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Selection Criteria for Drought Resistance
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INTRODUCTION

The region known as the Great Plains is one of harsh climatic extremes. It is characterized by persistent, rather high wind movement, frequent droughts, bitterly cold winters, hot dry summers, and seemingly endless areas of grass. The earliest settlers realized the need for trees in "The Great American Desert" and made every effort to establish trees in and around their homesteads. The establishment of windbreaks and other plantings is highly desirable for wildlife habitat, timber, ornamental use, and recreation sites, but most critical is the need for trees to provide protection for crops, livestock and humans from weather extremes.

In an area dominated by grass, tree survival is dependent upon the ability of individual trees to compete with the prairie. They must be able to withstand the temperature and moisture extremes of the region. Perhaps more than any other factor, available moisture is the limiting resource in determining tree survival and growth. "Drought resistance" as a characteristic of trees for use in the Great Plains is highly desirable.

What is Drought Resistance?

Drought resistance describes the relative abilities of different plant species to survive extended periods of reduced precipitation. The water holding capacity of the soil, the rate of evapotranspiration, and the type of root system of the individual plants are all important factors in determining the length of the dry period necessary to produce water stress and the resulting reduction in growth rate (Levitt, 1980; Kramer & Kozlowski, 1979).

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There has been considerable interest in drought induced inhibition of plant processes (Kramer, 1983; Pallardy et al., 1983; Kramer & Kozlowski, 1979; Levitt, 1980; Grace et al., 1981). However, no one factor related to drought stress is the cause of growth reduction. As stress develops, many of the metabolic processes can be inhibited. A tentative sketch of some processes affected by declining leaf water potentials might be as follows: at the onset of stress, cell expansion ceases or slows and is followed by a reduction of protein synthesis and cell division. Recent work on leaf expansion in corn indicates that some cell expansion may continue at much greater stress levels than formerly believed (Norman, personal communication). At moderate stress levels, stomatal aperture begins to decline resulting in reduced transpiration and carbon dioxide uptake. As stress becomes more severe, proline accumulates, photosynthesis may become minimal, and detrimental consequences such as leaf senescence, xylem cavitation, and eventually death, may occur. Variations in the level of such metabolic inhibitions depend upon genetic variation and stage of development as well as the severity of stress and the relative amount of time over which the stress developed (Slatyer, 1967; Hsiao, 1973; Kramer & Kozlowski, 1979; Kramer, 1983).

Many systems have been proposed to describe the adaptations or acclimation of plants to water stress (Levitt, 1980; Kramer, 1983). A discussion of the merits of each of these systems is not included here, however, it is necessary to define several terms.

Drought resistance in plants can be broken down into three major types: drought escaping, drought tolerating, and drought avoiding. Drought escaping plants complete their life cycles before severe water deficits occur. Drought tolerating plants possess the ability, through the properties of their protoplasm to survive desiccation. Drought avoiding plants are able to postpone dehydration through structural features affecting water absorption and loss (Levitt, 1980).

Higher plants are homoiohydric that is they are able to maintain a water potential higher than that of their atmospheric environment. But they are not perfectly so. Consequently, higher plants must possess at least some ability to resist drought. Tolerance and avoidance may be equally important in some plants, or one characteristic may be far more important than the other. A plant with a well-developed ability to avoid drought will not only survive drought, but will be able to continue to metabolize, develop, and grow. A plant that is highly drought tolerant may survive drought, but will not grow, since it does not have a positive turgor pressure and cannot prevent stress (Levitt, 1980).

The degree of tolerance to or avoidance of drought depends not only on such stable factors as the depth of rooting, cuticular resistance, and mesophyll resistance, but also on such dynamic plant characteristics as stomatal resistance, and relative changes in water potential and its components. In woody plants, avoidance or postponement factors are generally of greater importance than tolerating factors (Kramer & Kozlowski, 1979; Levitt, 1980).

The degree of tolerance to or avoidance of drought varies both between and within plant genera (Levitt, 1980). In a comparison of the two components of drought resistance in seedlings of post oak (Quercus stellata Wangenh.), black oak (Q. velutina Lam.), northern red oak (Q.

rubra L.), and white oak (*Q. alba* L.), post oak was determined to be the most drought resistant species. While there was little difference in drought resistance between white oak and black oak, northern red oak was the least resistant of all four. The high drought resistance of post oak was attributed to its greater drought tolerance. The low drought resistance of northern red oak was attributed to its low drought avoidance character. White oak and black oak showed no differences in either drought tolerance or drought avoidance values (Seidel, 1972).

Ecological and physiological studies have continued to show that various plant species have a preference for particular habitats and that this preference is based on the ability of a particular species to fully utilize the resources of a given site (Fralish et al., 1978; Hinckley et al., 1978; Pallardy et al., 1983). This information is valuable and should be utilized when selecting species to be used in the Great Plains.

From a tree improvement point of view, we are interested not only in which species are best adapted to our area, but we would also like to have the very "best" individuals from those species. That such differences exist is well established. Studies have shown within species variation in drought resistance in a number of species including *Pseudotsuga menziesii* (Mirb.) Franco (Pharis & Ferrell, 1966), *Pinus radiata* D. Don (Bennett & Rook, 1978), *Populus deltoides* (Coleman et al., 1982), and *Pinus taeda* L. (Kramer & Kozlowski, 1979).

Two avenues are open to us: we can select individuals which are drought resistant and/or we can breed for drought resistance. Both approaches are valid, however, for the breeding process to take place, one must have a collection of individuals with desirable traits. One must also decide exactly what those desirable traits are before being able to identify individuals with those traits. While many crop breeders have identified many cultivars with desirable traits, tree breeders are not as fortunate. The question becomes then, what are the selection criteria for drought resistance in tree species?

Selection Criteria for Drought Resistance

There are many reviews which deal with water stress and many of these have also included discussions of various characteristics which could enable plants to withstand periods of low water availability (Begg & Turner, 1976; Kozlowski, 1976; Tyree, 1976; Kramer & Kozlowski, 1979; Pallardy, 1981; Kramer, 1983). We have purposely limited our discussion of photosynthesis, fully aware that recent theories link photosynthesis to the control of stomata (Farquhar and Sharkey, 1982). It appears that photosynthesis and transpiration are much more intimately linked than simply that both processes must utilize the stomata for gaseous exchange. Future research dealing with stomatal resistance should consider the simultaneous measurement of resistance and photosynthesis. While most past and current studies do not measure both processes, new instrumentation is making these measurements possible and they should be included in future selection studies. Our discussion will be limited to three criteria: stomatal response, plant water potential and transpiration, and their interrelationships.

Stomatal Response and Transpiration

Considerable emphasis has been placed on stomatal response to drought and the importance of stomatal size and distribution in controlling water loss (Kozlowski, 1976; Ceulemans et al., 1978a; Kramer & Kozlowski, 1979; Parker, 1968; Siwecki & Kozlowski, 1973; Tobiessen & Kana, 1974). Not only are stomatal differences found among plants of different genera (Kozlowski, 1976; Parker, 1968; Tobiessen & Kana, 1974) but also within the same genera (Ceulemans et al., 1978b, Siwecki & Kozlowski, 1973) and between clones of the same species (Kelliher et al., 1980; Kelliher & Tauer, 1980; Coleman et al., 1982; Whitehead et al., 1983).

In most deciduous trees stomata occur only on the lower surface of the leaf. An exception occurs in Populus species which have stomata on both surfaces. In general, the number of stomata is inversely related to stomatal size (Table 1). For example, Acer saccharum and A. saccharinum have many small stomata while Fraxinus pennsylvanica and Gleditsia triacanthos have fewer large stomata. Quercus spp. are an exception in that they have a high frequency of large stomata. Considering their relative drought resistance this would indicate that while stomatal size and frequency may be important, stomatal control is more important, at least in oak species.

Table 1. Stomatal size and frequency (Kramer & Kozlowski, 1979).

Species	Stomatal Length μm	Stomatal Frequency* Number/ mm^2
A . <u>saccharinum</u>	17.3	418.8
A . <u>saccharum</u>	19.3	463.4
F . <u>pennsylvanica</u>	29.3	161.6
G . <u>triacanthos</u>	36.1	156.3
Q . <u>rubra</u>	26.7	532.1
Q . <u>macrocarpa</u>	24.0	575.9
Q . <u>plaustris</u>	30.9	530.4
P . <u>deltoides</u> - lower surface	--	226.6
P . <u>deltoides</u> - upper surface	--	186.9

*Lower surface only

Tobiessen & Kana (1974) compared Populus tremuloides L., P. grandidentata Michx. and Fraxinus americana L. with respect to stomatal closure and leaf water potential. They found that F. americana and P. grandidentata had smaller stomata, with a higher frequency, which closed at lower leaf water potentials than P. tremuloides. In contrast, Siwecki & Kozolowski (1973) measured stomatal size and frequency in several poplar

clones. They observed that P. deltoides and P. nigra had relatively large stomata which closed early (i.e. at higher water potentials) as the excised leaves dried. Ceulemans et al. (1978b) compared two clones, resulting from a cross of P. trichocarpa X P. deltoides (Unal 7 and 8) which showed greater transpiration rates than either P. trichocarpa or P. euramericana. As desiccation increased, transpiration rapidly decreased in Unal 7 and 8, more so than in P. trichocarpa or P. euramericana. The rapid decline in transpiration of the Unal clones under stress was attributed to the lower stomatal frequency and larger stomata which afforded greater control of water loss.

Kelliher and Tauer (1980) examined stomatal resistance values of two clones of P. deltoides, one originally from a dry site and another from a wet site. The plants were held at three soil moisture levels: control, moderate stress, and severe stress. Consistently lower stomatal resistance values were determined in the scions from the wet site, even under control conditions. Kelliher and Tauer (1980) suggested that drought resistance in individuals can be selected for at any given moisture level simply by choosing the clone with higher stomatal resistance.

Coleman et al. (1982) examined three clones of eastern cottonwood from Ohio, Missouri, and Nebraska. The Nebraska clone had greater leaf resistance and a lower transpiration rate than either the Ohio or Missouri clones. The Nebraska clone also had greater dry weights and a greater root:shoot ratio, which indicates that this clone may make more efficient use of its available water.

In a study of six clones of Pinus radiata D. Don, Whitehead and others (1983) showed differences in stomatal resistance between clones at three different water vapor saturation deficits (low = 0.2 kPa; medium = 1.0 kPa; high = 2.0 kPa). Differences between clones were greatest at the high deficits and less significant at lower deficits.

As these studies indicate, there appears to be a contradiction. The question needs to be asked, which mechanism indicates a drought resistant plant? Is it the plant that has the ability to close its stomata early at high water potentials, thus conserving water but reducing photosynthesis and perhaps allowing other plants to utilize the soil moisture it is trying to conserve? Or is it the plant that is able to keep its stomata open longer at lower water potentials, carrying on additional photosynthesis and utilizing additional soil moisture?

In a study of bur oak (Q. macrocarpa) currently underway at the University of Nebraska, Allen (unpublished data) found that of four provenances from Nebraska, North Dakota, Pennsylvania and Oklahoma, the Nebraska source had consistently lower leaf water potentials, higher stomatal resistances and lower transpiration rates than any of the other three provenances. This suggests that the Nebraska source tends to conserve water. When the same four sources were compared for diameter growth during a period of adequate soil moisture, the Nebraska source was lowest of the four sources.

The conflicting demands placed on stomata for control of water loss and for carbon dioxide exchange dictate that the plant find some means to meet both demands. At the stomatal level, a compromise between photoactive opening and hydroactive closure must be reached. For maximum

growth the stomata should stay open as long as possible, utilizing available soil moisture and photosynthesizing. For survival, they should close soon enough to ensure sufficient moisture to enable the plant to survive until the next resupply of soil moisture.

The relationship between stomatal size and frequency and the degree of control of stomatal aperture by water status is not clear. It appears that size and frequency are related so as to maximize transpiration and not to minimize water loss during periods of reduced moisture. For further development of this idea see Jarvis and Mansfield (1981), Allaway and Milthorpe (1976), Farquhar and Sharkey (1982), and Kramer (1983).

Plant Water Potential and Transpiration

Water potential of a tissue is a quantitative measure of plant water status and is related to the water content of the plant tissue (Hsiao, 1973; Slatyer, 1967). The level of water potential is directly correlated with the amount of water in the tissue (Slatyer, 1967; Tyree, 1976). At 100% tissue water content, the water potential is generally more than -1 bar (Tyree and Hammel, 1972). As tissue water content declines, so does the tissue water potential. A gradient in water potential from the soil through the plant and to the atmosphere is required for the proper functioning of the plant's water uptake and transpiration processes (Begg and Turner, 1976; Kramer and Kozlowski, 1979; Slatyer, 1967; Kramer, 1983). Moisture originating in the soil moves passively along this gradient in the soil-plant-atmosphere continuum. As the soil water potential becomes low, from drying, the plant must respond by lowering its water potential in order to maintain this free energy gradient and continue to absorb soil moisture (Begg and Turner, 1976; Slatyer, 1967). Without the addition of moisture into the soil, the plant will continue to lose water and the water potential of the plant will decline in response to soil moisture levels, resulting in the development of plant water stress.

As water stress increases, stomata close, decreasing water losses. The level of stress at which stomata close varies between species (Federer, 1980; Tobiessen & Kana, 1974; Federer & Gee, 1976) and within species (Siwecki & Kozlowski, 1973; Kelliher et al., 1980; Coleman et al., 1982).

As leaf water potential decreases, the stomata of Pinus ponderosa and P. contorta closed at between -14 to -17 bars while those of Pseudotsuga menziesii or Abies grandis closed at -19 to -22 bars and -25 bars, respectively (Lopushinsky, 1969). This was reflected in transpiration rates. At soil water potentials of -10 bars, transpiration rates of the two pines were only 12% of their maximum rate while those of P. menziesii and A. grandis were 27-37% of their maximum rates (Lopushinsky and Klock, 1974).

How important is this early closure? Water is held in a clay soil with greater tension than it is held in a sandy soil. Tyree (1976) suggests that "since stomata must remain open to sustain carbon dioxide assimilation, our success at increasing yield by increasing drought tolerance depends very strongly on soil characteristics." At any given soil water potential more water will be held in the clay soil than the sandy soil. Consequently a plant capable of maintaining open stomata at -10 bars will extract significantly more water from the clay soil than a

plant whose stomata close at -4 bars. However, on a sandy soil where there is less available moisture, this advantage is negligible.

From an ecological point of view this would explain the occurrence of the pines on drier sites. Since less water is held in sandy soils at lower soil water potentials, it is important that the pines described above close their stomata early so as to avoid depleting soil moisture to critical levels. Even though additional available moisture is limited, this moisture may be critical to the survival of plants adapted to these sites.

The water potential that a plant is capable of withstanding depends directly on the osmotic potential of the tissue (Begg and Turner, 1976; Kramer and Kozlowski, 1979; Tyree, 1976) and indirectly on the elasticity of the cell walls.

Osmotic pressures of fully turgid plant tissues vary between species from -15 to -50 bars (Kramer and Kozlowski, 1979). Since the movement of water requires a decreasing free energy gradient, the water potential of the plant must be lower than that of the soil. The tissue osmotic potential determines a lower limit of soil water potential which the plant is capable of exploiting. During water stress, cell turgor decreases to a zero. When turgor pressure reaches zero, the water potential is determined, for the most part, by osmotic pressures in the tissues. For this reason it is important to determine existing differences in osmotic potential when selecting for drought tolerance (Tyree, 1976).

Use of the pressure chamber for determination of osmotic pressures, incipient plasmolysis levels, and cell wall elasticity has recently been undertaken (Cheung et al., 1975; Tyree et al., 1978). Cheung et al. (1975) suggest that producing pressure-volume curves for plants can be a valuable tool for determining osmotic pressures of plant tissues and in assessing relative drought tolerance. Using this technique, Tyree et al. (1978) examined several poplar clones, including *P. deltoides*, *P. alba*, *P. nigra* and *P. deltoides* X *P. nigra*. Leaves of increasing age were examined. Osmotic potentials at full turgor increased with ontogeny; from -7 bars shortly after emergence to -15 bars at full expansion. Of the four clones, *P. deltoides* and *P. deltoides* X *P. nigra* had the most negative values of osmotic potential at full turgor (*P. deltoides* -17 bars, *P. deltoides* X *P. nigra* -16 bars).

At incipient plasmolysis, turgor has been reduced to zero and water potential is then determined by the solute concentration of the cell sap. The osmotic potential at incipient plasmolysis is an important parameter of drought resistance only if stomata are more sensitive to changes in water potential rather than to changes in vapor pressure deficit (Tyree, 1976). Even though stomata may begin to close at plasmolysis, a correlation between complete stomatal closure and osmotic pressure at plasmolysis may exist. If, however, stomata are more sensitive to vapor pressure than deficit than osmotic pressures, use of osmotic potentials at plasmolysis for a selection criteria could be futile since vapor pressure deficit would affect stomatal response to a greater extent than osmotic potential (Tyree, 1976).

Cell wall elasticity controls turgor pressure changes within individual cells when they lose a given amount of water (Begg and Turner,

1976; Tyree, 1976). Cells with rigid walls will experience greater declines in turgor pressure for a given amount of water loss than cells with less rigid walls (Cheung et al., 1975). Therefore, a plant with a more rigid cell wall would be better able to decrease its water potential with less water loss in response to desiccation than a plant with a less rigid cell wall. The elasticity of the cell wall (or bulk elastic modulus, Tyree and Hammel, 1972) can be an important factor in drought tolerance by controlling the rate of turgor loss during desiccation and as a result, the concentration of cell sap (Begg and Turner, 1976; Cheung et al., 1975; Tyree, 1976). A large bulk elastic modulus value (BEM) is desirable for superior drought tolerance (Tyree, 1976).

Cheung et al. (1976) compared Acer saccharum Marsh. and Populus balsamifera L. using the pressure-volume technique and found the poplar (BEM = 140 compared with BEM = 130 for A. saccharum) to have superior cell wall elasticity for drought tolerance. Tyree et al. (1978) calculated bulk elastic modulus and discovered no clear cut distinctions between poplars although a trend of increasing bulk elastic moduli was shown as leaf age increased, indicating drought tolerance is greater in older leaves.

Within species, seasonal and diurnal patterns of water potential were studied in four clones of scotch pine (Pinus sylvestris L.) at 20 years of age, from May to March of a single year (Hellkvist & Parsby, 1976). Water potentials were found to reach a minimum earlier in the day in the summer, with wider variations over the course of a single day. At both high and low evaporation rates, the fastest growing clone had the lowest water potential and the slowest growing clone, the highest. The differences between clones were constant under the same conditions and may be due to differences in osmotic potentials or stomatal behavior or a combination of both.

Conclusions

The selection and breeding of trees for drought resistance is relatively primitive when compared to efforts in various annual crops. This is certainly understandable given the length of time between generations. If we are going to select and eventually breed trees for drought resistance we must begin immediately.

We must define our goals and objectives. Are we to select/breed trees for survival or maximum wood production? Both goals, and others, are highly desirable but the mechanism that produces the greatest ability to survive drought may not be the one yielding maximum wood production. We must decide which objective to pursue or what balance to strike between these two.

We must continue to characterize the responses of our native trees to drought under field conditions. What type of mechanisms are involved in stomatal control? What is the "best" level of stomatal resistance to ensure adequate photosynthesis with minimum water loss? We must begin to look at water use efficiency and/or transpiration efficiency. New models of stomatal control dictate that we make measurements of stomatal resistance, transpiration, and photosynthesis simultaneously. Some of the recent advances in instrumentation provide us with this option.

We must begin to select the criteria we will use to identify a drought resistant individual.

Given the length of time between generations, we cannot afford to wait for the answers to the previous questions. We must continue our collection of promising species and the establishment of these plantings throughout the region. Collections such as the ponderosa pine study currently underway, will provide excellent opportunities in the future.

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