

Isohydric and anisohydric characterisation of vegetable crops

The classification of vegetables by their physiological responses to water stress



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Summary

Research on the physiological response of crop plants to drying soils and subsequent water stress has grouped plant behaviours as *isohydric* and *anisohydric*. Drying soil conditions, and hence declining soil and root water potentials, cause chemical signals—the most studied being abscisic acid (ABA)—and hydraulic signals to be transmitted to the leaf via xylem pathways.

Isohydric responses occur when receptors in and around stomatal guard cells react to both these chemical and hydraulic signals to close stomata, and maintain leaf water potential, despite declining soil and root water potentials. The result is relatively constant leaf water potential, but declining stomatal conductance as the stomata are closed. Consequently, there is little initial relationship between soil water potential and leaf water potential.

By contrast, anisohydric responses occur when receptors and guard cells do not react to hydraulic signals, but instead leaf water potentials decline in sync with declining soil and root water potentials, with little initial control of stomatal conductance. In anisohydric behaviour, there is a good initial relationship between soil water potential and leaf water potential.

In deciding what plant-based measurements may be useful in making irrigation decisions, the above discussion is important. For example, it would be sensible to focus plant-sensing using leaf water potential on vegetables showing predominantly anisohydric behaviour. Another example may be the use of regulated deficit irrigation—predominantly anisohydric vegetables may be at greater risk of sudden yield or quality deterioration, due to their less regulated stomatal control.

Researchers have attempted to allocate crops as isohydric or anisohydric. However, different cultivars within crops, and even the same cultivars grown in different environments/climates, can exhibit both response types. Nevertheless, understanding which behaviours predominate in which crops and circumstances may be beneficial. This paper describes different physiological water stress responses, attempts to classify vegetable crops according to reported water stress responses, and also discusses implications for irrigation decision-making.

Introduction

Higher plants exhibit control over water loss from their tissues—referred to as ‘homeohydric’ (Buckley 2005). However, different physiological characteristics that dictate the degree of control over leaf water potential can help to classify plants as either isohydric (having tight stomatal control and a minimum threshold of water potential that cause stomata to close) or anisohydric (having loose stomatal control and no discernable threshold of water potential maintenance) (Maseda and Fernández 2006).

These characteristics are significant, as they influence the physiological responses observed during water stress, and can affect the methods best suited to monitoring water stress. Stomatal conductance of a plant experiencing water stress can be correlated with changes in soil water in some plants but not in others; leaf water potential may be only weakly correlated with soil water or not at all (Comstock 2002). Jones (2008a) suggests that pre-dawn water potential measurements can be used as an accurate indication of current water potential for both isohydric and anisohydric plants, as pre-dawn water potential is unaffected by stomatal conductance and evaporative demand.

The main method plants signal to control stomatal conductance is by abscisic acid (ABA), produced by roots experiencing negative and declining soil water potentials. ABA is transported by the xylem; receptors in the stomatal guard cells respond by reducing stomatal aperture (Tardieu and Simonneau 1998). Another chemical signal, pH, has been observed to affect stomatal conductance (Comstock 2002). An increase in xylem pH, increasing alkalinity, can concentrate ABA near the guard cell without any increases in ABA in the xylem. This too can signal the guard cell to close stomata.

Many authors have observed that a hydraulic signal can also have a controlling effect on stomatal conductance, and this is what divides the two categories. However, these distinctions are not always ‘clear cut’. Anisohydric plants can display ‘near-isohydric’ characteristics and even cultivars of the same species can display opposite characteristics (Jones 2007). Some grape cultivars can display isohydric characteristics, while others display anisohydric characteristics (Jones 2007). The purpose of this paper is to describe the attributes that define isohydric and anisohydric plants, to begin categorising vegetable crop plants, and to assign suitable methods of measuring water potential accurately to each.

Isohydic characteristics

Definition

The isohydic characteristics of plants are evident in the tight and continuous control of leaf water potential by root-to-shoot signalling of hydraulic *and* chemical interactions, thus managing water loss through stomata, particularly during the initial onset of water stress.

Characteristics

Plants that display isohydic characteristics have tight and continuous water potential homeostasis through stomatal control. This means they constantly regulate their water loss within a certain range to avoid damaging water deficits occurring within the plant (Buckley 2005).

As soil water potential drops, the plant senses these changes and its response is to maintain leaf water potential, sometimes at the expense of water potential declines elsewhere in the plant, in order to maintain key physiological processes and prevent water loss. This means that water potential of the leaves remains relatively constant during the day and during periods of minor-moderate water stress events, regardless of soil water status (Jones and Tardieu 1998). This response is triggered by an interaction between hydraulic and chemical signals. Such signals can include a slight reduction in water potential and an increase in ABA concentration, which in turn initiate stomatal control of transpiration (Jones and Tardieu 1998).

Maintenance of leaf water potential is due to the controlling effect water potential has on stomatal conductance through an interaction with xylem ABA (Jones 2008a; Jones and Tardieu 1998). As leaf water potential declines to a threshold value, a chemical-based signal triggers stomatal control to prevent any further drops in water potential. Tardieu and Simonneau (1998) found that ABA concentration increases with decreases in measurements of pre-dawn water potential together, with stomatal aperture.

Consequences for plant-based sensing of water status

Even though leaf water potential has a controlling effect—through an interaction with ABA—on stomatal conductance, there is no statistical relationship between leaf water potential and stomatal conductance (Jones and Tardieu 1998). This is due to the fact that stomatal conductance declines in order to maintain leaf water potential.

Because of this, it has proven difficult to monitor accurately, using water potential measurements, the water status of plants that display isohydic characteristics. As these plants maintain leaf water status even when the soil water deficit is high, measurements of water potential are not sensitive to the deficits encountered by the roots in the soil. If the purpose of plant water status monitoring is to aid irrigation scheduling, without any reliance on soil water status monitors, then the irrigation manager could be deceived into thinking that there is adequate soil water due to the maintenance of leaf water potential. However, Jones (2008a) stated that measurements based on stomatal conductance are sensitive to declining soil water, and can give an accurate indication of declining stomatal aperture, and thus water stress, as a response to declining soil water potential.

Examples of vegetable plants that display isohydric characteristics

Bean	<i>Phaseolus vulgaris</i> L.	Wakrim <i>et al.</i> (2005)
Pepper	<i>Capsicum annuum</i> L. Vau. Maor	Yao <i>et al.</i> (2001)
Potato	<i>Solanum tuberosum</i> L.	Liu <i>et al.</i> (2005)
Sweetpotato	<i>Ipomoea batatas</i> L. Lam.	Sung (1981)
Iceberg lettuce	<i>Lactuca sativa</i> L.	Gallardo <i>et al.</i> (1996)

I have categorised these vegetable plants as displaying isohydric characteristics after examination of their water relations and responses to water stress, as researched and reported by those references mentioned above. For justification of isohydric classification, see **Appendix I**.

Examples of other plants that display isohydric characteristics

Almond	<i>Prunus dulcis</i> Mill. D . A Webb.	Tardieu and Simonneau (1998)
Barley	<i>Hordeum vulgare</i> L.	Jones (2004)
Peach	<i>Prunus persica</i> L. Batsch.	Tardieu and Simonneau (1998)
Sorghum	<i>Sorghum bicolor</i> L.	Jones and Tardieu (1998)
Soybean	<i>Glycine max</i> L. Merr.	Tardieu and Simonneau (1998)
Sunflower	<i>Helianthus annuus</i> L.	Jones (2007)
Wheat	<i>Triticum aestivum</i> L.	Tardieu and Simonneau (1998)

These plants were categorised as displaying isohydric characteristics by the authors.

Anisohydric characteristics

Definition

Anisohydric characteristics of plants can be seen in the loose, but not absent, stomatal control of leaf water potential (Jones 2008a) through long-distance signals such as ABA, which can be insensitive to mild water stress.

Characteristics

Plants that display anisohydric characteristics do maintain control over leaf water potential, but it is at a diminished rate when compared to isohydric plants. As soil water potential declines so too will leaf water potential (Jones 2007) until it reaches a threshold at which point stomata will begin to regulate water loss (Jones 2008a).

A number of authors have suggested that the reason for this is due to an absence of an interaction between chemical, hydraulic and even morphological signals (Comstock 2002; Jones 2008a; Jones and Tardieu 1998). Possibly the receptors that capture this signal are relatively insensitive, reducing the stomatal responses to fluctuations in water potential with changing evapotranspirative demand. While this process may maintain photosynthetic capacity during mild stress, these plants will continue to transpire until severe water stress ensues. By this time water potential may have already dropped significantly enough to impair the physiological processes of the plant, which may show visible signs of water stress (such as wilting), and may cause a significant shutdown of many growth processes.

The most commonly studied signals in anisohydric plants are chemical signals, which can include ABA and pH. Research conducted by Jones and Tardieu (1998) suggests that stomatal conductance depends on ABA concentration with no interaction with leaf water potential. As leaf water potential decreases, the sensitivity of receptors to ABA increases, but leaf water potential has no controlling effect on stomatal conductance (Tardieu and Davies 1993). Research suggests that in some plants that display anisohydric characteristics, the controlling signal may not be chemical, but other hydraulic or morphological pathways (Jones 2008b). However, I have not come across any research that specifically identifies these alternate signals in plants and how they may function.

Consequences for plant-based sensing of water status

In anisohydric plants, leaf water potential will decline as soil dries until it reaches a point where ABA receptors initiate declines in stomatal conductance. This means that measurements of leaf water potential to aid irrigation scheduling could make it difficult to distinguish between water stress as a result of substantially negative soil water potentials, or as a result of an increase in evaporative demand (Jones 2007).

However, stomatal conductance cannot be used as an effective method for irrigation scheduling as it is insensitive to declining soil water potentials. Therefore, to accurately measure the water status of anisohydric plants, leaf water potential is preferred, as it is sensitive to declining soil water potentials. In order to schedule irrigation using ψ_{leaf} , managers must understand and take into

account the normal diurnal fluctuations in leaf water potential. Small variations in leaf water potential may not mean that irrigation is required, as ψ_{soil} has not declined sufficiently to warrant re-wetting.

Examples of vegetable plants that display anisohydric characteristics

Cauliflower	<i>Brassica oleracea</i> L. var. Botrytis	Kochler <i>et al.</i> (2007)
Eggplant	<i>Solanum melongena</i> L.	Behboudian (1977)
Tomato	<i>Lycopersicon esculentum</i> L.	Sobeih <i>et al.</i> (2004)
Wild lettuce	<i>Lactuca serriola</i> L.	Gallardo <i>et al.</i> (1996)

I have categorised these vegetable plants as displaying anisohydric characteristics after examination of their water relations and responses to water stress as researched and reported by those references stated above. For justification of anisohydric classification, see **Appendix II**.

Examples of other plants that display anisohydric characteristics

Apple	<i>Malus domestica</i> Borkh.	Jones and Tardieu (1998)
Cowpea	<i>Vigna unguiculata</i> L. Walp.	Jones (2007)
Lupin	<i>Lupinus</i> spp. L.	Tardieu and Simonneau (1998)
Maize	<i>Zea mays</i> L.	Jones (2007)
Pea	<i>Pisum sativum</i> L.	Tardieu and Simonneau (1998)
Poplar	<i>Populus</i> spp. L.	Jones (2004)
Sugarcane	<i>Saccharum</i> spp. L.	Tardieu and Simonneau (1998)

These plants were categorised as displaying anisohydric characteristics by the authors.

Conclusion

Although these categories are useful to classify plants based on their water relations, it is important to note that these distinctions are not always clear.

As mentioned previously, different cultivars within a species may display completely opposite characteristics, and some plants may display both isohydric and anisohydric characteristics. Jones (2008b) states 'there is no pure isohydric or anisohydric plant, all plants are somewhere in between the theoretical extremes [of these classifications]'.

My literature review confirms this. An example is eggplant; the literature I have read suggests that eggplant is drought tolerant, compared to other closely related plants such as tomato and capsicum. Drought tolerance is a characteristic usually associated with isohydric plants. However, the data on eggplant's responses would classify it as displaying *anisohydric* characteristics. This is a very clear example of these classification boundaries being indistinct and this can limit their application to real-life decision-making and crop management.

However, having stated the problems associated with these classifications, there can also be advantages. For example, it would be sensible to focus plant-based sensing using leaf water potential on vegetables showing predominantly anisohydric behaviour. Another example may be the use of regulated deficit irrigation—predominantly anisohydric vegetables may be at greater risk of sudden yield or quality deterioration due to their less regulated stomatal control.

It is clear that although useful, there are disadvantages in the classification of plants by their responses to water stress. Considerable research and experimentation may be required to accurately appoint vegetable crop plants to these classifications—this could prove costly and time consuming. It may be more practical for crop managers or advisors to have an understanding of these characteristics and make observations of how a plant copes with water stress, and then to assign management strategies accurately. It is for this reason that I have compiled this information.

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Appendix I

Vegetable crops displaying isohydric characteristics

Vegetable crop	Justification	Source
Common bean (<i>Phaseolus vulgaris</i> L.)	This study found that, contrary to other studies, g_s and ψ_{leaf} decreased with water stress imposed in their partial root zone drying experimental plants. The authors stated that their hypothesis of a root-sourced signal to initiate stomatal closure was not supported, as there were no significant increases in ABA or xylem sap pH and concluded that a hydraulic signal was responsible for stomatal closure.	Wakrim <i>et al.</i> (2005)
Iceberg lettuce (<i>Lactuca sativa</i> L.)	The authors of this study tested two types of lettuce (cultivated and wild) for their rooting depth and water use efficiency by imposing water stress on the plants. They found that the ψ_{leaf} of the cultivated type, iceberg lettuce, did not reflect the ψ_{soil} , which indicates that this plant has isohydric characteristics. They also found that even though ψ_{soil} continued to drop, g_s increased at certain times over the next few days. This indicated that although the plant was experiencing water stressed conditions, it was able to continue photosynthesising during periods of low evaporative demand. This is a strong indication that this vegetable had isohydric characteristics.	Gallardo <i>et al.</i> (1996)
Potato (<i>Solanum tuberosum</i> L.)	This experiment found that as ψ_{soil} decreased in stressed treatments, g_s decreased but ψ_{leaf} remained similar to values in well-watered treatments, in the early stages of declining ψ_{soil} . This indicated the potato was displaying isohydric characteristics. However, as ψ_{root} fell to less than -0.4 MPa, ψ_{leaf} declined rapidly. In most commercial potato production situations, soil would not be dried to this extent, so this latter response is not as relevant.	Liu <i>et al.</i> (2005)
Pepper (<i>Capsicum annuum</i> L. vau. Maor)	A split-root study found that as soil dries g_s decreased without a significant decrease in ψ_{leaf} and after watering, the plants, (simulated by pressurising the soil/root zone) recovered quickly indicating that there was definitely a strong hydraulic signal.	Yao <i>et al.</i> (2001)
Sweetpotato (<i>Ipomoea batatas</i> L. Lam.)	This study conducted on sweet potato under drought conditions found that stomatal resistance increased with slight decreases in ψ_{leaf} . It also found that some varieties displayed more isohydric characteristics than others did. The variety Shin 31's ψ_{leaf} decreased to a certain point and then it was maintained, even though evaporative demand continued to increase.	Sung (1981)

Key

ψ_{leaf}	=	leaf water potential
ψ_{soil}	=	soil water potential
g_s	=	stomatal conductance

Appendix II

Vegetable crops displaying anisohydric characteristics

Vegetable crop	Justification	Source
Cauliflower (<i>Brassica oleracea</i> var. <i>Botrytis</i> L.)	This study used cauliflower plants under different irrigation regimes including well-watered, moderate, intermittent and severe water stress, to focus on the physiological characteristics of each treatment and develop a transpirational and stomatal model of cauliflower. The authors found that noon leaf water potentials were closely related to soil water potentials, which led to an increase in stomatal <i>resistance</i> . They concluded that ψ_{leaf} was a product of ψ_{soil} , which indicates that cauliflower is an anisohydric plant.	Kochler <i>et al.</i> (2007)
Eggplant (<i>Solanum melongena</i> L.)	This study used eggplant to study its physiological responses to water stress. The results of this study indicated that although ψ_{leaf} and ψ_{soil} showed a parallel relationship, which indicates that eggplant is an anisohydric plant; it was better able to maintain RWC when compared with other Solanaceous plants like capsicum and tomato. This means that it is an anisohydric plant with some isohydric characteristics of stomatal control for the maintenance of water content.	Behboudian (1977)
Tomato (<i>Lycopersicon esculentum</i>)	The results of this split-root study indicated that g_s decreased significantly in the droughted plants compared to the well-watered plants. This was accompanied by an increase in xylem pH, thought to cause ABA concentration increase in stomata guard cells. The authors also found that ψ_{leaf} did not decrease significantly in the droughted plants compared to the well-watered plants. This is consistent with the responses displayed by an anisohydric plant <i>during a split-root study</i> . The dry side of the root system produces ABA, which signals stomatal closure to prevent water loss. However, the well-watered side of the root system still provides enough water to the plant to maintain leaf water potential. This shows that stomata closed due to ABA, and not through an interaction between ABA and leaf water potential, as would be present in an isohydric plant.	Sobeih <i>et al.</i> (2004)
Wild lettuce (<i>Lactuca serriola</i> L.)	This study, previously mentioned, found that wild lettuce's ψ_{leaf} closely reflected the ψ_{soil} and g_s also rapidly decreased in parallel with ψ_{leaf} . This is strong evidence for anisohydric characteristics.	Gallardo <i>et al.</i> (1996)

Key

ψ_{leaf}	=	leaf water potential
ψ_{soil}	=	soil water potential
g_s	=	stomatal conductance