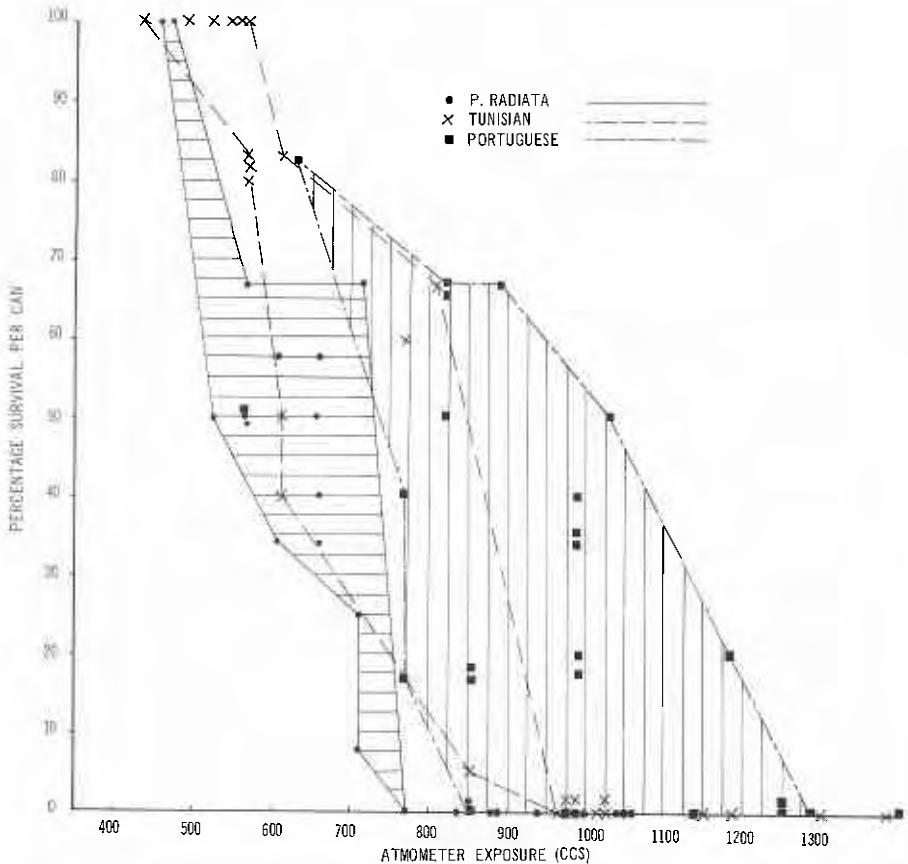


Figure 3.
Relationship between plant survival and total exposure to drought in Trial I.

half of the *P. radiata* plants have reached P.W. A comparable range for *P. pinaster* is for R.T. values of 70 per cent. and above; at this latter level all *P. radiata* plants had reached P.W.

It is not possible to relate a threshold R.T. value with the lethal limit (death point) for each plant group. From Figure 4 it can be seen that some deaths occurred with *P. radiata* between the R.T. limits of 65 to 77 per cent. For *P. pinaster* some mortality occurred between R.T. limits of 54 and 63 per cent. for the Tunisian and between 55 and 80 per cent. for the Portuguese provenance. A definite final lethal limit for the two provenances would appear to be at the 53 per cent. value as compared to the 65 per cent. value for *P. radiata*. Again, the indication is for differences between the two species.

Lethal limits for the two provenances of *P. pinaster* indicate (Figure 4) a more distinct and lower general limit for the Tunisian provenance. With the Portuguese provenance mortality was recorded at higher R.T. values. From Figure 1 however, it can be seen that for any exposure, values of R.T. for the Portuguese provenance are higher than those of the Tunisian plants. The two trends would tend to compensate to produce a similar result.

DISCUSSION

The results of this trial reveal that in the seedling form, *P. pinaster* is more resistant to drought than is *P. radiata*. This resistance consists of both a drought escaping effect, requiring a greater water loss to time of P.W., and a greater resistance to foliar desiccation following P.W. In both attributes the *P. pinaster* excelled.

Some concern is felt with the recording of lower pot weights at water capacity for *P. radiata*. The reason for this cannot be ascertained within the trial design. It may be explained by differences in fresh plant weight between species, by different root volumes for species or by differential influences of root rhizospheres on water repellence. Future work should keep this phenomenon in perspective when considering experimental design. Within the present study, the important point is to recognise that uniformity in pot size, soil volume, plant age and growing conditions were in fact achieved. Under these conditions *P. radiata* proved to be less drought resistant. Factors associated with the decreased pot weight could be important in decreasing drought avoidance and for the present, must be attributed to species effects.

The fact that the Portuguese provenance proved to be at least as resistant to drought as the Tunisian provenance was unexpected. The result is encouraging to breeding aims within the former population. It is suspected that the fact that a wide range of resistance (medium to relatively high) was revealed within the Portuguese population is significant. Results for *P. radiata* and the Tunisian provenance were much more uniform possibly indicating previous natural selection for this character or extreme variation within the Portuguese population. Further studies to investigate these possibilities are warranted. Current results do suggest however, that improvement work within the Portuguese population may provide for reasonable resistance to drought if selection is practised.

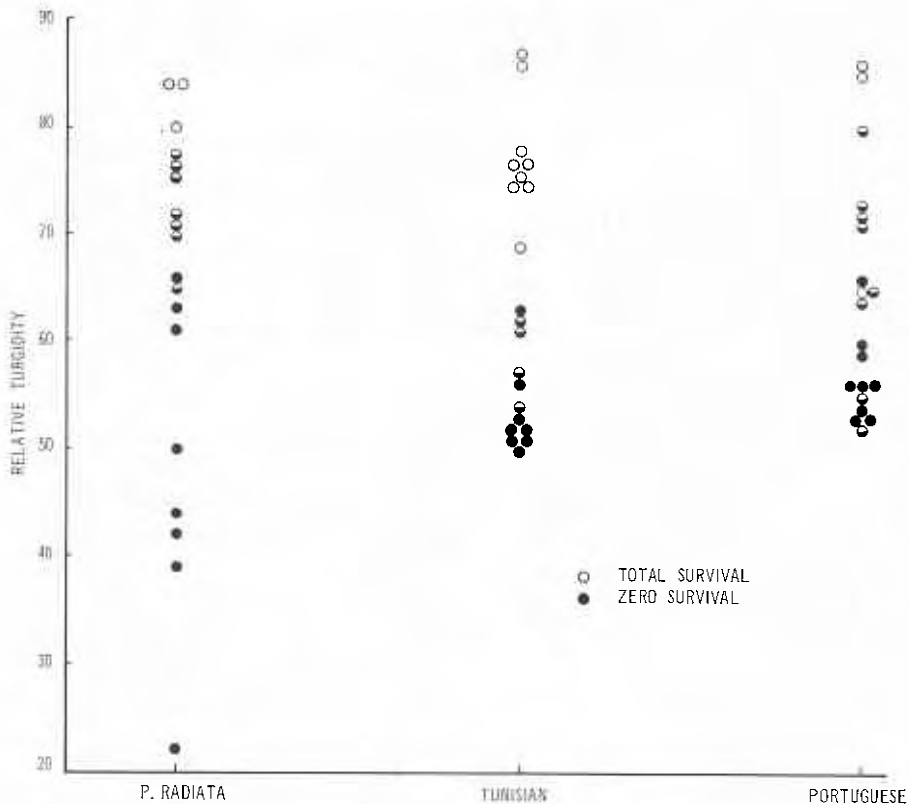


Figure 4.

Relationship between relative turgidity and the lethal point for *Pinus radiata* and *Pinus pinaster* provenances from Portugal and Tunisia.

Differences between the two provenances call for further provenance comparisons to define the total variability for the species.

Although the aims for the trial were satisfied by its implementation, the design employed was found to be very inefficient. In future it must be realized that the expression of P.W. may vary considerably both between species and between provenances of any one species. Comparative studies of drought tolerance must be based on plant water potential and on the period of exposure since watering ceased. Plant symptoms for each treatment group or pot weight are unsatisfactory bases for comparison of effects of drought.

Needle sampling procedures employed in this trial were exploratory. It was realized that R.T. values for species and provenances cannot be considered to represent similar water potentials and hence functional similarities. Foliar moisture sampling was employed, however, to determine whether the expense and time involved in sampling leaf water potentials is warranted in comparative studies. Results indicate that it is, provided that the trial design is sound in all other aspects and provided that water potential determinations are accurate. Differences for significance will be small. Because of this and the difficulties of obtaining water potential measurements with available apparatus,

it is proposed that further concentration will be on refining techniques for comparative work. Quantitative expression will only be attempted when the variability and limitation of comparative seedling studies are fully appreciated.

CONCLUSIONS

Pinus pinaster is much more resistant to drought than *Pinus radiata*. The Portuguese provenance was found to contain greater variability in drought resistance than either *P. radiata* or the Tunisian provenance of the species. Its overall resistance was, however, greater than both of these plant groups.

Results for the trial indicate that selection for drought resistance within the *P. pinaster* population from Portugal may be feasible. Such selection should provide for progeny with a relatively high resistance to drought.

TRIAL II

INTRODUCTION

A second trial investigating the resistance of seedlings of *Pinus pinaster* to drought was commenced in July 1966 and completed in February 1968. Two main objectives were specified:—

- (i) To compare the relative performances of seedlings of provenances from Portugal, France and Corsica under artificially induced drought.
- (ii) To compare the drought resistance of seedlings obtained by mass selection and controlled pollination in the breeding programme with that of routine seed.

The trial was similar in design to that previously reported. Early preparation precluded the use of improvements in techniques suggested from studying the results of Trial I. It was considered that the relation of survival with exposure since time of watering provided a useful means of comparing overall drought resistance.

PROCEDURE

Plant Source

Five plant sources were compared:—

- (1) *P. pinaster* R—routine imported Portuguese seed.
- (2) *P. pinaster* F.S.—a mixture of seed from full sib families obtained by crossing superior phenotypes raised from Portuguese seed in Western Australian plantations.
- (3) *P. pinaster* Landes—A mixture of seed from half sib progenies obtained from selected phenotypes in forests of the French Landes region.
- (4) *P. pinaster* Corsican—Plants mixed from five provenances imported from Corsica.
- (5) *P. radiata*—routine seed collected in South Australia.

Plants were potted from one year old nursery stock grown under identical conditions. All plants were vigorous and of medium size for the plant group represented in the nursery.

Potting

An equal weight of potting mixture (5.3kg.) was placed in each of 150 tins (seven inch (18cms) diameter, nine inches (23cms) deep). Eight seedlings of a single plant source were transplanted to a tin in July 1966, providing 30 pots for each plant source. After establishment, each pot was thinned to the six most uniform plants. Initially the pots were maintained in the shadehouse but they were transferred to the open for hardening off six months prior to commencing droughting. The potting mixture consisted of a 4:1:1:1 mixture of sand, loam, peat moss and rotted cow manure. Frequent watering and additions of liquid fertilizer promoted vigorous healthy growth during the maintenance period.

In January 1968 the heights of all plants were measured and the six poorest pots within each 30 pot plant group were discarded. The remaining 24 pots for each source were allocated to six treatment classes to provide comparable ranges of pot plant height classes within each treatment. Distribution of mean height within plant and treatment classes proved to be satisfactory (Table 4).

TABLE 4
Mean Plant Height (cms) Distribution within the Trial Design

Plant Source		Treatment	Replication
1. P.P.R.	46.3	A. 47.4	1. 46.1
2. P.P.F.S.	42.8	B. 48.4	2. 47.3
3. P.P.L.	43.7	C. 47.8	3. 46.5
4. P.P.C.	43.9	D. 49.4	4. 45.2
5. P. radiata	57.0	E. 45.2	
		F. 44.8	

Treatments

Six treatments were employed:—

- A. Droughted to P.W. and rewatered.
- B. P.W. + 3 evaporation days + rewatering.
- C. P.W. + 6 evaporation days + rewatering.
- D. P.W. + 9 evaporation days + rewatering.
- E. P.W. + 12 evaporation days + rewatering.
- F. P.W. + 15 evaporation days + rewatering.

An evaporation day was gauged as 40ccs. evaporation from a Livingston Atmometer maintained in the glasshouse.

Within each treatment 20 pots consisting of four of each of the five plant sources were allocated. All pots were randomly positioned on a separated glasshouse bench for each treatment. Treatment commenced on January 3.

On the evenings of January 4 and 5 all pots were heavily watered. Each pot was weighed (to 1.0 gram) on the morning of January 6 and watering was then discontinued. Each morning all plants were carefully inspected and when at least four of the six plants per pot were in a permanent wilt condition, the pot was considered to have reached P.W. At P.W. each pot was weighed, the atmometer record noted and treatment continued as specified. At the termination of each treatment all pots were weighed, the soil moisture percentage determined gravimetrically from five probe samples in the top two-thirds of the soil mix and the pots were rewatered. The pots were maintained in the shade house with watering for one month before the survival assessment was carried out.

Survival Scores

Survival value was determined from both mortality counts per pot and a weighted survival score. The score allowed a minimum of four points per plant (24 per pot) according to the following specifications:—

- 4 points—plant normally healthy.
- 3 points—slight needle damage.
- 2 points—dead tip.
- 1 point—dead tip plus needle damage.
- 0 points—plant dead.

TABLE 5

Mean Values for Atmometer Evaporation and Pot Water Loss to Condition of Permanent Wilting

Atmometer Loss to Permanent Wilting (ccs.)				Pot Evaluation to Permanent Wilting (ccs.)			
Plant		Treatment		Plant		Treatment	
3. P.P.L.	463	A.	505	3. P.P.L.	1,565	A.	1,653
5. P. radiata	465	B.	559	2. P.P.F.S.	1,591	B.	1,645
1. P.P.R.	536	C.	511	5. P. radiata	1,603	E.	1,631
2. P.P.F.S.	580	D.	545	1. P.P.R.	1,649	C.	1,620
4. P.P.C.	645	E.	538	4. P.P.C.	1,722	F.	1,614
		F.	596			D.	1,592

RESULTS

Permanent Wilting

Values for amount of atmometer evaporation and water loss per pot from time of cessation of watering to P.W. (Table 5) differed significantly both between plant sources and within treatment groups. For pot water loss five of the six treatments are in agreement, treatments A or D being out of phase with the other five. If the trial had been suitably controlled, differences between treatments in these two aspects should not have resulted. The only explanation offering for the discrepancy is that the large number of pots and the physical need to distribute them in treatment blocks, rather than replication units, has led to differential exposure of treatments in the glasshouse. This suggestion is not consistent with the fact that treatments which lost least water (D) did not experience the shortest exposure or time to P.W. Treatment A which lost most water also received the least exposure time (Table 5). The discrepancy cannot be related directly to differences in mean plant height per treatment (Table 4). In practice it is believed that the magnitude of the differences within treatments are of little significance.

Differences in exposure time (atmometer loss) and pot water loss between plant groups up to P.W. were significant and to be expected from results of previous trials. The condition of P.W. was detected from visual symptoms of needle and tip wilting in the early morning. This must vary with the condition and type of needle as well as through any physiological factors. From experience

it was anticipated that *P. radiata* would show first signs of stress, the Portuguese provenance next, then Landes and lastly the Corsican. This had been the trend with the exception of the Landes provenance which wilted before the Portuguese.

TABLE 6

Mean Values of Atmometer Exposure and Soil Moisture Percentage Measured for Treatment

Total Atmometer Exposure Received by Treatments (ecs.)				Soil Moisture Percentage Prior to Rewatering			
Plant		Treatment		Plant		Treatment	
5. <i>P. radiata</i>	683 (17)	A.	532	5. <i>P. radiata</i>	2.6	A.	3.4
3. P.P.L.	708 (18)	B.	663	1. P.P.R.	2.7	B.	3.3
1. P.P.R.	799 (20)	C.	706	2. P.P.F.S.	3.2	C.	3.2
2. P.P.F.S.	826 (21)	D.	804	4. P.P.C.	3.4	D.	2.8
4. P.P.C.	884 (22)	E.	928	3. P.P.L.	3.4	E.	2.9
		F.	1,049			F.	2.7

Treatments

Results for total exposure and residual soil moisture (Table 6) indicate that the objective to obtain increasingly greater exposure and desiccation over the treatments range was achieved. Both survival scores and mortality counts (Table 7) show increasingly greater plant damage with length of the drought treatment.

Within plant sources, different groups were subjected to different exposure periods (Table 6), *P. radiata* experiencing five days less exposure than the Corsican source. This is the result of variable time to P.W. and commencement of the desiccation stage. Results for survival and soil moisture are hence not statistically comparable over the trial period within the design specification.

TABLE 7

Mean Values Obtained for Mortality and Survival Scores

Mortality per Treatment				Survival Value per Treatment			
Plant		Treatment		Plant		Treatment	
2. P.P.F.S.	14	A.	5	2. P.P.F.S.	29	A.	61
1. P.P.R.	16	B.	9	1. P.P.R.	21	B.	36
5. <i>P. radiata</i>	16	C.	17	5. <i>P. radiata</i>	20	C.	15
3. P.P.L.	18	D.	20	3. P.P.L.	19	D.	6
4. P.P.C.	18	E.	23	4. P.P.C.	12	E.	2
		F.	23			F.	1

Values recorded for mortality and survival value (Table 7) do in fact indicate a superiority of the Portuguese sources, particularly the P.P.F.S. source, over *P. radiata*. This is despite the fact that the latter source received four days less exposure. The order of differences obtained however, suggests that it could be extremely difficult to attach statistical significance to such a ranking, even if exposure was constant for all species and treatments. Survival means for each plant source were assessed from 24 pots or 124 separate plants. The order of differences obtained for a range of species and provenances suggests that the experimental approach may be rather ineffective and insensitive.

Survival Values

Having proven from results that control within the experimental design was inadequate, the trial objective was analysed on a non statistical basis. To compensate for varying exposure with plant group, the survival value for each trial unit (one pot with six plants) was plotted against the accumulated atmometer loss (exposure) between cessation of watering and re-commencement of watering (Figure 5).

It is obvious (Figure 5) that, within the limits of the study, *P. pinaster* is much more drought resistant than *P. radiata*. *Pinus pinaster* F.S. forms a population cluster completely separate from that of *P. radiata* and shows superior drought resistance throughout its whole range. The scatter for

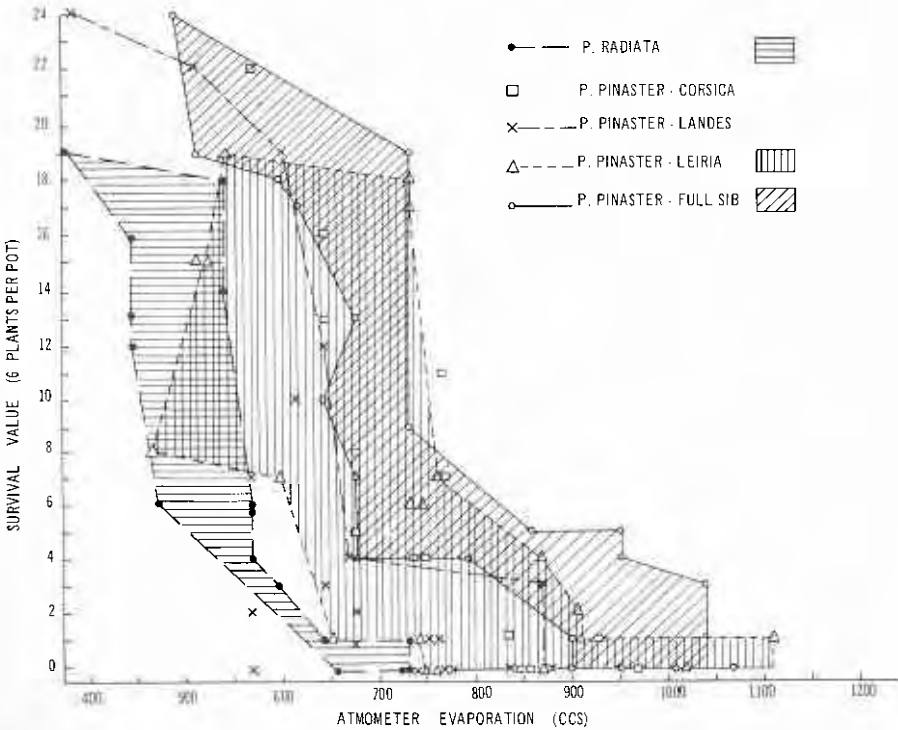


Figure 5.
Relationship between survival value and total drought exposure for *P. radiata* and four provenances of *Pinus pinaster*.

P. pinaster R is broader and partly overlaps both of these clusters. Corsican data have a distribution similar to P.P.F.S. in the region of high drought resistance. Landes occupied a position generally between that of P.P.F.S. and *P. radiata* with some overlap. Relative positions of decreasing drought resistance for these populations would be *P. pinaster* F.S. and Corsican, *P. pinaster* R, Landes and then *P. radiata*.

DISCUSSION

Current results largely confirm those of the previous trial in that P.W. as a determination point in comparing species is quite variable. *P. radiata* attains a condition of P.W. with less exposure and less water loss than similarly aged *P. pinaster* under similar conditions. Permanent wilting, since it is associated with different drought stresses for different plants, cannot be employed as a diagnostic medium in studies of drought resistance based on comparable drought exposure and expression of results as ultimate mortality. Permanent wilting obviously has physiological significance and, as mentioned in Trial I, could be a valuable study aspect if associated with accurate measurements of plant water potential.

Definition of comparable drought resistance from analysis of scatter diagrams relating survival against exposure has proved quite successful in both Trials I and II. Suitable means to compare both provenances within a species, and separate species, have resulted. The success of this technique is dependent on the accuracy of determination of a relatively large number of points within any exposure period. To this end, the use of ordered, regulated treatments, with adequate replication of plant sources, provided for acceptable point dispersion and continuity.

It is also recommended that the system of survival scores be utilized rather than a direct record of mortalities. Mortality counts are too restrictive and only utilize a small part of information, concerning treatment effects and plant recovery, available from a full consideration of plant damage due to water stress. Survival scores, although subjective, were of sound precision when assessed by several different persons. The allowance of a one month recovery period prior to assessment removed any doubt concerning the relative extent of individual plant damage.

As for Trial I, results from the current study show that *P. radiata* has a relative narrow range of low resistance to drought, while routine seed sources of Portuguese *P. pinaster* have a wide amplitude of resistance which extends from relatively low to very high limits. This trial was successful in showing that mass selection within the Portuguese provenance has restricted the amplitude of resistance while also extending the average range of resistance of the F.S. source beyond that of the non-selected Portuguese population.

The fact that the narrowed amplitude of the F.S. population occupies the high resistance range of the unselected source possibly reflects that selection, within local plantations, is within site conditions more drought prone than is the norm of the natural forests of Leira in Portugal. The current breeding programme is probably selecting to advantage for drought resistance.

Little is known of the actual origin of the Corsican provenance mixture used in this study. The population is of similar amplitude and range as the F.S. provenance. General knowledge of forest conditions in Corsica, the stiff, short

nature of needles and slow shoot growth lead to an expectation that this provenance would prove relatively drought resistant. These have been the experimental indications.

Results suggest that the Landes provenance is the least drought resistant of the *P. pinaster* provenances. Again, this is not entirely unexpected. The source represents a half sib family mixture from vigorous phenotypes selected in the central and southern Landes region which would be less drought prone than the Portuguese forests at Leira.

CONCLUSIONS

Useful comparisons of drought resistance can be made from the technique adopted.

P. pinaster F.S. and Corsican provenance proved most drought resistant, *P. pinaster* Routine, and Landes were then ranked in that order. *Pinus radiata* was the least resistant to drought of all plant sources tested.

TRIAL III

INTRODUCTION

A further drought trial initiated in 1967 had three main objectives:—

- (i) To compare the relative resistances of provenances of *Pinus pinaster* to drought.
- (ii) To compare the drought resistance of *P. pinaster* with other species used for commercial planting.
- (iii) To develop improved techniques for comparing drought resistance of seedlings.

The trial compared six month old seedlings of seven different plant sources under six droughting treatments.

PROCEDURE

Plant Sources

Ninety-six pots, nine inches (23cms) deep, seven inches (18cms) diameter, were filled with an equal weight of soil mix containing sand, loam and peat moss in the proportions 3:1:1. The air dry weight of mix per pot was 5.2kg. and it was added over 0.4kg. of cinders placed on the perforated bottom to facilitate drainage.

Six plant sources were employed in the trial, viz.:—

- (1) *P. pinaster* F.S.—a mixture of full sib families prepared for the breeding programme.
- (2) *P. pinaster* R.—routine seed imported from Portugal.
- (3) *P. elliottii*—seed imported from Queensland.
- (4) *P. brutia*—seed imported from Cyprus.
- (5) *P. radiata*—routine seed.
- (6) *P. pinaster* Corsican 1—a provenance imported from Corsica.
- (7) *P. pinaster* Corsican 2—a second provenance imported from Corsica.
- (8) *P. taeda*—seed imported from Queensland.

Seed of each plant group was stratified and sown into the pots in August 1967. Twelve pots were allocated to each plant group and 25 seeds were sown into each pot. The pots were maintained in the shadehouse until October 1967 when each pot was thinned down to the nine most uniform plants per pot. Pots were then moved to an unshaded glasshouse, watered regularly and provided with liquid fertilizer.

In late December 1967, six seeds of dwarf sunflowers were sown in each pot. Following germination these were thinned to the three plants most uniformly distributed around the pot.

On the evenings of February 14 and 15 the pots were heavily watered and weighed on the morning of February 16. Watering was then discontinued. All pots were inspected daily at 8 a.m. for signs of permanent wilting of the sunflowers (Figure 6). As each pot attained the P.W. condition it was allocated to a droughting treatment and placed in a second glasshouse.



Figure 6.

Sunflowers used to produce a standard soil moisture potential in treatment units. The pines are *P. pinaster* full sib and *P. brutia*.

Treatments

Six treatments were employed:—

- A. Permanent wilting (P.W.) + rewatering.
- B. P.W. + 3 days exposure + rewatering.

- C. P.W. + 6 days exposure + rewatering.
- D. P.W. + 10 days exposure + rewatering.
- E. P.W. + 14 days exposure + rewatering.
- F. P.W. + 19 days exposure + rewatering.

To control the trial under variable weather conditions an exposure day was considered as 30ccs. evaporation from a Livingston atmometer maintained in the glasshouse.

As plant units reached P.W they were weighed and allocated to treatment F, then E down to treatment A last. This procedure commenced the treatments with longest duration first, shortened the overall length of the trial and reduced the overall daily variability within the trial.

TABLE 8
Mean Height of Seedlings (cms) for Plant and Treatment Classes

Plant Sources				Treatment	Replication		
1.	Pinaster F.S.	12.9	A.	15.0	1.	15.1
2.	Pinaster R	17.5	B.	14.4	2.	13.7
3.	Elliottii	15.0	C.	14.6		
4.	Brutia	7.2	D.	13.8		
5.	Radiata	18.4	E.	14.0		
6.	Corsican 1	14.5	F.	14.7		
7.	Corsican 2	14.3				
8.	Taeda	15.7				

When the cumulative atmometer record indicated that a treatment unit had reached the prescribed exposure, the pot was weighed, eight soil probe samples were taken and grouped and the pot was rewatered. Soil moisture percentages were determined by gravimetric means and the pots were maintained in the shadehouse with watering.

Following a one month recovery period in the shadehouse each pot was assessed for number of dead plants and a survival score. Survival scores utilized the four point system described in Trial II and aggregated a total of 36 points per pot. With two pots per plant—treatment class, mortality and survival were assessable on a basis of 18 plants.

RESULTS

Permanent Wilting

The distribution of seedling heights within plant and treatment classes is recorded in Table 8. Plants are smaller and much younger than those used in the previous two trials. Establishments of plants and the uniformity of individuals within the pots after thinning were excellent.

Sunflower germination and development was satisfactory and the plants proved to be a sensitive and effective method of drying all treatment units to a common water potential. In most instances pot drying, due to the number

of plants per pot (Figure 6) was uniform and all three sunflowers were found to reach P.W. on the same morning. Pot water losses, as determined by weighing for either plant or treatment classes, were all within ± 2 per cent. of the mean value. In effect the use of sunflowers permitted the desiccation exposure to commence at a common water potential.

TABLE 9

Number of Plants Permanently Wilted at Moisture Potential Indicated by Permanent Wilting of Sunflowers

Plant Source	Treatment						Total
	A	B	C	D	E	F	
1. <i>P. pinaster</i> F.S.	7	4	5	7	2	16	41
2. <i>P. pinaster</i> R.	6	4	4	4	12	30
3. <i>P. elliottii</i>	4	2	2	3	4	15
4. <i>P. brutia</i>	8	10	8	10	10	6	52
5. <i>P. radiata</i>	11	18	17	15	18	18	97
6. <i>P. pinaster</i> Corsican 1	1	1	2
7. <i>P. pinaster</i> Corsican 2	1	3	8	12
8. <i>P. taeda</i>	3	1	2	4	6	16
Total	41	38	37	38	41	70	265

The number of plants in the P.W. condition at sunflower P.W. varied greatly with plant group (Table 9). Variation between treatment groups was minimal except for treatment F which was the first set up. A period of rapid initial drying and conservative estimation must have influenced this anomaly. Further estimation was constant for all selections. Results in Table 9 again confirm the fact that *P. radiata* enters a stage of P.W. at lower water potentials than *P. pinaster*.

Mortality and Survival Values

Survival values were expressed as percentages and transformed as angle arcsines for analysis. Mortality values were analysed using a square root transform. The analyses proved to be highly significant and established that the plant by treatment interaction was significant at the one per cent. level. Results for the main effects and the interaction are presented in Table 10 and displayed in Figure 7.

Pinus brutia proved to be the most drought resistant being virtually unaffected by the treatments. The two Corsican provenances were next in order of resistance. Results for these two provenances were remarkably similar suggesting precision within the trial procedure. Portuguese *P. pinaster*, both routine and full sib ranked next in resistance. *P. radiata*, *P. elliottii* and *P. taeda* were similar in order and of lowest resistance.

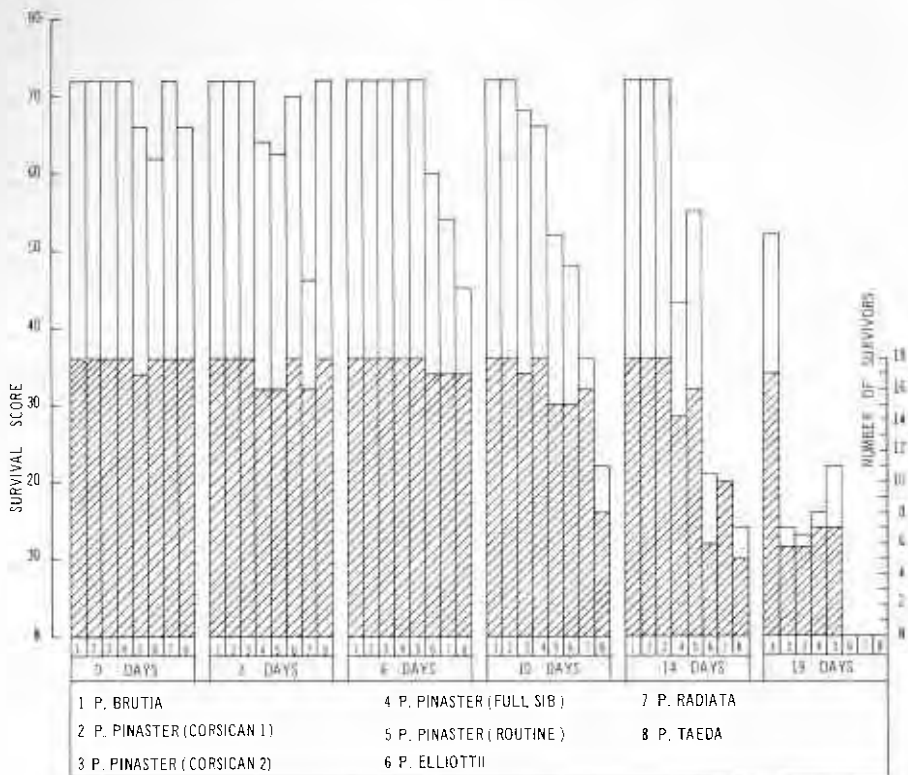


Figure 7.

Histograms showing variation in mortality and survival value of *Pinus radiata*, *P. elliotii*, *P. taeda*, *P. brutia* and four provenances of *P. pinaster* under six drought treatments.

TABLE 10

Means for Survival Scores and Mortalities for Plant and Treatment Groups. Significance is at the 0.01 level

Survival Score				Mortality			
Plant Source		Treatment		Plant Source		Treatment	
P. brutia	68.7	A.	69.2	P. brutia	0.2	A.	0.1
Corsican 1	62.3	B.	66.2	Corsican 1	2.0	B.	0.7
Corsican 2	61.5	C.	64.9	Corsican 2	2.2	C.	0.4
P. pinaster F.S.	55.5	D.	54.2	P. pinaster F.S.	2.8	D.	2.4
P. pinaster R.	54.5	E.	46.0	P. pinaster R.	3.2	E.	4.9
P. elliotii	43.5	F.	14.4	P. radiata	5.2	F.	12.5
P. radiata	38.0			P. elliotii	5.7		
P. taeda	36.5			P. taeda	7.0		

Soil moisture

Residual soil moisture data (Table 11) showed that progressive soil drying accompanied increasing exposure by treatment. Agreement between replicates was excellent. Both the means for plant groups and treatments were significant at the one per cent. level. The plant by treatment interaction did not prove to be significant. Multiple range tests against plant means revealed that the *P. radiata* mean was significantly different from the other seven.

No practical significance can be associated with soil moisture values. *P. radiata* reached P.W. first (Table 9) and soil drying was least. *P. brutia* however, which was most drought resistant, also had a relatively high residual soil moisture and it will be seen from Table 9 that this species entered P.W. at a rate only second to *P. radiata*. On the other hand, the Corsican group which was delayed in P.W. also had relatively high soil moisture.

The soil mixture used did not allow for a wide range of soil moisture residuals over the exposure range employed. For this trial, it is suggested that moisture residuals purely serve to show that the progressive range of treatments employed was effective.

TABLE 11

Means Obtained for Soil Moisture Percentages in Plant and Treatment Classes. Significance is at the 0.01 level.

Plant Source		Treatment	Replication
<i>P. radiata</i>	3.71	A. 3.92	1. 3.40
Corsican 1	3.59	B. 3.61	2. 3.39
<i>P. brutia</i>	3.46	D. 3.33	
<i>P. pinaster</i> F. S.	3.44	E. 3.31	
Corsican 2	3.37	C. 3.25	
<i>P. elliottii</i>	3.33	F. 2.98	
<i>P. pinaster</i> R	3.19		
<i>P. taeda</i>	3.10		

DISCUSSION

Drought Resistance

This third trial confirms Trials I and II in showing that *P. pinaster* is more drought resistant than *P. radiata*. It also confirms results from Trial II to show that Portuguese seed modified by the tree breeding programme is at least as drought resistant as routine seed of this provenance. The latter conclusion, although only based on seedling material, provides confidence for future results of the breeding programme. It will be many years and the programme will be greatly developed before an absolute result, based on mature trees in the field, will be forthcoming.

Trial III shows that the Corsican provenance is more resistant to drought than Portuguese material at low to moderate exposure and of similar value at high exposure. Again this confirms results of Trial II but the more sensitive design and control of the current study has improved understanding of the nature of the two provenances.

Comparison of *P. pinaster* with *P. radiata*, *P. elliotii* and *P. taeda* places the former species in a perspective of resistance related to pines normally used for afforestation in Australia. In many cases in Western Australia, all four species could be considered for planting in the same situation. Although it is believed that management practices such as cultivation and heavy thinning would have greatest impact in determining stand development on such sites, an idea of relative drought resistance may assist interpretation of anomalous performance.

Pinus brutia proved to be the most drought resistant of all species tested. This confirms results obtained from arboreta trials in semi-arid areas of Western Australia. In certain cases, all *P. pinaster* have died or suffered severely from drought while the *P. brutia* plants are developing at a slower rate but with no apparent drought effects. It is expected that *P. halepensis* would prove to be even more resistant than *P. brutia*.

The nature of the interaction expressed in Figure 7 suggests that mean resistance per plant source may be of little significance unless the treatment range is clearly defined. *P. elliotii* and *P. taeda*, over treatments A and B for instance, aggregated 132 and 138 points for survival respectively, and no mortalities. *P. pinaster* F.S. aggregated 136 points for survival and two mortalities over the same treatment range. At P.W. numbers of plants in permanent wilting were 6, 3 and 11 respectively. It is believed that this data shows that the first two species have a high resistance to mild drought; possibly higher than *P. pinaster*. Over the whole range of treatments, *P. pinaster* showed quite superior resistance to severe drought. *P. radiata* showed relatively high susceptibility to mild drought. Survival and mortality aggregates for *P. radiata* treatments A and E were 118 and 2 respectively while at sunflower P.W., 29 plants were permanently wilted.

Individual results for survival and mortality in plant by treatment classes indicate that had the relatively similar and mild treatments C and D been used to increase the overall range of severity of treatments, i.e. an intensified exposure within treatments B and C and extended exposure beyond F, the significance of results would have altered to the favour of *P. pinaster*. Since the definition of treatment stages and the treatment range is arbitrary, significance of main effects (Table 10) is of little practical consequence.

Trial Design

With successive trials, the design and technique was improved. The fact that in Trial III the interaction between plant and treatment effects proved to be highly significant suggests that the scatter display of results (Figures 3 and 5) is a sound method of assessment. The amplitude of response over a wide treatment range is more meaningful than is a mean value for a single plant group.

Variation in plants within sources and the necessity of having a relatively large number of plants to assess survival effectively, necessitates the use of statistical control. For any interpretation of results it is essential to ensure that each plant source is equally well represented over the range of treatments. Pot weighing, leaf turgidity sampling and soil moisture determination incorporated in the trials did not necessarily improve the amount of information obtained. They were most useful in determining the effectiveness of control within the experiments.

A major problem associated with the procedure utilized is the variation in exposure involved. Use of an evaporation day, from atmometer readings, is reasonably sound. It is obvious however, that a time factor is operative and this can be most important. Whether drying to say 100ccs exposure occurs over three days or six days can influence plant response. This is clearly indicated in Table 9 where pots selected at the first evidence of sunflower P.W., following a very hot period, had twice the number of pines wilted as did the latter selections. Ideally, a drought chamber providing standard temperatures, radiation and evaporation rates is the answer. If however, large plants and large numbers need to be screened, expense is prohibitive. Influences of variable duration of exposure can be reduced in the glasshouse approach utilized by determining exposure time from a standard evaporation source, designing treatments to cover a wide range of exposure conditions and ensuring that all plants utilized within a single treatment are associated with the same time period.

A further problem associated with the approach is to pre-set treatment levels which will adequately cover a suitable exposure range. Depending on size of plants, condition of plants, container size and weather conditions, the same atmometer loss (exposure) will produce different plant response. Useful results were only obtained in the present studies by starting at P.W. and allowing for a wide range of treatments which could be adjusted to include severe drought conditions. To do such, and use scatter analyses effectively, a relatively large number of treatments and experience in gauging plant stress and response are required.

Sunflowers were used effectively to set a standard start point to commence the trial. This was effective with small plants but some problems could arise in growing sunflowers under crowded, two year old plants.

CONCLUSIONS

Pinus pinaster has been shown to be more drought resistant than *P. radiata*, *P. elliottii* and *P. taeda*. Within provenances of *P. pinaster* resistance to drought is variable decreasing from Corsica, Portugal, Landes and Tunisia in that order. Plants obtained from the Western Australian breeding programme show at least the drought resistance of the natural Portuguese source and there is an indication that selection may be improving the average drought resistance of the population.

DROUGHT RESISTANCE AND SILVICULTURE

INTRODUCTION

The principal objectives of this study were to obtain experimental indications of the extent that *P. pinaster* was more drought resistant than *P. radiata*, to indicate the range and ranking of drought resistance for certain provenances of *P. pinaster* and particularly to compare the drought resistance of selectivity improved seed of the Portuguese provenance with that of the parent population. These objectives have been achieved by the techniques employed.

Evidence has been presented to suggest that drought resistance, as determined by glasshouse procedures, reflects the overall resistance of the species under natural conditions of competition. This knowledge is sufficient to decide that the current breeding programme within the Portuguese population is proceeding satisfactorily. Wherever the Portuguese provenance is currently being planted in Western Australia, improved seed should cope with the situation equally as well but with a promise of increased yield due to improvements in form and vigour. To achieve this additional vigour however, some silvicultural manipulation may be desirable. Knowledge of natural drought resistance alone will not necessarily determine the use of species under managed, plantation conditions.

SILVICULTURE MANIPULATION

Levitt (1962) considers that drought resistance is a complex interaction of plant and environmental factors and that its direct measurement, in absolute terms, has not yet been attained. He emphasizes that measurement of drought resistance will not necessarily predict growth and yield under conditions of drought. The plant with the highest drought resistance will always give the highest yield in a drought that it can survive but that is severe enough to kill all others; but it will not necessarily give the highest yield under conditions of moderate drought. When considering commercial plant production, therefore, a definition of drought resistance is of little value to yield and economic considerations unless it can be related to the maximum conditions of drought, imposed under management conditions, within a rotation.

From the viewpoint of absolute wood production, commercial forestry is greatly dependent on the use of species with an inherently low drought resistance, i.e. *P. radiata*, *Enc. regnans*, *Enc. diversicolor*, and sites which do not experience severe drought stress during the rotation. One can generally accept that in any droughty site within its resistance range, the species with the greatest commercial production has a relatively low drought resistance. Species with a high resistance to drought, e.g. *P. halepensis*, *P. brutia*, *P. pinaster*, *Enc. macrorrhyncha*, will have a relatively low absolute production when grown under mesic conditions. A major aspect of inherent drought resistance in trees is the natural regulation of growth rates to relatively low levels (Hopkins 1964; Bolotin 1967). Larcher (1960) demonstrated that some species of relatively low drought resistance have a capacity to continue a high rate of assimilation up to the critical wilting stage.

Under managed conditions, water availability can be regulated on a marginal site to meet the requirements of a developing stand. Nursery practice, ploughing, weed control, care to spacing and season of planting, subsequent

cultivation and progressive thinning may grow an economic crop of *P. radiata* on sites from which it would be naturally excluded by drought and competitor species. One hundred stems of mature *P. radiata* grown under such conditions may be more economical than a healthy, unthinned stand of *P. pinaster* on the same site. The ability to vary competition through silvicultural manipulation reduced the utility of a direct expression of the natural drought resistance of a species.

Drought problems in commercial forestry are hence a compromise between droughtiness of a site, the range and cost of silvicultural manipulation and the relative drought resistance and potential for production of a species. It is still desirable to have an expression of the absolute or natural drought resistance of a species. It is however, equally essential to define the droughtiness of a site and to realize the economic and biological returns possible from that site under a range of silvicultural alternatives.

GENERAL

Within objectives set for the study, results are satisfactory. Further information has been provided concerning provenance variation in *P. pinaster*. Aspects of the local breeding programme, concerning drought response, have been placed into perspective. Study results also offer a useful direction upon which to base detailed work concerning physiological or functional aspects of drought resistance in the conifers concerned. In a field of study which is seriously lacking in factual data, the simple, direct approaches employed provided useful results.

A knowledge of natural drought resistance will assist afforestation schemes in selecting species for testing on sites available for planting. The major economic advantage however, must come from testing species on sites and relating economic returns with the costs of silvicultural manipulation. Very resistant species usually have slow growth rates and very droughty sites will only support limited production. Commercial production in plantation practice will usually come from the least drought resistant species which will provide an economic return on the site.

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