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THE RELATIONSHIP BETWEEN MATRIC WATER
AND RELATED PHYSIOLOGICAL PROPERTIES

by

Hussain Ali Al-Saadi

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Plant Physiology

(Botany)

Approved:

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H. Al-Saadi

Hussain Ali Al-Saadi

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	ii
LIST OF TABLES	v
LIST OF FIGURES	vi
ABSTRACT	vii
INTRODUCTION	1
REVIEW OF LITERATURE	2
Proteins and matric binding forces	6
Matric water and the cell walls	6
Matric water and the effect of age and season	8
MATERIALS AND METHODS	12
Pressure membrane apparatus	12
Preparation of plant materials	14
Effect of age and season	16
Different plant parts	16
Temperature hardiness and water stress in Sunflower	17
Cold hardiness, photoperiod, and moisture stress in Cabbage	19
Protein extraction	20
Cell wall isolation	22
Nomenclature	22
Statistical analysis	23
RESULTS	24
Effect of season and age on matric water and water content	24
Regression analysis	28
Matric water of different plant parts	31
Temperature hardiness and moisture stress in Sunflower	35
Cold hardiness, photoperiod and moisture stress in Cabbage	38

TABLE OF CONTENTS (Continued)

	Page
Matric water of crude protein and cell wall materials	41
DISCUSSION	43
SUMMARY	52
LITERATURE CITED	54
APPENDIX	60
VITA	66

LIST OF TABLES

Table	Page
1. Summary table illustrating the relation of matric water binding forces and water content to some physiological properties	10
2. The effects of age and season on the matric water and the original moisture content of the leaves	25
3. Regression analysis of variance showing the effect of age and season on the matric water and moisture content	30
4. Matric water and the original moisture content of different plant parts	36
5. Matric water determination under water stress and different temperature regimes in Sunflower plants	37
6. The relations of matric water to cold hardiness, photo-period, and water stress in Cabbage	40
7. Matric water of crude protein and cell wall material of plant leaves	42
8. The replicated values of matric water in relation to age and season	61
9. Replicated values of matric water of different plant parts	63
10. Replicated values of matric water under water stress and different temperature regimes in Sunflower plants	64
11. Replicated values of matric water of different treatments in Cabbage	65

LIST OF FIGURES

Figure	Page
1. A. Water content of several biocolloids as a function of the matric potential	
B. Water content of frozen and thawed potato tuber, mangel root and asparagus stem tissues as a function of the matric potential (Adapted from Wiebe, 1966)	15
2. Matric water and the original moisture content in relation to age in coniferous trees	27
3. Matric water and the original moisture content in relation to age in deciduous trees	29
4. Regression lines of several trees illustrating the relation of matric water original moisture content of the tree leaves	32
5. Regression lines illustrate the relations of matric water and original moisture content of conifer leaves to the inverse of their age in months	33
6. Matric water and the original moisture content of different parts of <u>Helianthus</u> , <u>Geranium</u> , <u>Malva</u> , and <u>Acer</u>	34
7. Matric water of Sunflower leaves at different temperatures	39

ABSTRACT

The Relationship Between Matric Water and
Related Physiological Properties

by

Hussain Ali Al-Saadi

Utah State University, 1972

Major Professor: Herman H. Wiebe
Department: Botany

Matric water was measured as the water retained by plant material on a pressure membrane or ultra filter after equilibration under 20 bars nitrogen gas pressure and the removal of free water. At increasing pressures lesser amounts of water are held by matric or colloidal surface forces. Twenty bars pressure, supplied by cylinder nitrogen for 48 hours, was used in this study. Matric water was expressed as a percent of either (a) the dry weight or (b) the original water content. Plant material was oven dried, ground, and then saturated with water prior to the determination.

The matric water values of different aged leaves from a number of local species were studied. The highest values of matric water were found in the younger leaves. Both matric water and original moisture content were higher for spring than for fall or midwinter values. The linear relationship between matric water and original moisture content was established

for all trees studied. Another linear relation was found between either the matric water or the water content of the tree leaves and the inverse of their age in months.

Petioles had a higher matric water value as well as a water content than leaf blades in all the species studied. Roots and old stems had the lowest values of matric water.

The matric water values increased during the cold hardening of Cabbage leaves. No appreciable differences in the matric water values for Sunflower leaves grown under different temperatures were found.

The crude protein and cell wall materials were isolated and their matric water values studied. Crude proteins had a higher value of matric water than cell wall materials alone. The matric water values of several biocolloidal materials were determined also. Agar had the highest value of matric water, fibrous cellulose the lowest, and the proteins had intermediate values.

(75 pages)

INTRODUCTION

The concept of water binding forces (matric forces) has been used in attempts to supply a basis of explanation for such physiological processes as the swelling of animal tissue; and in edema, the drought and frost hardiness in plants, as well as the imbibition process in colloidal systems generally.

Matric potential is a measure of the lowering of chemical activity of water which results when water is bound at interfaces with solids. Such binding occurs in plant cell walls and in cytoplasm. It is contrasted with osmotic potential, which is a measure of the water potential lowering by soluble solutes. Although significant matric potential may develop in some dehydrating plant tissues, matric potential has seldom been evaluated in studies of plant water relations. Ignoring this component may introduce errors in estimates of the contribution of osmotic potential to the total water potential.

In this study I report on the matric water of various plant parts; I also studied the influence of age and season on matric water. The influences of environmental factors, such as heat, cold, photoperiod, and drought stress on matric water were also studied. The original moisture contents of the plant materials were also measured and related to their matric water values. I also extracted the cell wall material and crude protein and studied their matric water.

REVIEW OF LITERATURE

The imbibition pressure, recently called "matric potential," is a pressure against which a colloid will imbibe a liquid or, conversely, the pressure which is required to force the dispersion out of a gel (Gortner, 1949). As the amount of imbibed water in a colloid increases, the imbibitional and swelling forces decrease. For example, the amount of imbibed water bound per gram to dry stipe of the brown alga "Elk Kelp" increased with increased hydration, but not proportionately. In fact, the percentage of imbibed water bound decreased with increased hydration (Chrysler, 1934).

Gortner (1930) maintained that an appreciable fraction of water in organisms is not "free" as judged by the fact that only part of it freezes, even at low temperature. He listed two hypotheses of the nature of bound water: (1) an oriented adsorption of the water dipoles at the interface, and (2) an oriented adsorption of hydrogen and hydroxyl ions.

Water in protoplasm occurs in two forms, free and bound (Giese, 1957). Free water is that which is available for metabolic processes, while bound water is attached to protein molecules by the formation of hydrogen bonds and, therefore, forms part of the structure of protoplasm. However, Briggs (1932) defined bound water as the water in a colloid-crystalloid system which is associated with the colloid, together with those ions which form a part of the colloid complex.

Surface forces of proteins, other molecules of the protoplasm, cellulose of plant cell, and clay particles of soil also influence diffusion pressure of water. In soil science this phenomenon is called "moisture tension," "soil water suction" or "matric suction" (Richards, 1941; Richards and Fireman, 1943; Reitemeier and Richards, 1944; Richards, 1947; Taylor, Evans, and Kemper, 1961). Plant physiologists have called it "imbibition pressure," while the term "matric water" or "matric potential" has recently come into use by both groups (Taylor and Slatyer, 1961; Collis-George and Sands, 1962; Gardner and Ehlig, 1965; Kramer, Knipling, and Miller, 1966; Wiebe, 1966; Boyer, 1967; Slatyer, 1967; Wilson, 1967; Barrs, 1968; Sutcliffe, 1968; Taylor, 1968; Kramer, 1969; Salisbury and Ross, 1969; Nobel, 1970; Al-Saadi and Wiebe, In Press).

The tension with which water molecules are held on an imbibing surface is a function of their water potential, the nature of the surface (especially the charge), and the distance between the water molecules and the surface (Salisbury and Ross, 1969). The closer the water molecules are to the surface, the more firmly they will be held. The tenacity with which they are held may be expressed in terms of chemical potential or water potential. The hydrating, often highly irregular and porous surface (colloid or gel-like material, such as the cell wall), is referred to as the matrix, and its potential is called matric potential.

In non-vacuolated cells, typically meristematic, or cells in which the vacuole is small and may be a gel, much of the water will be

retained by matric forces and relatively little free water "solution" may exist (Slayter, 1967). As cell water content decreases, the osmotic and matric forces increase in magnitude since both are dependent on water concentration.

Often the matric potential is ignored or it is treated as a part of the osmotic or pressure potential (Briggs, 1967; Nobel, 1970). In most plant tissues the matric potential does not exceed value of -1 bar. Several studies indicate that matric forces may be responsible for a significant fraction of the total water potential in some plants, especially when tissue water content is low as in the case of seeds (Dainty, 1963; Wiebe, 1966; Boyer, 1967; Wilson, 1967; Noy-Meir and Ginzburg, 1969; Miller, 1971). These findings suggest that a full interpretation of changes in plant water potential may require an estimate of its matric component.

Wilson (1967) concluded that bound water content, which is believed equivalent to matric forces, decreases as relative water content falls. He indicated that the matric potential originates in forces of capillary, adsorption, and hydration. Capillary menisci occur in the intercellular space and at the outer surface of cell walls. Within the walls, spaces between the microfibrils are so small--usually less than $100 \overset{\circ}{\text{A}}$ (Preston, 1952; Siegel, 1962)--that the forces can be regarded as adsorptive rather than capillary. Adsorption (imbibitional force) is likely to predominate in the protoplasm but may also be present in the vacuole if it contains colloids. Newton and Gortner (1922) showed that percentage bound water increased regularly with colloidal concentrations.

The matric force field decreases gradually with distance from surface, though there is no sharp distinction between those water molecules which are "bound" to the surface and those which are not (Walter, 1955).

Bound water reduces vapor pressure, remains unfrozen at temperatures far below zero, does not function as a solvent, and seems to be unavailable for physiological processes (Kramer, 1969). Kramer provisionally and arbitrarily defined bound water as that remaining unfrozen at -20 to -25 C. Some water may remain unfrozen at much lower temperatures (Lloyd and Moran, 1934).

Methods for determining bound water (matric water) were discussed by Gortner (1937) and Kramer (1955). A recent method was developed by Wiebe (1966), using the pressure membrane apparatus, which previously had been used to study soil moisture tension. This method was followed in the present study.

Shull (1924) has discussed certain phases of imbibition (matric forces) as related to botanical problems, and noted that dried seeds will adsorb water from a saturated solution of lithium chloride until they attain a water content of about 8-9 percent. Since a saturated solution of lithium chloride has an osmotic pressure of approximately 1000 atmospheres, it is evident that imbibition pressure (matric potential) of seed colloids may reach enormous values. Levitt (1954) also noted that the amount of such bound water is retained against forces of evaporation of well over 1000 atmospheres in some aqueous gels which are highly hydrophilic.

Proteins and matric binding forces

The proteins in colloidal state are typical lyophilic colloids (Gortner, 1930). In the plant kingdom the polysaccharides and proteins in colloidal state are, in general, highly hydrophilic and attract considerable quantities of water.

Bull (1944) found that the amount of water held by a protein molecule in solution should depend principally upon the extent of the total hydrophilic surface exposed to the water. In 1951, he indicated that there is no fundamental difference between adsorption and chemical binding, and that identical types of forces operate in both. Proteins are particularly effective in binding water because they bind it in two places, by the hydrophilic end groups of the side chains and by the oxygen and nitrogen atoms of the peptide linkage.

Mellon, Korn, and Hoover (1947) found that the polar amino group, which constitutes less than 1 percent of the total weight of the protein, can account for about one-quarter of the total adsorption. This indicates that the specific sites (the polar groups) are relatively more important, and that general surface adsorption plays a less important role. They also found that when the relative humidity is above 70 percent, there is a rapid increase in the water adsorbed by amino groups.

Matric water and the cell walls

The cell wall has characteristics of a hydrophilic gel (Levitt, 1954). Evidence of matric forces in the cell wall and cytoplasm was discussed by Babbitt (1942), Carr and Gaff (1961), and Boyer (1967). Barrs (1968) indicated

that matric potential arising from the imbibitional forces of colloids in the cell wall by capillary matric forces is released when the cell is immersed in solution and, consequently, is able to cause dilution.

Water is an important constituent of the cell wall, and the water content of the wall is one of its most variable features (Northcote, 1972). The amount of water within the wall matrix can be controlled to some extent by the deposition of polysaccharide filler material which forms close intermolecular associations and gel-like structures, or by a non-wettable filler such as lignin.

Gaff and Carr (1961), proposed that the cell wall, not the protoplast, acts as the main pathway for extrafascicular movement of water, and that in the leaf the cell wall water operates as a buffer against loss of water from the protoplast. The buffering capacity of the water in the wall may be a factor in the "hardening off" of plants to drought. This may occur through an increased production of hemicellulose and pectin substances, coupled with a decrease in protein synthesis.

Large cell wall:protoplast ratios may occur either in cells with thick cell walls, or in tissues with small closely-packed cells (Miller, 1971). The large cell wall:vacuole ratio in xerophytes may be responsible for adding measurable and often quite large matric components to the water potential.

Geometric changes in the wall structure during changes in cell water content affect the interfibrillar distances in the wall matrix, and probably cause variations in the matric potential (Weatherly, 1966). Because solutes

are actively absorbed by the protoplast, the cell wall solution is diluted and most of the forces holding water in the wall are matric forces.

The results of studies by both Teoh, Aylmore, and Quirk (1967) and Noy-Neir and Ginzburg (1969) have suggested that cell walls have a higher (more complex) structure in xerophytes than in other plants.

Differences in the sorption-description isotherm found for the various wall materials suggest that an important factor enabling a drought species to endure prolonged water stress is the relatively greater tenacity with which its cell wall water is held in comparison with that of mesophytes (Teoh, Aylmore, and Quirk, 1967).

Matric water and the effect of age and season

Although several studies have already shown that a gradual steepening of desorption curves may be correlated with increasing tissue or plant age (Knipling, 1967; Millar, Duysen and Norum, 1970) and with drought hardening (Knipling, 1967), evaluation of the importance of matric potential in these ecologically significant phenomena has rarely been attempted.

Knipling (1967) concluded that increased leaf dry weight, decreased cell wall elasticity, and increased osmotic potential accompanied leaf aging.

Meyer (1928) found relatively little change in the water content of leaves of pitch pine from summer to winter, but much less of the total sap could be expressed at a given pressure from the cold-resistant winter leaves. The increased water retaining power of the cold resistant (leaves) was attributed to an increase in colloidal gels capable of binding water.

The seasonal variation in the relative proportion of bound and unbound water is the most important factor in the cellular physiology of the leaves in relation to cold resistance of pitch pine (Meyer, 1928). That this seasonal variation in the proportion of bound water is due primarily to the seasonal changes in the amount and condition of the cell colloids appears to be reasonably well established. In 1932, Meyer found that no evidence could be obtained by the pressure dehydration method of any significant increase in the amount of bound water in the pine leaf tissue in winter as compared with summer. Conversely, Steinmetz (1926) found higher percentage of bound water for the alfalfa samples taken during winter and early spring than for late summer samples.

Grandfield (1943) found total water increased through the early fall, began to decrease the latter part of October, and reached minimum in January. Bound water calculated as a percentage of total water, was opposite to that of total water, and there were no reverse changes in the early fall, as the case of total water. The rapid increase in the percentage of bound water from October 6 to January 2 coincides with an increase in cold resistance and with an increase in sugar.

In studies on seasonal and diurnal changes in the water content of pear leaves, Ackley (1954) found that the water content decreased from 73 to 59 percent of their fresh weight from May to August, although the weight of water per leaf remained practically unchanged.

Several physiological properties, as related to bound water or matric water are summarized in Table 1. These illustrations indicate that

Table 1. Summary table illustrating the relation of extric water binding forces and water content to some physiological properties

Conclusion	Plants, plant materials studied, or other remarks	References cited
1. There is a correlation between bound water and hydrophilic colloids	Vegetable crops Cereals and other crops Soybeans, sunflower, milo and cabbage Acorary with drought plus trees	Rosa, 1921. Newton and Martin, 1930. Greathouse, 1932. Hankel, 1961. Kushnirenko, 1964.
2. The amount of hydrophilous colloids such as pentosans increases during the cold "hardening off" process	Cabbage and few other vegetables	Rosa, 1921
3. Pentosans and proteins do not increase during the cold "hardening off" process	Winter wheat No apparent connection between cold resistance and pentosan content of the leaves of conifers	Newton and Brown, 1926. Doyle and Clinch, 1926.
4. Total moisture content is correlated inversely with cold hardness	Vegetable crops Winter wheat Cabbage and milo Apple twigs Frost hardness has been correlated directly with dry matter content.	Rosa, 1921. Newton and Brown, 1926. Greathouse, 1932. Stark, 1936. Levitt, 1956.
5. Bound water or water-retaining power is correlated with cold hardness	Vegetable crops Review article Soybean, sunflower, milo and cabbage No significant differences in bound water of apple twigs between resistance and non-resistant varieties Alfalfa Cabbage	Rosa, 1921 Gortner, 1932. Greathouse, 1932. Stark, 1936. Grandfield, 1943. Levitt, 1959.
6. There is no correlation found between bound water and cold hardness	Alfalfa Alfalfa Pitch pine	Steinmetz, 1926. Weiner, 1929 Meyer, 1932.
7. There is no effects of photoperiod on growth or on frost hardness	Cabbage	Kohn and Levitt, 1965.
8. The protoplasmic colloidal-chemical properties play an essential role in the resistance of plants to high temperature and drought	The degree of hydration of colloids, and the increased content of bound water are also important aspects of heat-resistance	Hankel, 1961, 1964.
9. There is a correlation between bound water and drought resistance	Vegetable crops Cereals and other crop plants. Bound water in cabbage and milo increases under less soil moisture cond- Review articles Corn	Rosa, 1921. Newton and Martin, 1930. Greathouse, 1932. Gortner, 1932, 1937. Shchukina, 1965.
10. There is no correlation between bound water and drought resistance	Loblolly pine and short leaf pine Prairie grasses Fruit trees Wide range of several species	Schopmeyer, 1939. Whitman, 1941. Kushnirenko, 1964. Al-Saadi and Wiebe, (in press)
11. The plants exposed to drought "hardening off" conditions increase in dry substances and decrease in moisture content	Milo and cabbage (Especially in Early Jersey Wakefield variety)	Greathouse, 1932.

the condition of the water in a biological system has a marked effect on the properties of the protoplasm, and give evidence in support of the supposition that matric water is closely related to many physiological processes carried on by a living cell.

Bound water was found to be related to several physiological processes such as frost hardiness and drought resistance. However, several other investigations did not find any correlation between bound water and several different physiological processes (Table 1). This work is intended to clarify the relation of matric water to its various physiological properties.

MATERIALS AND METHODS

The matric water of plant materials was measured with a pressure membrane apparatus (Wiebe, 1966; Al-Saadi, 1970). The pressure membrane method has been used since 1940 for measuring matric potential (moisture (moisture tension) of soils at various soil moisture contents, for determining the water release curves of soils (Richards, 1941; Reitmeier and Richards, 1944) and for soil solution studies.

The pressure membrane apparatus was used originally for ultra-filtration in chemical work; it was also used for extracting solutions for analysis from saline soils. It has been useful for studying the moisture retention characteristics of soils and other material, and for the calibration of soil moisture instruments (Richards, 1947).

Pressure membrane apparatus

This method is based on the availability of cellulose membranes which, when wet and properly supported, withstand a large gas pressure differential without allowing the gas to flow through the pores. Molecules of water or solutes which come in contact with the membrane on the higher pressure side can, however, pass through to the low or atmospheric pressure side. The moisture diffuses from the plant material and passes through the membrane. This process continues until the surface forces which retain water in the material (and which increase during moisture

extraction) balance the water extraction force established at the membrane by the pressure difference across the membrane. The amount of moisture retained in plant material after sufficient time to reach equilibrium depends on gas pressure in the chamber and on the characteristics of the material. The higher the pressure, the more moisture is removed, and the less moisture is retained in the material (Al-Saadi, 1970).

The pressure membrane apparatus used was a commercial product, similar to that described by Richards (1947). Nylon cloth was used instead of metal screen to provide drainage under the membrane (Wiebe, 1966; Al-Saadi, 1970). It supplied uniform support for the membrane, allowing liquid to pass through the membrane and move freely toward the outflow tube. The membrane used was grade B-17 (Schleicher and Schull, Keene, New Hampshire) with a nominal pore diameter of 20-35 μ . This had proved to be most satisfactory in previous studies (Wiebe and Zielinska, 1972).

To determine the water content associated with a particular potential, the apparatus, nylon drain cloth, and pre-wetted membrane were assembled. Ground plant material, wetted to saturation, was placed on the membrane in small rubber rings (about 3 cm in diameter and 7 mm deep), covered with a layer of sheet plastic and then with sponge rubber (10 cm in diameter and 4 cm deep) in a plastic bag; the latter pressed gently against the plant material, insuring good contact between the tissue and the membrane. The lid was closed, tightened, and compressed air was admitted to the apparatus. The entire assembly procedure required less than 5 minutes, so evaporation water loss was negligible.

The solution began to run out of the drain within a few seconds after the pressure was applied. The initial rapid rate then decreased after about 6 hours. In most instances no additional solution drained after 24 hours and it is presumed the material was approaching equilibrium. After 48 hours the material was removed, placed in tared stoppered bottles, weighed, oven-dried at 105 C for 24 hours, and reweighed to determine the water content as a percentage of dry weight. The matric water values of plant material in this study were expressed in terms of the moisture remaining at 20 bar pressure supplied as a percent of the oven dry weight of the material. Matric bound water was defined by the 20 bar matric water values divided by the percentage of original water content on a dry weight basis.

The moisture release curves for different plant materials as well as for several biocolloids stabilized at a pressure of 15 bars or more are given (Fig. 1). On this basis the author used 20 bars pressure for moisture extraction from plant material. It was supplied by cylinder nitrogen, and applied continuously for 48 hours.

Preparation of plant materials

Plant leaves, stems, and roots or other parts were collected and promptly weighed on a field balance, dried in a forced air oven at 65-70 C for 4 days, and reweighed to determine the water content as a percentage of the dry or fresh weight. They were then ground in a Wiley mill to pass through a 40 mesh screen and stored in stoppered bottles until used.

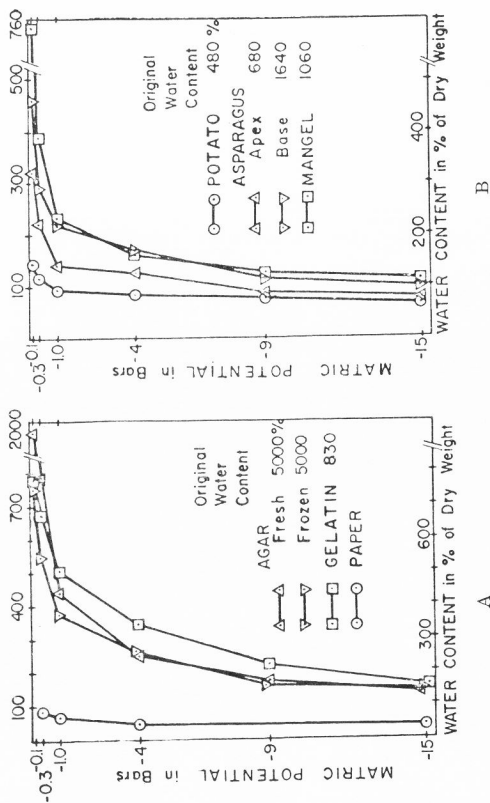


Figure 1. A. Water content of frozen and thawed potato tuber, mangel root and asparagus stem tissues as a function of the matric potential (Adapted from Wiebe, 1966).
 B. Water content of several biocolloids as a function of the matric potential.

Samples of the ground plant material were moistened to complete saturation with distilled water. The moistening process required about 6 hours. The moistened sample was then used to make matric water determinations.

Effects of age and season

Leaves from deciduous and coniferous trees were collected from different areas near Logan, Utah, at various times in 1970-1971. The exact locations of these species are indicated in the Appendix and the dates of collections are given in the result section.

For each conifer species, 3 leaf samples representing 3 different years of growth were taken on each sampling date. In deciduous trees the young leaf blades from the current seasons were collected. In maple, however, three leaf blade samples of different ages were taken: Buds, young leaves which were produced throughout the season, and mature leaves.

Different plant parts

Parts were chosen for the study depended on the species, but generally consisted of leaves, petioles, stems, and roots.

Greenhouse grown Sunflower plants were used when they were 80 cm tall and six to eight weeks old. The first set was harvested in January, 1972, the other in May of the same year. Eight different parts were collected from each plant, consisting of 1. Buds within the first top 1 cm. Three samples were taken from the top 4 cm's; 2. Leaf blades; 3. Leaf petioles; 4. Stems.

Three samples were taken from the lowest 4 cm just above the cotyledons position: 5. Leaf blades; 6. Leaf petioles; 7. Stem; and 8. Roots.

Several plant species, other than Sunflowers, were collected from different areas near Logan, Utah, to compare the moisture content and the matric water of different plant parts. Sections of dry kelp stipe were moistened until saturated and then transferred to the pressure membrane apparatus to determine matric water content.

The matric water and the moisture content of "water storage tissue" were studied in two greenhouse-grown succulent species (Gasteria and Opuntia). It was possible to dissect 3 layers, each representing a different tissue; namely, cuticle and epidermis, green chlorenchyma, and the water storage tissue. The tissues were dissected rather rapidly, so there was some cross contamination by adjacent tissues with the exception of the water storage tissue. Then plant material was then oven dried and prepared as previously indicated.

Temperature hardiness and water stress in Sunflower

Greenhouse-grown Sunflower plants were also used to study the influences of temperature and moisture stress. Mature plants were randomly divided into six groups, using dice, each group consisting of 22 plants, and were treated as follows:

Group 10 M was transferred to a growth chamber kept at 10 C during the day and 8 C at night, and watered regularly.

Group 20 M was transferred to a growth chamber at 20 C during the day and 16 C during the night, and watered regularly.

Group 30 M was transferred to a growth chamber kept at 30 C during the day and 25 C at night, also watered regularly.

Group 30 D was transferred to the same growth chamber used by group 30 M, but the plants were given several moisture stress cycles.

Group 40 M was transferred to a growth chamber kept at 40 C during the day and 33 C during the night, and watered regularly.

Group 40 D was transferred to the same growth chamber as that of group 40 M, but these plants also were given several moisture stress cycles.

The moisture stress cycles were provided by keeping the plants dry (without watering), until they wilted and then giving them about 10-15 ml water per plant for recovery which completed one moisture stress cycle. Eleven cycles were provided for both groups 30 D and 40 D during the treatment period.

Fourteen hours light and 10 hours dark were provided during the treatment period for all growth chambers. Light intensities in the growth chambers were 1700-1900 f. c. near the top of the plants, measured by the light meter.

All mature leaf blades were harvested after one week of the temperature and moisture stress treatments, although a few leaf blades were harvested after the fourth moisture stress cycle in the 30 D and 40 D treatment groups.

This experiment was repeated twice, the dates of harvest being February 11 and May 19, 1972.

Cold hardiness, photoperiod, and moisture stress in Cabbage

Greenhouse-grown Cabbage (Brassica oleracea capitata var. Early Jersey Wakerfield) was used to study the relations of matric water to cold hardiness.

The plants, after reaching the mature stage, were divided into 3 groups, each group consisting of 18 plants, and treated as follows:

Group 1 was first hardened (Levitt, 1959) for 2 weeks in usual way by transferring to cold growth chamber (+4 C) with 8 hours of light per day. The plants were watered regularly.

Groups 2 and 3 were treated similarly as a control experiment (treatment), and transferred into two separated growth chambers, both kept at 25 C during the day and 20 C during the night. The only difference between the chambers was the photoperiod, of which two were provided; one growth chamber programmed for a short day (8:16), the other for a long day (16:8).

This experiment was repeated three times with harvesting dates of 29 April, 12 May, and 7 September, 1972.

The last two repetitions had, in addition to the aforementioned treatment, two more treatments dealing with water stress. The two additional groups were treated with the warm treatments, but subjected to fifteen moisture stress cycles during the treatment period of 2 weeks. Each moisture

stress cycle was provided by the same procedure given for sunflower plants indicated earlier.

In summary, five treatments were performed on cabbage plants:

1. Cold temperature with short day (SD) condition
2. Warm with short day (SD) condition
3. Warm with long day (LD) condition
4. Warm with SD and water stress condition
5. Warm with LD and water stress condition.

Leaf blades without the midribs and buds with one or two leaves were used for matrix water determination.

Protein extraction

Two different species, spinach and sugar beet, were used in this experiment. Leaves with midribs removed were randomly divided into two sets. One set was used for protein extraction and the other was used for direct matrix water determination of the whole leaf.

Two methods were applied for crude protein extraction.

In the first, a domestic brand meat grinder, hand powered, was used for making the initial spinach leaf pulp. The pulp was homogenized for 10 minutes with distilled water (30 ml water each 100 gm fresh weight) in a Waring Blender. The homogenate mash was then squeezed and filtered through a small bag of cotton lawn, using a pressure of 2000 pounds per square inch in a hydraulic press. This separated a green extract, heavily

charged with protein, from the pasty mass of cell wall debris (Chibnall, 1939).

The mash was centrifuged for 5 minutes at 500 g to remove the excess debris (whole cells, starch grains, and whole chloroplasts). Microscopic examination of the supernatant suspension revealed numerous chloroplast fragments but almost no cell debris. The supernatant was then lyophilized for 20 hours and a dry crude protein was obtained. The dry protein was treated in the same manner as the dry plant material used for matric water determination.

In the second method, sugar beet leaves were frozen in liquid nitrogen and then ground, while frozen, using a mortar and pestle. After avaporation of the nitrogen, part of the slurry was placed in the pressure membrane apparatus for direct matric water determination for the whole leaves. The remainder was squeezed and filtered through a small bag of cloth lawn, using pressure of 2000 pounds per square inch in hydraulic press. Then the juice (crude protein) was taken directly to the pressure membrane apparatus for matric water determination.

The matric water values of several protein and carbohydrate biocolloids, including casein, gelatin fibrous cellulose, and agar, were studied also. The dry powders of these biocolloids were moistened until saturated with distilled water for several hours and then transferred to the pressure membrane apparatus for matric water determination.

Cell wall isolation

Spinach leaves were used for the extraction of cell wall material. Excised leaves were divided into two comparable halves with the midribs removed. One set was used for cell wall isolation and the other was used for direct matric water determination of the whole leaves.

The residue from the first step in protein extraction was collected and washed with distilled water. Then ethanolamine was added and homogenized with the residue in a Waring Blender and centrifuged. This procedure removes the cytoplasm from the cell wall (Gaff and Carr, 1961) and, presumably, removes any protein constituent present in the wall.

The residue was subjected to this treatment repeatedly until, on centrifuging, the supernatant ethanolamine was light in color. The residue was washed several times with distilled water and centrifuged. Then the residue, which consisted mainly of cell wall material, was taken directly to the pressure membrane apparatus for matric water determination.

Nomenclature

Morphological and floral characteristics were used to identify the plant species. The binomial system and the authority for each species follows Holmgren (1972), Bailey (1949), Higgins (1960), and Holmgren and Reveal (1966). Complete names and authorities of species studied are given in the result section. For convenience, in the text they will generally be referred to by generic name or common name.

Statistical analysis

An analysis of variance was conducted to determine any significant differences among the different treatments, using formulas given in Scheffe (1959) and Ostle (1963). Several regression analyses of variance were conducted and the regression lines were determined. The correlation coefficients for the regression analysis were obtained.

RESULTS

Effect of season and age on matric water
and water content

The seasonal matric water trends of different trees were similar in all species studied (Fig. 2, Table 2, and Table 8 (see Appendix for Table 8)).

In the first year growth of conifer leaves both the matric water and the original water content were highest in the spring while the needles were young and still expanding (Table 2 and Fig. 2). Both values dropped sharply between June 15 and July 22, during which time the needles nearly reached their mature size, and continued to drop during the remainder of the first season. Midwinter values (December) did not appreciably differ from fall values.

In the second and fifth years the matric water and moisture content of conifer leaves declined slightly. Nor did they change significantly throughout the season.

In pine leaves the basal part is meristematic and through most of the first growing season, affording an opportunity to compare the matric water of this basal, elongating portion of the needles with the tip, more mature portions. Although the base contained higher water content in June and July of the first year than the tip, the matric water content was not significantly different. Both showed the same seasonal and yearly trend characteristics of other conifers.

Table 2. The effects of age and season on the matric water and the original moisture content of the leaves

Plant species	Date	Age (year growth)	H ₂ O %		20 bar matric water	Matric bound water
			Fresh weight basis	Dry weight basis		
<i>Picea pungens</i> (Lambert.) Engelm.	6-15-1970	First	80	404	166	41
		Second	47	89	66	74
		Fifth	41	81	59	73
	6-26-1971	First	73	248	123	50
		Second	55	121	72	59
		Fifth	51	103	70	68
	7-21-1970	First	63	169	89	52
		Second	55	123	76	62
		Fifth	51	105	68	65
	9-13-1970	First	59	144	88	61
		Second	55	122	71	58
		Fifth	52	107	71	66
	12-25-1970	First	59	140	72	52
		Second	57	130	70	54
		Fifth	54	116	79	68
12-17-1971	First	58	135	79	58	
	Second	54	118	73	62	
	Fifth	53	111	82	74	
<i>Abies lasiocarpa</i> (Hook.) Nutt.	6-24-1970	First	72	259	137	53
		Second	48	94	105	112
		Fifth	45	82	79	96
	6-19-1971	First	65	185	123	67
		Second	45	81	95	118
		Fifth	43	75	101	135
	7-20-1970	First	67	199	115	58
		Second	53	114	83	73
		Fifth	52	108	83	77
	9-12-1970	First	53	111	100	90
		Second	50	100	85	86
		Fifth	47	88	109	123
	12-31-1970	First	55	121	103	85
		Second	53	113	100	89
		Fifth	51	104	87	83
12-18-1971	First	55	122	114	93	
	Second	55	121	121	100	
	Fifth	50	99	116	117	
<i>Pseudotsuga pensil-</i> <i>vica</i> Mirb.	6-24-1970	First	75	298	105	35
		Second	47	88	73	83
		Fifth	41	70	77	110
	6-19-1971	First	61	156	83	100
		Second	41	70	70	100
		Fifth	37	58	63	108
	7-20-1970	First	64	178	103	58
		Second	47	90	81	91
		Fifth	42	73	76	104
	9-12-1970	First	55	121	84	69
		Second	50	100	68	68
		Fifth	44	80	86	108
	12-24-1970	First	54	118	71	60
		Second	51	103	71	69
		Fifth	47	89	70	80
12-18-1971	First	55	120	70	58	
	Second	53	113	79	70	
	Fifth	48	92	77	84	

Table 2. Continued

Plant species	Date	Age (year growth)	H ₂ O %		20 bar metric water	Metric bound water
			Fresh weight basis	Dry weight basis		
<i>Pinus ponderosa</i> Laws.	6-18-1970	First base	77	344	121	35
		tip	70	230	124	54
		Fifth	50	101	78	77
	6-26-1971	First base	76	314	132	42
		tip	67	202	106	52
		Fifth	52	110	68	62
	7-22-1970	First base	73	253	107	42
		tip	61	156	93	60
		Fifth	52	106	72	68
	9-13-1970	First base	56	127	72	57
		tip	58	138	79	57
		Fifth	50	99	72	73
	12-25-1970	First base	55	119	73	62
		tip	55	123	80	65
		Fifth	53	114	77	67
	12-17-1971	First base	56	126	69	55
		tip	55	140	70	56
		Fifth	53	115	95	83
<i>Acer Negundo</i> L. var. <i>interius</i> (Britt.) Sarg.	6-30-1970	Buds	75	304	219	72
		Young leaves	77	329	235	71
		Mature leaves	74	279	130	47
	6-30-1971	Buds	73	266	218	82
		Young leaves	76	310	260	84
		Mature leaves	71	239	159	67
	7-30-1970	Young leaves	76	323	257	80
		Mature leaves	71	230	119	52
	9-14-1970	Young leaves	74	278	207	74
		Mature leaves	67	198	121	61
	9-24-1971	Young leaves	74	282	246	86
		Mature leaves	66	191	155	81
<i>Populus tremulo-</i> <i>ides</i> Michx.	6-23-1970		70	232	112	48
	6-19-1971		76	307	143	47
	7-20-1970		60	149	105	71
	9-12-1970		53	112	108	96
	9-25-1971		65	188	119	63

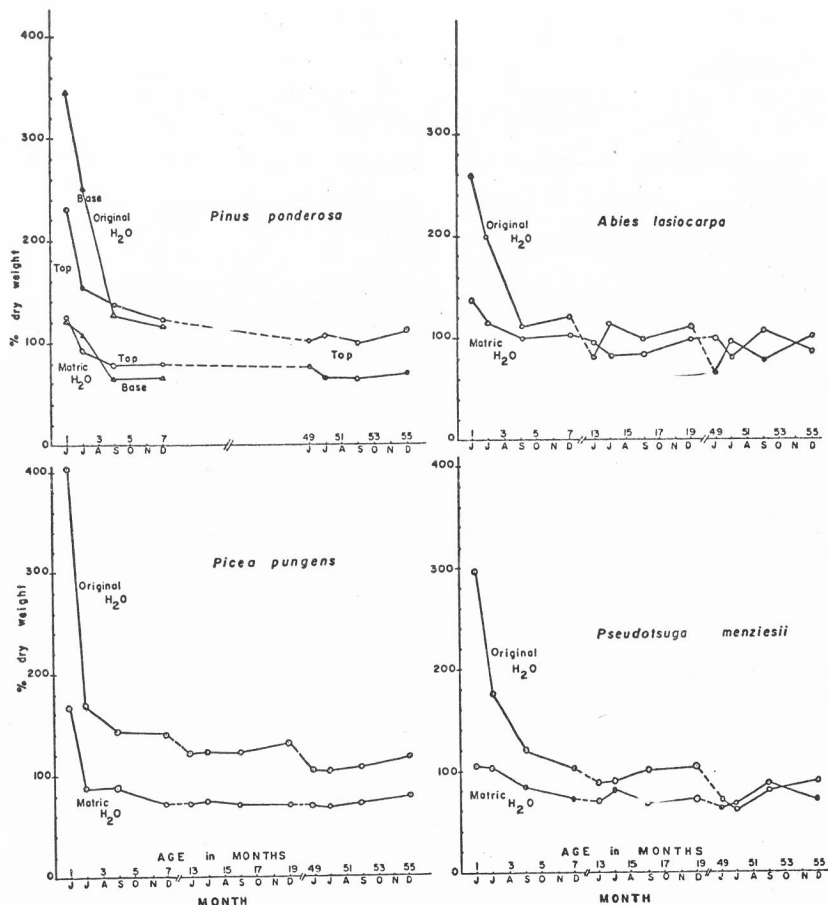


Figure 2. Matric water and the original moisture content in relation to age in coniferous trees.

In Box Elder both matric water and original water content were higher in young leaves than in old leaves, while buds had intermediate values. There was a slight decline in matric water through the summer. Box Elder produces new leaves throughout the summer, those produced in spring had higher fresh and matric water contents than those formed later (Fig. 3). Matric water constituted somewhat more than half of the leaf water content.

The moisture content of Aspen leaves was also high in the spring, dropped sharply during the summer and continued to decrease until autumn (Fig. 3). Similarly, the matric water was also higher in spring and dropped, but not sharply, in summer and continued to decrease when the leaves reached the mature stage in September. Matric water accounted for about half of the total in June, and somewhat more than half in September.

Regression analysis

The regression analysis of variance was used to study the relations between the variables matric water (Y), moisture content, and age. The following equation was used in determining if any linear relation existed between matric water or original moisture content and age.

$$Y = b_0 + b_1 X.$$

Where b_1 is an arithmetic coefficient, b_0 is a constant, and X is the moisture content of the leaves. A highly significant linear relation was found between the matric water and the moisture content in all species studies (Table 3). The straight lines of the species, which related the matric water

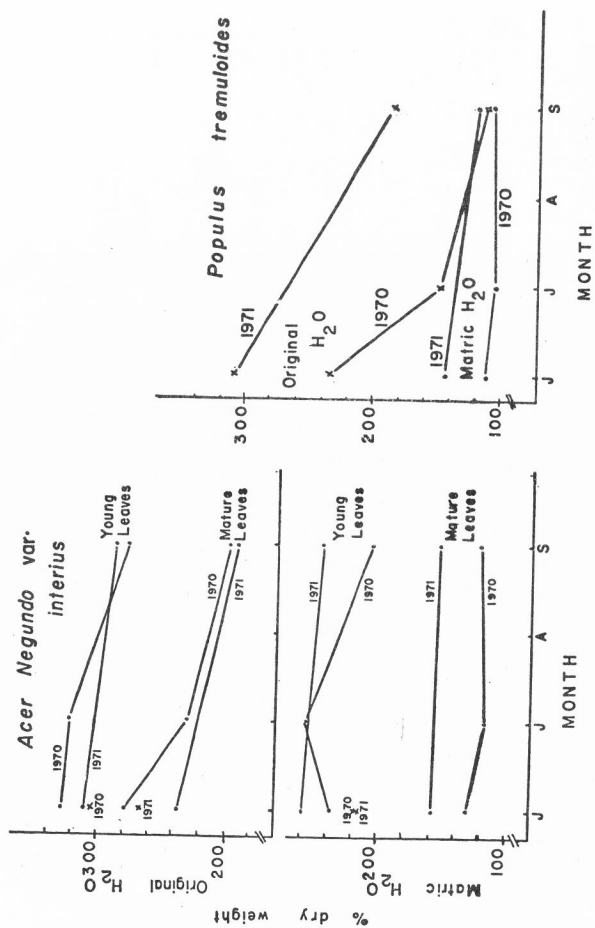


Figure 3. . Matric water and the original moisture content in relation to age in deciduous trees.

Table 3. Regression analysis of variance showing the effect of age and season on the matric water and moisture content

Plant species	Number of observations	Relations between the three variables, matric water, moisture content, and age	Correlation coefficient (r)	Tabulated F value at 95% significant
Linear relation between matric water (Y) and moisture content (X) described by the following equation: $Y = b_0 + b_1 X$				
<i>Picea pungens</i>	18	$Y = 35.06 + 0.33 X$	0.98	404.75
<i>Abies lasiocarpa</i>	18	$Y = 74.92 + 0.23 X$	0.69	14.11
<i>Pseudotsuga menziesii</i>	18	$Y = 60.39 + 0.16 X$	0.79	25.69
<i>Pinus ponderosa</i>	18	$Y = 48.14 + 0.25 X$	0.91	73.61
<i>Acer negundo</i>	12	$Y = -58.21 + 0.94 X$	0.80	18.07
<i>Populus tremuloides</i>	5	$Y = 82.88 + 0.18 X$	0.87	9.17
All observations	89	$Y = 33.63 + 0.45 X$	0.79	141.65
Linear relations between the matric water (Y) and the inverse or inverse square of the age (X) (number of months for the leaves been on the tree), described by the following equation: $Y = b_0 + b_1/X + b_2/X^2$				
<i>Picea pungens</i>	12	$Y = 70.57 + 94.82/X^2$	0.98	193.66
<i>Abies lasiocarpa</i>	12	$Y = 89.90 + 48.00/X$	0.83	22.74
<i>Pseudotsuga menziesii</i>	12	$Y = 73.78 + 35.66/X$	0.84	28.08
All observations	36	$Y = 75.90 + 58.24/X$	0.77	49.79
Linear relations between the moisture content (Y) and the inverse or inverse square of the age (X), described by the following equation: $Y = b_0 + b_1/X + b_2/X^2$				
<i>Picea pungens</i>	12	$Y = 111.48 + 290.11/X^2$	0.98	251.74
<i>Abies lasiocarpa</i>	12	$Y = 92.49 + 171.51/X$	0.97	144.72
<i>Pseudotsuga menziesii</i>	12	$Y = 76.99 + 216.71/X$	0.99	497.94
All observations	36	$Y = 87.28 + 222.14/X$	0.93	231.21

and the original water content, are shown in Fig. 4. No significant linear relation was found between either matric water or original moisture content and age.

Plotting the matric water or the original moisture content with age in Fig. 2 also illustrated the non-linear relations. Plotting the matric water or the original moisture content with the inverse of age (Fig. 5), however, gave a significant linear relation. Another regression analysis of variance was used to test the relations between the matric water (Y) or the original moisture content (Y) and the inverse or the inverse square of age (X), using the following equation:

$$Y = b_0 + b_1/X + b_2/X^2$$

where b_0 is a constant, b_1 and b_2 are arithmetic coefficients. High significant relations were found in all species tested between the matric water or the moisture content and inverse of age as shown in Table 3. In Picea the relations were more significant with the inverse square of age.

Matric water of different plant parts

Both matric water and total water content were consistently higher in petioles than in leaf blades for Sunflower, Geranium, Malva and Box Elder (Fig. 6). The reason for this is not yet apparent; presumably the blade has a higher porportion of lipoidal material such as cuticle and chloroplasts which would contribute to the dry weight, but not to matric water holding forces.

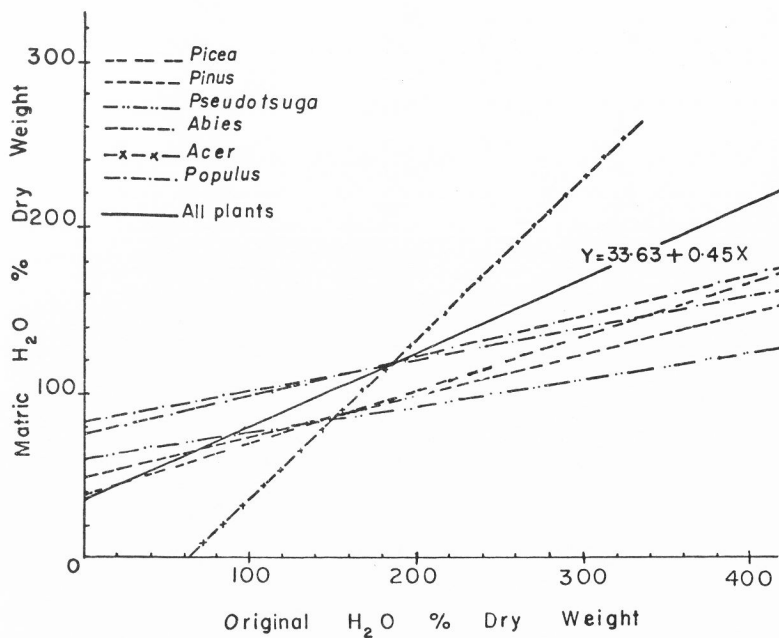


Figure 4. Regression lines of several trees illustrating the relation of matric water to original moisture content of the tree leaves.

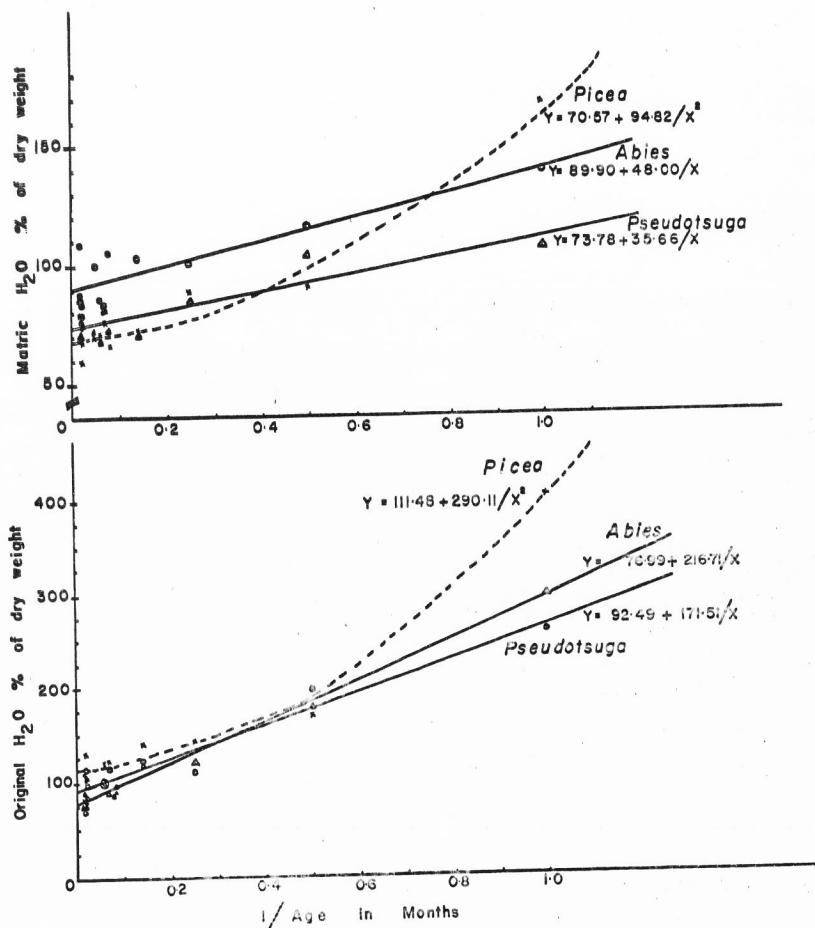


Figure 5. Regression lines illustrate the relations of matric water and original moisture content of conifer leaves to the inverse of their age in months.

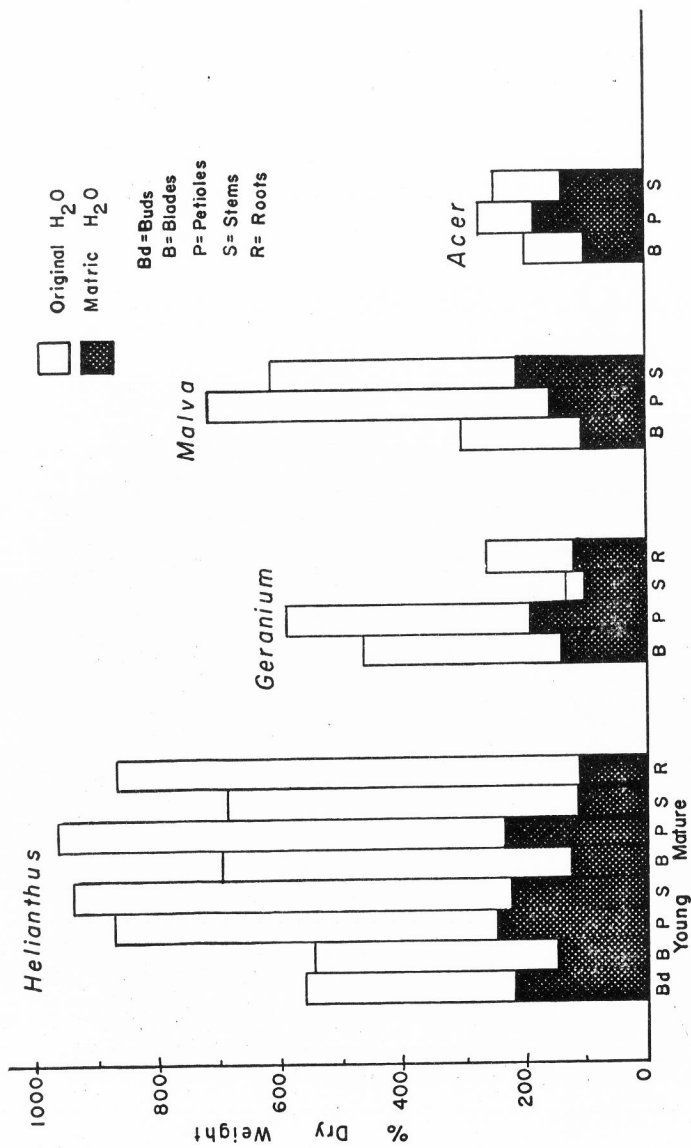


Figure 6. Matric water and the original moisture content of different parts of *Helianthus*, *Geranium*, *Malva*, and *Acer*.

Stem matric water values were more variable, being higher than petiole values in Malva, but lower in the other species. Root values, where studied, were about the same as stem values (Fig. 6 and Table 4).

Three species were studied for the comparison between the matric water of their leaves and flowers. The matric water values of the flower parts were higher than the leaves (Table 4). This difference in matric water values was significant, except in the case of Alfalfa.

The water storage tissues of the two succulent plants were higher in their matric water and moisture content than in the mesophyll or the cuticle portion. A significant difference among the three parts was found in Gasteria plant but was not significant in Opuntia plant. The values of the matric bound water values were very similar in both species for all three parts.

In all plants studied, the highest moisture content was found to be 98 percent as a percentage of fresh weight which was associated with the water storage tissues of Gasteria. On the other hand, the highest matric water was found to be 747 which was associated with kelp stipe.

The replicated values of matric water for all plant parts are given in Table 9 (see Appendix).

Temperature hardiness and moisture stress in Sunflower

The matric water and the original moisture content of Sunflower leaves were determined under four different temperatures ranging 10 C-40 C, and shown in Table 5 and Table 10 (see Appendix for Table 10).

Table 4. Matric water and the original moisture content of different plant parts

Plant species	Part of plant	Repl- cate	H ₂ O %		20 bar Matric water	Matric Bound water
			Fresh weight basis	Dry weight basis		
<i>Helianthus annuus</i> L.	Buds	1*	87	641	205	32
		2**	83	480	231	48
	Top 4 cm:					
		Leave blades	1	87	691	158
	Leave petioles	2	80	411	140	34
		1	91	1023	242	24
	Stems	2	88	714	254	36
		1	92	1085	105	19
	Base 4 cm:					
		Leave blades	2	89	768	237
	Leave petioles	1	90	881	118	13
		2	83	498	138	28
	Stems	1	92	1101	193	18
		2	89	820	270	33
	Roots	1	90	855	108	13
		2	84	512	125	24
	F ratio	1	91	1057	125	12
Tabulated F ⁺	2	87	689	101	15	
				13.1		
				3.79		
<i>Geranium Frenconii</i> Torr.	Leave blades		82	464	137	30
	Leave petioles		86	589	189	32
	Stems		57	132	101	77
	Roots		73	256	114	44
F ratio				75.66		
Tabulated F ⁺				4.07		
<i>Malva rotundifolia</i> L.	Leave blades		75	298	95	32
	Leave petioles		88	711	151	21
	Stems		86	609	218	36
F ratio				32.87		
Tabulated F ⁺				5.14		
<i>Acer platanoides</i> L.	Leave blades		66	196	93	48
	Leave petioles		73	274	185	57
	Stems		71	242	132	55
F ratio				83.31		
Tabulated F ⁺				5.14		
<i>Cynoglossum officinale</i> L.	Flowers		85	552	310	56
	Leaves		85	556	208	37
F ratio				88.17		
Tabulated F ⁺				7.71		
<i>Medicago sativa</i> L.	Flowers		79	380	160	42
	Leaves		75	292	151	52
F ratio				2.65		
Tabulated F ⁺				7.71		
<i>Mellilotus officinalis</i> (L.) Lam.	Flowers		76	323	176	54
	Leaves		76	324	141	43
F ratio				51.15		
Tabulated F ⁺				7.71		
<i>Opuntia fragilis</i> (Nutt.) Haw.	Cutical		82	443	87	20
	Mesophyll		90	870	75	9
	Water storage tissue		95	2070	89	4
F ratio				1.04		
Tabulated F ⁺				5.14		
<i>Gasteria verrucosa</i> (Mill.) Duv.	Cuticle		81	433	191	21
	Mesophyll		90	938	120	13
	Water storage tissue		98	4271	152	4
F ratio				288.08		
Tabulated F ⁺				5.14		
Kelp stipe		92	1134	747**	66	

* Plants were harvested on Jan 23, 1972; ** Plants were harvested on May 24, 1972
⁺ Tabulated F on 95% significant; ** Average of three readings 702, 766, and 773

Table 5. Matric water determination under water stress and different temperature regimes in sunflower plants

Temperature treatment day:night	Replicate	H ₂ O %		20 bar water	Matric water	Matric Bound water
		Fresh weight basis	Dry weight basis			
Moisture conditions 10:8	1*	84	533	143		27
	2**	80	404	137		54
20:16	1	82	444	121		27
	2	83	499	129		26
30:25	1	84	523	128		25
	2	82	468	149		32
40:33	1	86	616	131		21
	2	84	510	142		28
F ratio for above treatments						
Tabulated F ⁺					1.46	
Water stress condition						
30:25	1	87	678	129		19
	2	81	424	158		37
40:33	1	87	642	126		20
	2	83	478	132		28
F ratio for dry vs moist treatments						
Tabulated F ⁺					2.67	
					161.00	

*Plants were harvested on Feb 11, 1972; ** Plants were harvested on May 29, 1972

+ Tabulated F on 95% significant

In the two time replications, the lowest values of matric water were associated with the 20 C moisture treatment (Fig. 7). No significant differences, however, were found by simple analysis of variance among the different temperature treatments.

Moisture stress had variable, statistically insignificant, influence on matric water (Table 5).

Cold hardiness, photoperiod and moisture stress in Cabbage

The matric water values of buds were significantly higher than those of leaves in all treatments. In addition, the moisture content in buds tended to be higher than that of leaves (Table 6 and Table 11 (see Appendix for Table 11)). The proportion of water bound by matric forces was as expected higher in buds than in leaves.

The matric water values in buds under cold treatment were higher than those under warm treatment, but because of variability among the different treatments, were not significantly different at the 95 percent level.

The higher matric water values in leaves were associated with cold treatment and were significantly different from those under the warm treatment (Table 6).

In warm treatment, the matric water values of leaves under the short day condition were somewhat higher than under the long day condition, but this difference did not reach statistical significance.

Under the moisture stress, the leaves had higher, but not significantly different matric water from those under moist conditions.

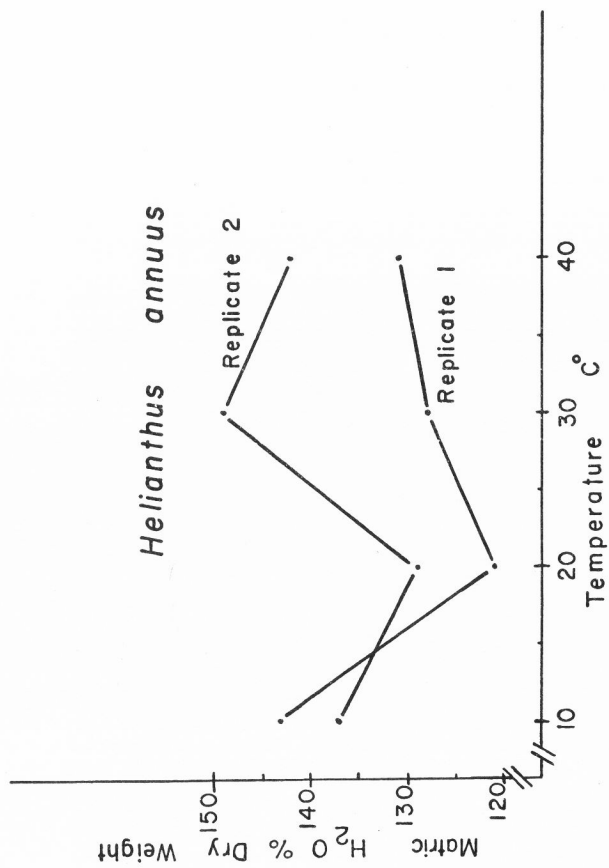


Figure 7. Matric water of Sunflower leaves at different temperatures.

Table 6. The relations of matric water to cold hardiness, photoperiod, and water stress in cabbage

Part of plant	Treatment	Repl- cate	H ₂ O %		20 bar matric water	Matric bound water	Tabulated F at 95% signifi- cant	
			Fresh weight basis	Dry weight basis				
Buds	Control	1*	87	659	438	67		
	Warm, SD	2**	87	655	543	83		
		3*	89	773	493	64		
		Average		88	682	491	71	
		Cold, SD	1	85	558	469	84	
	Cold, SD	2	84	539	586	108		
		3	85	568	493	87		
		Average		85	555	516	93	
		Warm, LD	1	87	649	453	70	
	Warm, LD	2	87	645	433	66		
		3	84	544	455	89		
		Average		86	613	447	75	
		SD, Under stress	2	84	517	469	91	
	SD, Under stress	3	86	635	470	74		
		Average		85	576	470	83	
		LD, Under stress	2	81	426	444	104	
	LD, Under stress	3	82	457	418	91		
		Average		82	442	431	98	
F ratio s:								
Cold vs Control					0.89	18.5		
LD vs Control					2.50	18.5		
Dry vs Moist					9.58	161.0		
Leaves	Control	1	87	640	169	26		
	Warm, SD	2	84	517	179	36		
		3	83	482	151	31		
		Average		85	546	166	31	
		Cold, SD	1	86	627	186	30	
	Cold, SD	2	85	554	238	43		
		3	84	524	230	44		
		Average		85	568	218	39	
		Warm, LD	1	81	432	153	35	
	Warm, LD	2	82	449	163	36		
		3	74	282	152	54		
		Average		79	388	156	42	
		SD, Under stress	2	85	567	191	34	
	SD, Under stress	3	82	451	158	35		
		Average		84	509	175	35	
		LD, Under stress	2	81	426	181	43	
	LD, Under stress	3	77	375	150	46		
		Average		79	375	166	45	
F ratio s:								
Cold vs Control					90.02	7.71		
LD vs Control					0.26	10.10		
Dry vs Moist					10.02	161.00		

* Plants were harvested at April 16, 1972; ** Plants were harvested at April 29, 1972

† Plants were harvested at September 7, 1972

Matric water of crude protein and
cell wall materials

The crude protein extracted from the spinach leaves had higher matric water values than the pure cell wall material (Table 7). On the other hand, higher matric water values were found for the crude cell wall, which were comparable to that of whole leaves. There were no appreciable differences between the crude protein extracted from the sugar beet leaves and the whole leaves in their matric water values.

The matric water values of the proteins casein, gelatin, and gluten, were similar to the values found in the crude proteins extracted from the spinach and sugar beet leaves. The cellulose had low matric water, while agar had a high value (Table 7).

Table 7. Matric water of crude protein and cell wall material of plant leaves

Plant species or Biocolloids	H ₂ O %		Repli- cate	Matric water			
	Fresh weight basis	Dry weight basis		Whole leaves protein	Crude cell- wall	Pure cell wall	Biocolloids
<i>Spinacia oleracea</i> L.	89	824	1	78	70	71	66
	85			85	75	75	70
			2	88	79	90	73
<i>Beta vulgaris</i> L.			3	90	80	90	75
				100	82	96	80
				104	99	119	83
			Average	91	81	90	74
	88	733	1*	112	121		
				96	155		
			2**	124			
Casein				126			86
Gelatin				124			82
Gluten				149			124
Fibrous cellulose							157
Agar							90
							100
							25
							26
							294
							319

* Matric water determined by the drying usual method. ** Matric water determined by using leaves frozen in liquid nitrogen

DISCUSSION

For deciduous and conifer leaves less than one year in age, the high moisture content found in early spring dropped during the summer and continued to drop for the remainder of the season. The same results were found by other investigators (Grandfield, 1943; Ackley, 1954). However, Meyer (1928) found relatively little change in the water content of pitch pine leaves from July 27 (59.4 percent) to October 29 (63 percent). In the present works, there were no appreciable differences in the moisture content of conifer leaves between one and four years of age throughout the entire season (June to December).

The high matric water values in deciduous and conifer leaves in early spring may be a function of a higher ratio of hydrophilic/hydrophobic colloidal materials in enlarging cells. These hydrophilic colloids are capable of adsorbing water molecules and increase the matric holding capacity of the leaves. Newton and Gortner (1922) showed that the percentages of bound water calculated by a freezing point depression obtained with gum acacia sols increased regularly with the concentration of the sols.

Information dealing with the effect of age and season on the matric or bound water of the leaves is limited. Meyer (1932) studied the seasonal variation of pine-leaf tissue collected in Ohio and its effect on bound water, as calculated by the calorimetric method. He found no appreciable differences in the bound water of pitch pine leaves between August and January. In the present work, there were no significant differences in matric water

values for conifer leaves between one and four years of age throughout the season.

During the spring while the leaves were young, much of the water content was held by other than matric forces, i. e., osmotic forces. However, in late season (December) most of the leaf water content was held mainly by the matric forces in all species studied. This higher proportion of water being held by matric forces may be explained by the lower moisture content of late summer leaves, which generally gives a higher ratio of matric water to total water.

In a previous study (Al-Saadi and Wiebe, In Press), a positive correlation was found between the matric water and the original moisture content of leaves from a wide range of species. In the present study the same relation was found, also with very high correlation coefficient values, reaching 0.98 in some species. The high correlation found between the matric water and moisture content of the leaves may be due to the fact that larger matric water forces cause more water molecules to be retained in the particular tissue and which are a part of the total water content. In the interest of establishing this relation as an arithmetic expression, all the observations from six species, four conifer and two deciduous trees, were combined and a regression analysis of variance was conducted. The linear relation between the matric water and original moisture content is represented in the following equation

$$Y = 33.63 + 0.45 X$$

where Y is the matric water and X is the original moisture content of the leaves, and both variables are expressed on the basis of leaf dry weight. From this relation we may conclude that the matric water values are lower than the original moisture content of the leaves when both are expressed on the leaf dry weight basis. This was found to be true in all the cases studied.

By knowing this information, we might generalize and apply the above equation to give a rough estimation value of the matric water simply by knowing the original moisture content of certain leaves. This relation could be applied for several species, especially for the coniferous and deciduous trees which have been studied in this work as well as those of the previous work (Al-Saadi, 1970).

I also established a linear relationship between the matric water and the inverse of age in months

$$Y = 75.99 + 58.24/X$$

where Y is the matric water and X is the age in months.

Because of the high correlation between the matric water and the original moisture content, it is possible to predict that the inverse of age should also be related to the original moisture content as well. This is confirmed by the following equation

$$Y = 87.28 + 222.14/X$$

where Y is the original moisture content and X refers to the age in months.

With the approach of maturity the moisture content of leaf tissue decreased rather rapidly in Sunflower and Soybean plants (Greathouse, 1932). In the present study the same conclusion was found for all conifer trees as well as for Box Elder and Sunflower plants.

After studying several species, it became well established that the highest matric water values as well as the highest original moisture content were found in leaf petioles. This may be due to a higher hydrophilic colloidal material build up in the petioles, specially the polysaccharides which may be involved in the support function in collenchyma. The leaf blades would have a higher proportion of lipoidal materials such as cuticle and chloroplast material which would contribute to the dry weight, but not to matric water holding forces. The influence of leaf blade proteins in increasing matric water was apparently more than over balanced by the above non-hydrophilic substances.

Both Sunflower and Cabbage had higher values of matric water and moisture content in buds than in leaves, probably due to a higher protein level in the buds.

Roots had the lowest matric water values among the plant parts. Old stems also had low matric water values. These low values for matric water in old stems may be due to lignins. Lignins may play a similar role in the large roots sampled.

Flower buds had higher matric water values than leaves for all species studied, probably because of the high concentration of proteins found in them.

Cactus and Gasteria juices were extremely viscous and difficult to press out, suggesting a high colloidal content (Newton and Martin, 1930). This was, however, not confirmed by matric water measurements which would suggest a very low colloidal capacity for holding water in these succulents. The osmotic potential of water storage is generally also low. Water retention in cells is generally attributed to osmotic and matric forces (Newton and Martin, 1930), but neither seems as important in these succulents as in the other species studied. Cactus is known to have a wide spreading but very shallow root system which enables it to absorb water quickly after a rain. Since the soil water after a rain is held at high potentials, plant water potentials do not need to be very low in order to absorb this water from the soil. However, two other properties of succulents may be important in water storage: 1. thin walled cells capable of extreme and rapid enlargement as they absorb water and 2. a very effective cuticle, plus physiological adaptations such as crassulacean metabolism and the daytime closure of stomates which conserve water.

Among all the plant parts studied, the highest original moisture contents were associated with the water storage tissues of the two succulent plants, Opuntia and Gasteria. Similar high moisture contents were also reported by Henkel (1964) in several succulent plants.

Briggs (1932) studied several colloidal materials and obtained the highest values of bound water with agar, a carbohydrate material similar in composition to kelp stipe; which may be taken as evidence that kelp stipe has a relatively high water-binding capacity. In this study the highest

matric water value found was also associated with kelp stipe and equaled more than two times the value found for agar.

The slight increase in matric water in Cabbage plants, when subjected to periodical wiltings, may suggest the increase of hydrophilic colloids, although this increase does not reach significant levels. The Sunflower responses were similar to those found in Cabbage under moisture stress, except under high temperature (40 C), where the reverse response was found. High temperature may affect the synthesis of some hydrophilic colloids. Carr and Gaff (1961) concluded that in the drought-hardening of plants there is an increase of the amount of cell wall and the hardening process may consist essentially in the development of greater wall-water capacity. Greathouse (1932) also found that the bound water in Cabbage and Milo leaves increases under reduced soil moisture or drought conditions. Several researchers reported the positive relationship between the bound water in leaves of several species and the corresponding drought resistances (Rosa, 1921; Newton and Martin, 1930; Shchukina, 1965). Conversely, other investigators did not find any relationship between bound water and drought resistance (Schopmeyer, 1939; Whitman, 1941; Kushnirenko, 1964, Al-Saadi and Wiebe, In Press).

In 1955, Kramer concluded that the attempts to explain cold and drought resistance of plants as the results of high bound water content were not satisfactory. He also added that changes in bound water content usually result from changes in total water content and in chemical composition and are not themselves the cause of cold or drought resistance. In the present

study, a marked increase in the matric water values were found when the Cabbage plants were exposed to a cold temperature (+4 C). This increase in water-retaining power of the tissue is due primarily to an increase in the imbibitional forces of the cell. Rosa (1921) found that pentosans accumulate in Cabbage and other vegetables during the "hardening off" process, and that this accumulation may be brought about by exposure to low temperature. Bound water or water-retaining power, was found to be positively correlated with cold hardiness in several species by Rosa (1921), Greathouse (1932), Stark (1936), Grandfield (1943), and Levitt (1959). However, other investigators did not find any relationship between bound water and cold hardiness (Steinmetz, 1926; Weimer, 1929; Meyer, 1932).

Gelatin had rather high matric water value among the biocolloidal proteins studied. Wiebe (1966) obtained similar values of matric water in gelatin.

Pure cellulose was found to have a low matric water value. Filter paper, which consists of cellulose fibers, has a similarly low matric water value (Wiebe, 1966). The matric water of extracted cell wall material was three times as high as that of extracted cellulose, although it was lower than matric water of crude protein. Leaf cell wall materials consist of, in addition to cellulose, pectins and other polysaccharides, as well as hemicellulose which may have a higher water retaining power.

The matric water values for the crude protein extracted from spinach leaves were consistent with the findings for casein and gluten, while the values of matric water for crude protein extracted from sugar beets agreed very much

with the values of matric water for gelatin. It may be concluded from this that different species may have different abilities to retain water in respect to the protein composition in the leaf tissues.

Most of the matric potential in the leaves was attributed to the cell walls (Kramer, 1955; Boyer, 1967). Kramer (1955) concluded that because much of the bound water in plants occur in the cell wall, it can scarcely affect the protoplasm, and water held so firmly that it cannot function as a solvent can scarcely take part in physiological processes.

In studying the effects of hydration on physiological processes such as photosynthesis, respiration, stomatal movements, etc., it is clear that the water status of the protoplast rather than that of the whole leaf (including as it does the water of the cell walls) is the operative factor, although the cell wall water may be involved in affecting rates of diffusion through the cell wall. (Gaff and Carr, 1961).

The hydrated cell wall serves as a buffer against loss of water from the protoplast during temporary adverse conditions. The thicker the cell wall, the greater the buffering effect of the wall against unfavorable, transient forces (Gaff and Carr, 1961). They estimated that as much as 40 percent of the cell water content in Eucalyptus leaves may be found in the cell wall.

Although the matric potential in most fresh plant tissues does not exceed value of -1 bar (Boyer, 1967), in certain cases it may reach extremely low values, especially in dry seeds (Shull, 1924) and gels (Levitt, 1954).

In conclusion, the matric water of the leaves is related positively to the inverse of their age in deciduous and conifer trees. The matric water

was found to be related to cold hardiness in Cabbage and also, though not significantly, to moisture stress in Cabbage and Sunflower. The changes in water binding forces, or matric water, during the cold hardiness or moisture stress conditions may be due to the changes in the amount of hydrophilic colloidal materials which account for water binding in plants.

SUMMARY

Matric water was measured as the water retained by plant material on a pressure membrane or ultra filter after equilibration under 20 bars nitrogen gas pressures and the removal of free water. At increasing pressures lesser amounts of water are held by matric or colloidal surface forces. Twenty bars pressure, supplied by cylinder nitrogen for 48 hours, was used in this study. Matric water was expressed as a percent of either (a) the dry weight or (b) the original water content. Plant material was oven dried, ground, and then saturated with water prior to the determination.

The matric water values of different aged leaves from a number of local species were studied. The highest values of matric water were found in the younger leaves. Both matric water and original moisture content were higher for spring than for fall or midwinter. The linear relationship between matric water and original moisture content was established for all trees studied. Another linear relation was found between either the matric water or the water content of the tree leaves and the inverse of their age in months.

Petioles had a higher matric water value as well as the water content than leaf blades in all the species studied. Roots and old stems had the lowest values of matric water.

The matric water values increased during the cold hardening of Cabbage leaves. No appreciable differences in the matric water values for Sunflower leaves grown under different temperatures were found.

The crude protein and the cell wall materials were isolated and their matric water values studied. Crude proteins had a higher value of matric water. The matric water values of several biocolloidal materials were determined also. Agar had the highest value of matric water, fibrous cellulose the lowest, and the proteins had intermediate values.

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APPENDIX

Table 8. The replicated values of metric water in relation to age and season
 a. *Fagus*, *Abies*, and *Fraxinifera*

Plant species and location	Date of collection	Metric water		
		First year growth	Second year growth	Fifth year growth
<i>A. Fagus PURGURUS</i> (Leinert) Engelm Near Utah State University Logan, Utah.	6-15-1970	168	66	61
		169	64	64
		162	63	61
	6-26-1971	113	71	68
		134	76	76
		121	69	66
	7-21-1970	94	76	75
		85	76	63
		87	76	66
	9-13-1970	88	73	76
		87	66	71
		90	72	66
12-25-1970	71	73	71	
	64	71	81	
	79	65	87	
12-17-1971	85	74	87	
	77	75	80	
	74	70	78	
<i>Abies LEUCOCARPA</i> (Hook) Nutt. Logan Canyon, 33 miles north Logan, elevation about 7000 feet	6-24-1970	131	106	73
		140	104	83
		141	104	80
	6-19-1971	120	95	101
		127	95	101
		123	96	101
	7-20-1970	112	87	88
		117	78	82
		115	83	79
	9-12-1970	103	93	103
		93	77	104
		104	86	119
12-31-1970	105	99	89	
	96	93	85	
	111	109	87	
12-18-1971	106	121	116	
	121	132	124	
	114	110	107	
<i>Fraxinifera macrantha</i> Nutt. Logan Canyon, 33 miles north Logan, elevation about 7600 feet	6-24-1970	105	72	86
		108	75	76
		103	73	69
	6-19-1971	84	68	67
		83	76	61
		83	66	61
	7-20-1970	101	77	76
		106	80	75
		103	86	78
	9-12-1970	83	66	87
		86	66	78
		82	71	94
12-24-1970	71	66	66	
	71	68	63	
	72	77	76	
12-18-1971	66	72	76	
	70	92	82	
	73	72	71	

Table 8. Continued.

b. *Pinus*

Plant species and location	Date of collection	Metric water		
		First year growth		Fifth year growth
		Base part	Top part	Mature part
<i>B. Pinus ponderosa</i> Laws.	6-18-1970	122	124	87
		117	123	76
		125	124	71
Near Utah State University Logan, Utah.	6-26-1971	129	110	66
		127	104	73
		139	104	65
	7-22-1970	108	95	73
		99	95	69
		114	90	75
	9-13-1970	73	76	75
		73	82	77
		71	79	65
	12-25-1970	79	86	81
		75	82	81
		67	71	69
	12-17-1971	66	81	86
		73	78	98
		68	75	101

c. *Acer, Populus.*

Plant species and location	Date of collection	Metric water		
		Buds	Young leaves	Mature leaves
<i>Acer Negundo</i> L. var. <i>interius</i> . (Britt.) Sarg.	6-30-1970	217	243	134
		212	216	145
		229	245	111
Near Utah State University Logan, Utah.	6-30-1971	226	243	152
		223	237	166
		205	262	161
	7-30-1970		254	109
			283	123
			235	125
	9-14-1970		198	124
			219	122
			204	116
	9-24-1971		242	160
			243	158
			253	148
<i>Populus tremuloides</i> Michx.	6-23-1970			110
				109
				115
Logan Canyon, 30 miles north Logan, elevation about 8000 feet.	6-19-1971			137
				145
				147
	7-20-1970			109
				101
				105
	9-12-1970			108
				106
				109
	9-25-1971			121
				114
				122

Table 9. Replicated values of matric water of different plant parts

a. Helianthus

Plant species	Young (top 4 cms.)				Mature (base 4 cms.)			Roots
	Buds	Leaf blades	Leaf petioles	Stems	Leaf blades	Leaf petioles	Stems	
<u>Helianthus annuus</u> L.	196	151	223	208	129	204	105	126
1*	225	179	255	208	106	180	116	139
	195	145	247	199	119	195	102	110
	226	144	256	227	146	257	129	99
2*	221	130	257	227	137	289	127	104
	246	145	251	258	131	265	119	101

b. Geranium, Malva, Acer, Cynoglossum, Medicago, Melilotus, Opuntia, and Gasteria.

Plant species	Cuticle	Mesophyll	Water storage tissue	Flowers	Leaf blades	Leaf petioles	Stems	Roots
<u>Geranium Fremontii</u> Torr.					132	180	105	109
					137	186	93	111
					142	202	102	120
<u>Malva rotundifolia</u> L.					77	162	221	
					92	123	224	
					115	169	209	
<u>Acer platanoides</u> L.					98	187	126	
					79	179	137	
					107	188	133	
<u>Cynoglossum officinale</u> L.				315	229			
				309	199			
				306	196			
<u>Medicago sativa</u> L.				163	145			
				167	150			
				151	157			
<u>Melilotus officinalis</u> (L) Lam.				181	135			
				168	142			
				177	145			
<u>Opuntia fragilis</u>	90	77	85					
(Nutt) Haw.	72	69	107					
	101	81	75					
<u>Gasteria verrucosa</u>	95	135	144					
(Mill.) Duv.	106	114	161					
	72	110	151					

* See table 4. foot note

Table 10. Replicated values of matric water under water stress and different temperature regimes in sunflower plants

Replicate	Treatments					
	10M	20M	30M	40M	30D	40D
1*	124	108	110	120	132	126
	154	142	139	133	131	130
	150	114	135	140	125	122
2*	138	140	138	126	134	130
	139	124	151	154	150	143
	134	123	159	146	192	122

* See table 5 the foot note

Table 11. Replicated values of matric water of different treatments in cabbage

	Replicate	Cold	Warm				
			SD	Moist	LD	Dry	
				SD Control		SD	LD
Buds	1*	463	453	417			
		487	440	479			
		457	422	440			
	2*	605	514	474	436	465	
		531	517	396	493	421	
		615	598	430	479	447	
	3*	460	431	457	468	390	
		447	541	426	451	409	
		573	565	482	491	456	
Leaves	1	180	158	122			
		146	153	156			
		232	196	182			
	2	226	179	171	177	159	
		229	164	146	165	199	
		259	195	171	235	185	
	3	187	159	118	163	129	
		183	166	131	168	139	
		232	151	128	169	142	
		191	131	169	126	144	
		228	137	178	166	165	
		247	160	187	154	180	
		243					
		265					
	297						

* See table 6. the foot note

VITA

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List of Publications:

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Wiebe, H. H. , H. A. Al-Saadi, and S. L. Kimball. Photosynthesis in the anomalous secondary wood of Atriplex confertifolia stems. (To be published in Planta.)

Al-Saadi, H. A. , and H. H. Wiebe. Physiology of the armed parenchyma in conifer leaves. (In preparation.)

Al-Saadi, H. A. , and H. H. Wiebe. The effect of age and season on the matric water of plant leaves. (In preparation.)

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