FACTORS THAT PREDISPOSE *PINUS PINASTER* TO DROUGHT DEATH

Physiology

Physiology of Drought Stress

Growth rate and Tree Form

Water plays a central role in plant growth. Not only do plants transpire water as part of their metabolic process they also store water. Over 50%of the total fresh weight of a tree consists of water, but the water concentration varies widely in different parts of the tree and with species, age, site and season (Kramer and Kozlowski 1979). Therefore as plants grow their demand for water increases and the demand on the environment to supply it also increases.

Hence, rapid growth and the development of large foliar biomass will speed up this demand for water and also increase competition between trees.

Inherent Physiology

Plants differ widely in their stomatal response to drought stress. This variability is at least partly associated with the existence of drought adaptation strategies based on (1) drought avoidance, which is generally found in species with high sensitivity to drought, or (2) drought tolerance, which is found in species with lower stomatal responsiveness but displaying structural and functional adaptive traits such as osmoregulation, allowing the plant improved tolerance of reduced water status (Picon *et al*. 1996).

Soil Water Availability

Soil water potential decreases as soils dry. This reduces the driving force for the movement of water from soil to roots. Additionally the resistance to water movement through the soil increases because the larger pores are emptied first. The resistance to water absorption by roots increases due to the shrinkage of roots and soil resulting in a decrease in root-soil contact. Root permeability also decreases due to an increase in root suberization in drying soil. (Kramer and Boyer 1995).

These limiting effects of low soil water potential increase as atmospheric conditions favour high potential rates of transpiration. The practical significance of this is that on sunny days rapidly transpiring plants can often develop water deficits in moist soil, but in cool cloudy weather plants may show little stress even in a relatively dry soil (Kramer and Boyer 1995).

Predawn Leaf Water Potential and Homeostasis

Water Potential is a common physiological measurement used to assess the general water status of a plant. A value of zero indicates the absence of water stress, while increasingly negative values depict increasing severity of water stress.

It has been assumed that before sunrise plants will be in equilibrium with the soil's water potential, therefore making PDWP a more sensitive indicator of soil water availability.

Hydrologic homeostasis is a physiological trait that allows plants to maintain their leaf water potential above a certain threshold level through stomatal control. Threshold levels will vary between species and are triggered by soil water availability and environmental conditions. Most plants can survive short periods of high water stress but will eventually die if it is prolonged. Again the degree and duration of water stress that eventually leads to drought death will vary between species. Water Stress Integral (calculated as water stress days), provides a measure of a plant's ability to withstand prolonged drought.

Soil Structure and Volume

There is evidence that the soil in the immediate vicinity of roots of actively transpiring plants often tends to become temporarily dry, increasing the resistance to water flow through the soil towards the plant root surfaces. This drying of soil around roots emphasizes the importance of root extension into previously unoccupied soil. It has been suggested that an increase in root depth is more important for postponing the onset of water stress than increasing root length density (cm of roots per cm^3 of soil) in the surface soil (Kramer and Boyer 1995). Therefore the importance of adequate soil depth, without impeding layers, for storing and accessing soil water is crucial to plant survival in drought conditions.

Physiological Traits of *Pinus pinaster*

To better understand the ecophysiology of *P. pinaster* in WA it is useful to understand the environment in which the genotypes currently planted here originated, and drought response findings from research around the world.

Range

Pinus pinaster (Maritime Pine) is native to S.W. Europe and N.W. Africa. In France, Algeria, Tunisia and Italy the distribution is mainly coastal, but in Portugal, Spain, Morocco and Corsica the tree grows from near the coast to far inland and high into the mountains, with marked differences in habit and rate of growth between the coastal and inland forms. It thrives best in the mild and relatively moist climate of the southern Atlantic coast of France (the Landes of Gascony), the Atlantic coast of Portugal north of Lisbon and the north coast of Spain (Scott 1962). The absence of the species from the Mediterranean east of the Adriatic may be due to the climate there being too dry (Scott 1962).

In these areas where *P. pinaster* grows best the climate is wet and mild. Mean average rainfall in Landes France is between 700mm and 1200mm and even higher in the north of Spain. In the Leiria region of Portugal mean annual rainfall is 800mm and mean average temperatures are 13ºC – 15ºC (Scott 1962). It is interesting to note that when looking at suitable climates when introducing Atlantic provenances (Leirian and Landes) of *P. pinaster* into Western Australia Prescott and Lane-Poole (1947) considered the optimum locations to be around Collie, Donnybrook and Bridgetown, which are vastly different from the areas in which we are now trying to establish plantations. Later assessments by Hopkins (in Havel 1976), considered that the area of the Gnangara and Yanchep plantations to be the northern limit of pine planting based on the reliability of rainfall and suitable edaphic-topographic associations to concentrate and conserve water.

The Leirian strain dominates the plantations established in Western Australia. Of the various provenances it is among the fastest growing with reasonable form. It comes from an area that has moderately high rainfall (~800mm) and cool temperatures. It therefore has some of the least well developed drought avoidance adaptations and is also susceptible to frost damage. Frost susceptibility was not considered an obstacle to its development in WA as it has been grown in close proximity to the coast where frosts are infrequent and not severe. Moving the planting of this species inland may not cause problems, while the frost frequency is higher the severity is usually within acceptable limits (down to -8.0ºC).

In Western Australia *P. pinaster* has a reputation as a drought hardy species suitable for growing in the medium rainfall zone (400mm – 600mm) of Western Australia. It is however a drought avoiding species rather than a drought tolerant species as it;

- Displays a high stomatal sensitivity(responsiveness) to drought stress (or water deficit)
- Has decreasing CO_2 assimilation in response to drought which is associated with increasing water use efficiency. ;(Picon *et al*. 1996).

Martinez-Vilalta and Pinol (2002) showed through comparative $\delta^{13}C$ data that *P. pinaster* had higher water use efficiency than either *P. nigra* and *P. sylvestris*. Granier *et al*. (1990) showed that stomatal control (in response to vapour pressure deficit) in *P. pinaster* in Landes (France) limited the daily transpiration to a maximum of 3.5mm day^{-1}, well below the Penman Potential Evaporation (PET) for that site of 6.8 mm day^{-1} (0.51 of maximum) and below the average ratio of tree transpiration to PET of 0.55. This supports the classification by Picon *et al*. (1996) that it is a drought avoiding rather than a drought tolerant species.
It is however, known to tolerate considerable summer drought, although this feature varies greatly between the different provenances, with the inland Spain and Moroccan mountain provenances being the most adapted to dry conditions. Unfortunately the form and vigour of these provenances make them unsuitable for commercial plantation development.
Studies with 3 year-old seedlings from 5 provenances that differed in climatic conditions (Landes France, mean RF 1280mm Temp 13.5ºC, Tunisia RF 1044mm T 18ºC, Leiria, Portugal RF 764mm, T 16ºC, Porto Vecchio France RF 657mm, T 15.5ºC, Morocco RF 650mm T ?) showed that there was significant differences in osmotic adjustment ,which contributes to drought resistance in woody plants, and a clear negative relationship between osmotic adjustment and annual rainfall at the geographical origins of the provenances such that trees originating from the Landes site (RF 1280mm) showed less capacity for osmotic adjustment than trees originating from Morocco (RF 650mm) (Nguyen- queyrens and Bouchet-Lannat 2003). They also stated that little is known about the adaptive processes involved that could serve as criteria for selection and breeding of more drought-tolerant genotypes.
Trials in New Zealand demonstrated that trees from different provenances reacted differently to stocking levels. They found the wide bushy crowns of the Atlantic coast provenances (Leirian and Landes) were apparently intolerant of competition and the best grown ones effectively thinned themselves. In other words competition for resources by these trees resulted in mortality. On the other hand the Corsican provenances retained close to their original stocking even though they are not noted as being particularly drought hardy (Knowles and Miller 1989).

A very valuable feature of *P. pinaster* is that it tolerates very poor infertile soils, especially sands, where few if any other useful timber trees will grow. It has a very low nutrient requirement for adequate growth.
P. pinaster is able to grow in a wide range of acidic soils changing its root system in relation to soil conditions. Soil pH does not influence lateral root initiation but it does have an impact on root length. In soils <3.5 pH and >6.5 pH root elongation is reduced (Arduini *et al*. 1998). As mentioned earlier root extension into previously unoccupied soil is an important factor in drought avoidance and therefore soil pH may have an influence in this process. Most soils in WA fall within the acceptable pH range except possibly some calcareous coastal sands, which may be higher than pH 6.5.

Long drought periods cause severe damage, especially to the Portuguese provenance, and this damage may continue after drought conditions end, possibly owing to the action of fungi that are not normally pathogenic (Scott 1962)
Manion (1981) has suggested that the multiplicity of factors which cause tree decline and death fall into three groups;

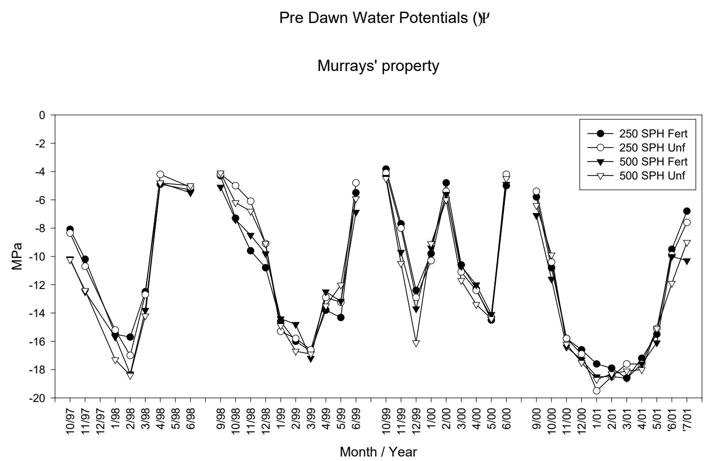
Predisposing Factors – long-term factors such as climate, soil type, aspect, landscape position, genotype, stand structure and stocking. These factors weaken trees growing in inappropriate locations.

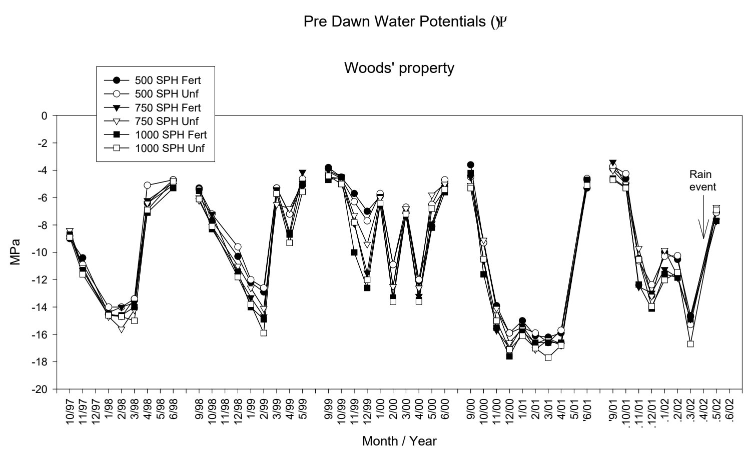
Inciting Factors – short-term factors such as drought, frost and insect defoliation which produce a sudden injury from which the tree has difficulty recovering.

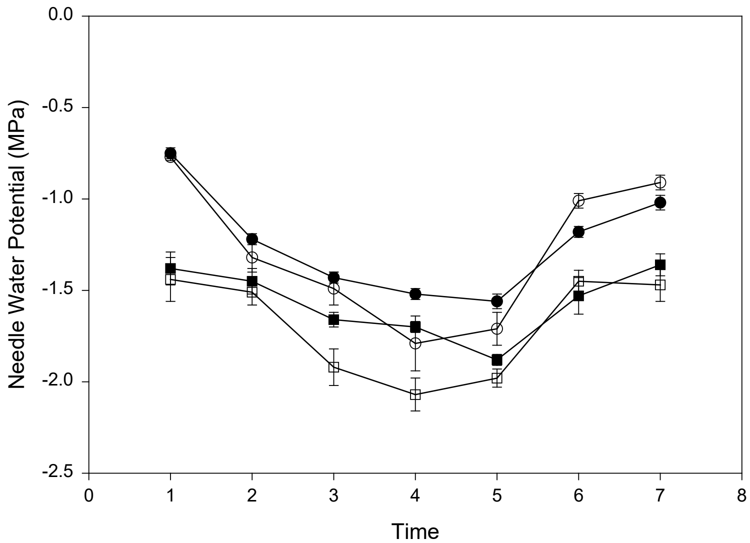
Contributing Factors – long-term factors such as secondary insect attack, cankers, and fungi which are able to invade only a weakened host. They are often very conspicuous but are best regarded as indicators of a severely stressed or dying tree.

Research Results from Western Australia

Evidence of hydraulic homeostasis was shown by Delzon *et al*. (2004) with a threshold level of -2.0 MPa and being independent of tree age and height. This is supported by data collected here in WA that shows mean pre-dawn water potentials remaining above -2.0 MPa. Extensive drought deaths occurred in 2000/01 at Murrays' plantation (right side of top figure) east of Wickepin. Although the threshold of -2.0 MPa was not breached it remained at or near this level for several months eventually leading to extensive mortality. The Water Stress Index (WSI) in relation to this collapse was greater than 500 MPa days. In the same year at Woods plantation near Dandaragan the duration of severe water stress was the same but the level was not as great leading to a WSI of approx 460 MPa





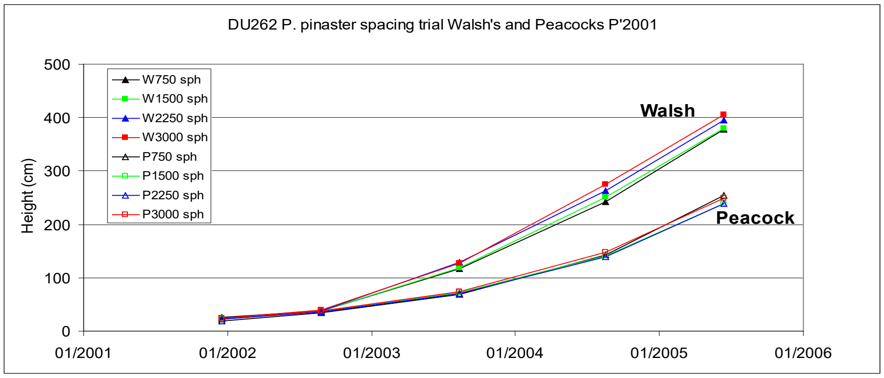


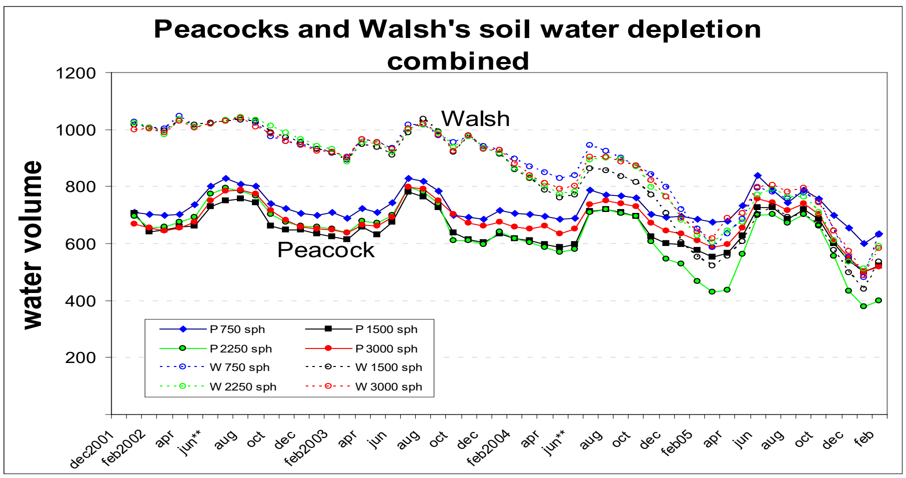
Maximum water stress in trees is experienced during the day and the standard measure is midday water potential. The figure above shows the diurnal range of leaf water potentials at the end of summer for two different stockings (250 and 750 stems/ha) of *P. pinaster* growing on the coastal plain at McLarty. The hydraulic homeostasis of -2.0 MPa appears to hold even under these late summer conditions.

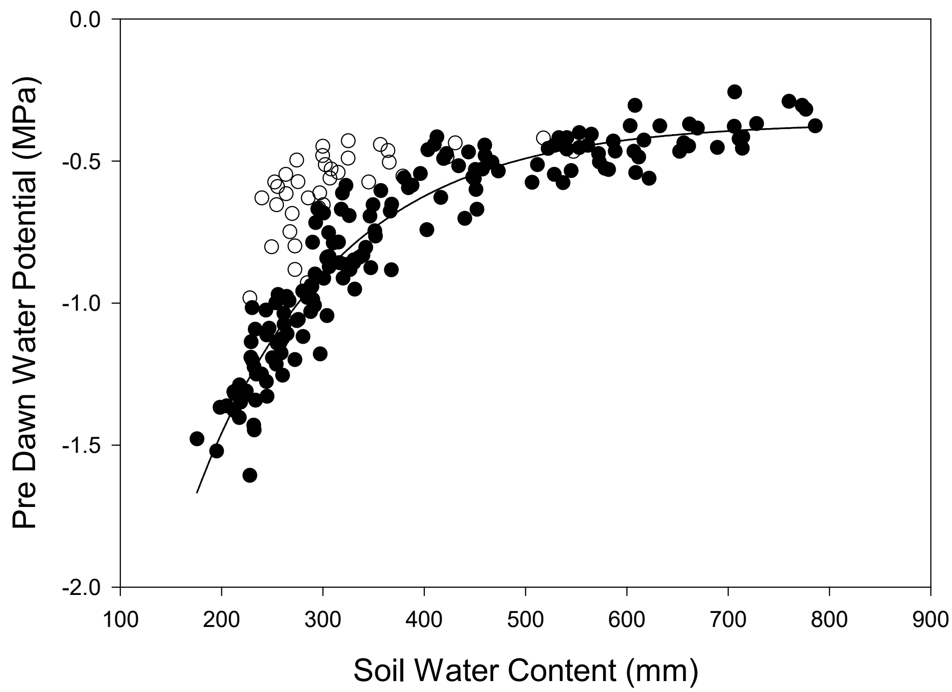
Growth and soil water depletion by 4 year-old *P. pinaster* plantations north of Perth are shown in the following two figures. The trees were planted at 750, 1500, 2250 and 3000 stems per hectare (sph) and monthly soil water measurements have been collected since planting. Height growth has been measured annually. Peacocks is located east of Badgingarra, and high in the landscape. It is a deep coarse sand with water table below 6m and hence considered a dry site. Walsh's is located SW of Moora low in the landscape and adjacent to an uncleared swamp the soil is also a sand to loamy sand. At the time of establishment the water table was generally within 1 – 1.5m of the surface, and is considered a wet site. Long term average rainfall is the same for both sites at approx 550mm, however evaporation estimates indicate Peacocks to be approx 100 – 150mm higher than Walsh's.

Growth and biomass at Walsh's is nearly double that of Peacocks and can be attributed to the abundant supply of water near to the surface plus annual rainfall, while Peacocks has been surviving on what can be stored from annual rainfall alone.
The mining of the abundant soil water by trees at Walshs in order to sustain their rapid growth is evident in the trace of soil water depletion shown in the lower figure. While the pattern at Peacocks is uniform in wetting and drying from winter to summer, with variation of approx 200mm each year (with the exception of the last year where 250-300mm have been extracted), Walshs shows a steady decline to a stage now where it has the same amount of water available as Peacocks. hence the trees at Walsh's having dried the soil profile out through their rapid growth are now relying on annual rainfall to supply water. Therefore the prospect of much larger trees at Walsh's having to survive on rainfall alone would indicate that, given a "normal" period of years ahead (age 5–6) will see extensive drought deaths in this plantation, particularly in the higher stocked plots.

Only in the past 18 months has there been any indication of the higher stocked areas using more water and drying the soil to a greater extent than the lowest stocked areas.







The graph above clearly demonstrates the strong relationship between total soil water content to 8m (mm) and leaf water potential (MPa) for *P.pinaster* at McLarty plantation over a three year period. This indicates the importance of soil water availability in determining le level of drought stress experience by *P. pinaster*.
Although *P. Pinaster* has some capacity to withstand summer droughts and possess adaptations that that make it effective at drought avoidance we have now taken the Leirian provenance well outside of its natural climatic range and therefore these tolerances are pushed to the limits and beyond. Exacerbating this alienation are the ex-farmland sites on which most of the new plantations have been established. These sites have artificially high soil water contents and generally raised fertility which favours rapid early growth. When this soil water is depleted and trees have to rely on annual rainfall alone, the larger canopies developed under the initially favorable water and nutrient supplies will likely predispose the trees to drought death even in "normal" years.
The extent to which other factors such as soil pH influence *P. pinaster* growth and drought avoidance in drier climates are not known, however given the generally acidic nature of WA soils this may not be an issue..

The focus of FPC's *P. pinaster* tree breeding since 1996 has been toward improved drought tolerance (avoidance) and improved stem form on farmland. The strategy to date in improving drought tolerance has concentrated on crossings within the Leirian provenance and the development of *P. pinaster* x *P. brutia* hybrids. Trial plantings have been established but are not yet old enough to conduct a thorough assessment. Trees in seed orchards have also been established and some seed is now becoming available. Unsuccessful (due to contract conditions) attempts have been made to collect genetic material from Leirian provenances grown on the coastal plain of Morrocco. The trees in this area seem to have adapted to a much lower rainfall than in its original range in

Portugal. Incorporating this capacity into the current *P. pinaster* population may increase its capacity to withstand drought conditions.

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