

The relationship between plant growth and water consumption : a history from the classical four elements to modern stable isotopes

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Key message

The history of the relationship between plant growth and water consumption is retraced by elucidating the progression of scientific questions posed through the centuries : from a purely philosophical question, to conceptual and methodological developments towards a research interest in plant functioning and their relationship to the environment.

Abstract

Context : The relationship between plant growth and water consumption has for a long time occupied the minds of philosophers and natural scientists. The ratio between biomass accumulation and water consumption is known as water use efficiency and is widely relevant today in fields as diverse as crop improvement, forest ecology and climate change. Defined at scales varying from single leaf physiology to whole plants, it shows how botanical investigations changed through time, generally in tandem with developing disciplines and improving methods. The history started as a purely philosophical question by Greek philosophers of how plants grow, progressed through thought and actual experiments, towards an interest in plant functioning and their relationship to the environment.

Aims : This article retraces this history by elucidating the progression of scientific questions posed through the centuries, presents the main methodological and conceptual developments.

Conclusion : Research on water use efficiency followed a path from the whole plant to molecular mechanisms and is still a very active research field across nearly all levels of botanical research.

Keywords

Transpiration efficiency; water use efficiency; plant physiology; botanical history

Introduction

The ratio of biomass accumulation per unit water consumption is known today as water use efficiency (WUE) and is widely relevant to agriculture (e.g. Blum 2009; Tallec et al. 2013; Vadez et al. 2014;), to forest ecology (e.g. Linares and Camarero 2012; Lévesque et al. 2014), and in the context of global climate change (Cernusak et al. 2019). This ratio can be defined at various levels, from the physiological functioning of a leaf to the whole plant and at the ecosystem level. The main subject of this historical review is at the whole plant level. It can be simply measured by quantifying the amount of water given to a plant and the plant's increase in biomass during the experiment. The ratio of biomass produced divided by the cumulative water lost during growth is termed whole plant transpiration efficiency ($TE = \text{biomass produced} / \text{water lost}$). Historically, the ratio has also been calculated in its inverted form (water lost / biomass produced) and various terms have been used to denote these ratios (see Box 1). As knowledge, concepts and technology advanced, it became desirable to measure TE also at the leaf level. Some history of the technological advances and their use at the whole leaf level are included here. Establishing historical precedence for scientific discoveries was made more difficult by the availability of historic written evidence. Also, toward the beginning of the 20th century, publications became too numerous to allow a comprehensive review. Even though this review is focussed on tree ecology, to show the historical continuity it was necessary to also include bibliography on other plant types.

Box 1 : Short history of names for TE

Hellriegel (1883) called the ratio of transpiration divided by the amount of dry plant biomass produced "relative Verdunstungsgrösse" which translates into English as "**relative transpiration**".

Leather (1910) defined the "**transpiration ratio**" as the water transpired divided by the weight of dry plant produced.

Kearney and Shantz (1911) defined the plant's "**water requirement**" as the quantity of water consumed per pound of dry matter, a term widely used in the first half of the 20th century.

Maximov (1929) first introduced the term "**efficiency of transpiration**" to mean biomass produced divided by the amount of water used.

In the 1940's several authors started using "**efficiency of water use**" (Roeser 1940; Thornthwaite 1947)

In the late 1940's and early 1950's the term "**water use efficiency**" came into common use (e.g. Hobart and Harris 1946; Dreibelbis and Harrold 1958; P. Brown and Shrader 1959) as plant dry biomass produced divided by water used.

I) What is plant matter made off ?

Various Greek philosophers were interested in how substances can change from one thing into another. Thales (624 – c. 546 BC) thought that all things come from water, whereas Anaximenes argued that “penuma” (air) should be the basis of all things (Egerton 2001a). These assertions were the basis of more than 2000 years of philosophical dispute.

In “De Causis Plantarum”, Theophrastus (371-287 BC) assumed that plants draw nutrition, which consisted of varying amounts of the four elementary humours, from the earth through their roots (Morton 1981). Some centuries later, in a Christian work translated in 400 AD from Greek into Latin and known as “pseudo-Clement’s Recognitions”, an apparent thought experiment was described to “ prove that nothing is supplied to seeds from the substance of the earth, but that they are entirely derived from the element of water and the spirit (spiritus) that is in it » (Egerton 2004c). This thought experiment revealed a small amount of progress in scientific thinking because the question was posed more precisely than before. It stood out at a time when botany mainly consisted of naming plants and “theoretical botany effectually went out of existence” (Morton 1981). The author of this thought experiment, described in “pseudo-Clement’s Recognitions”, suggested putting earth into big barrels, growing herbaceous plants in it for several years, then harvesting them and weighing them. His hypothesis was that the weight of the earth would not have changed, and the author used this as an argument that the vegetation biomass could have come only from water.

It appears that the question of how plant matter is produced, was not pursued in Roman or Arabic writings, which were more concerned with agricultural (the former) and medical (the latter) aspects of plant sciences. (Egerton 2001c; 2002). Not until the high middle ages was a renewed interest shown in plant growth. Adelard of Bath, a 12th century AD English natural philosopher, devoted the first four chapters of “Quaestiones Naturales” (c. 1130-1140; Morton 1981) to the question of what plant matter is made of. He argued, within the concepts of the four elements theory, « by just as much as water differs from earth, by so much does it afford less nourishment to roots, I mean than earth does », clearly being in favour of earth as the source for plant nourishment. His arguments were only theoretical and speculative.

A major step occurred in botanical sciences between the 15th and 16th centuries; scholars began making experiments to test antique and medieval hypotheses against observations in nature (Egerton 2003). In the mid-15th century, and probably related to the translation and printing of the botanical books by Theophrastus (Morton 1981), the thought experiment from “Recognitions...” was taken up by Nicholas of Cusa in the fourth part of his “Idiota de mente”, “De staticis experiments”. At a time that the naming of plants for pharmacology was the major interest of savants, he proposed experimental investigations. Nicholas of Cusa described the same thought

experiment as did pseudo-Clement's Recognitions; he concluded similarly that "the collected herbs have weight mainly from water" (1450; translation into English by Hopkins 1996). Cusa additionally suggested that the plants should be burned at the end of the experiment and the ash weight be taken into account. It is not clear whether the thought experiment was ever physically done.

In the 16th century, botanical science began to separate from medical sciences, with the establishment of lectureships in universities (e.g. Padua in 1533) and the establishment of botanical gardens (Egerton 2003). The bases existed for advancing science in the 17th century of Enlightenment. Francis Bacon, an influential philosopher of his time, conducted a series of plant growth experiments which are reported in his "de Augmentis Scientiarum" (1623; Spedding et al. 1900). Bacon discovered that some plants sprouted more quickly in water than in soil (Egerton 2004b). He concluded that "for nourishment the water is almost all in all, and that the earth doth but keep the plant upright, and save it from over-heat and over-cold" (Hershey 2003), thus still upholding the theory proposed by Thales and Nicholas of Cusa. In "The History of the Propagation and Improvement of Vegetables", Robert Sharrock (1660) reported that some plants both rooted and grew entirely in water. Although he noted different amounts of transpiration over time, he did not discuss this in relation to plant growth.

In 1662 Johannes Baptista van Helmont published his now-famous willow experiments (van Helmont 1662). This maybe the fist report of an experiment that was based on the thought experiment of Nicholas of Cusa (Hershey 2003) with the minor differences of beginning with dried soil and not using herbaceous plants, but rather a willow tree. After weighing this soil, he irrigated it with rain water and planted the weighed stem of a willow tree. The experiment ran for five years. At the end, the tree was weighed again, as was the dried soil. He found the soil weighed about two ounces less than at the beginning of the experiment, whereas 164 pounds of wood, bark and roots were produced. He concluded that the organic matter could only have come out of the water. Helmont was unaware of the existence of carbon dioxide, but he did know of "gas sylvestre". He also knew that burning oak charcoal would produce nearly the same amount of gas sylvestre and ash. However he did not connect this information with the plant growth he had observed (Hershey 2003). Robert Boyle published similar experiments in "The sceptical Chymist" (Boyle 1661). Boyle claimed that he had done his experiments before he knew of Helmont's (Egerton 2004c), although he discussed Helmont's results and arguments in detail in his book. Boyle doubted the direct transformation of water into plant matter. He admitted, however, that it might be possible that other substances contained in the water could generate new matter (Boyle 1661). In the 1660's, Edme Mariotte also criticised van Helmont's theory that water alone constituted the only element to produce plant matter. He thought similarly to Boyle that elements in the water could contribute to

the plant matter. He also showed that nitrogen compounds were important for plant growth (Bugler 1950).

John Woodward, in his “Some Thoughts and Experiments Concerning Vegetation” (Woodward 1699) again took up the question of what comprised the source of plant growth. Woodward criticised Helmont's and Boyle's experiments, mainly on the precision of weighing the dry soil before and after the experiment, but also the contamination of the irrigation water by terrestrial vegetable or mineral matter. Consequently, he developed a series of hydroponics experiments, where by growing plants in sealed vials, in different types of water and weighing them regularly over the same time period, he could calculate how much biomass was gained over a set time period. He was able to draw a series of conclusions from these experiments by calculating the ratio of water lost to plant mass gained in the same period of time, thereby calculating the inverse of transpiration efficiency. **This was probably the first time that the inverse of transpiration efficiency was calculated using experimental data.** He showed that 50 to 700 times as much water was lost than biomass gained. He also reported that plants grown in water containing more terrestrial matter grew more and with less water consumed. From these observations, he concluded that water serves only as a vehicle for the terrestrial matter that forms vegetables and that vegetable matter is not formed out of water. He is still remembered more for his geological publications (Porter 1979) than for his contributions to botany (Stanhill 1986).

In his “history of ecology” series, Egerton (2004c) nicely sums this period thusly: “each of these authors (Bacon, Boyle, Helmont, Sharrock) built upon the work of his predecessors and improved somewhat the understanding of plant growth and how to study it. However, they still fell short of a basic understanding of plant growth. Before that could be achieved, chemists would have to identify the gases in the air.”. This series of studies shows that from the end of the 17th century onwards, experiments replaced speculation (Morton 1981), in botany many as well as in many other areas of science.

From the end of the 17th century, the question of how plants grow was still unresolved, although it was known that nutrients were conducted from the roots in the ascending sap to the leaves, and a vague idea of photosynthesis was beginning to develop. A major improvement in the understanding of how transpiration and its variations work, was the discovery of cells by Robert Hooke towards the middle of the 17th century (Egerton 2005), and subsequently the discovery of stomata on leaf surfaces. One of the first to describe stomata may have been Malpighii in this “Anatomy of Plants” (Malpighii 1675; Möbius 1901). Based on Malpighii's and Grew's (1682) studies, John Ray suggested in his “Historia Plantarum” (Ray 1686) that the apertures in the leaves, when open, would give off either breath or liquid. Ray may have been the first to have connected stomata with transpiration. He also suggested that the loss of water by evaporation is compensated

constantly by water from the stem and thus, transpiration results from a constant water flux. He also observed that sap ascends the stems of trees in sap-bearing vessels, which do not contain valves. He did, however, admit that it cannot be capillary forces that make water go up tall trees.

Ideas on photosynthesis developed slowly from the middle of the 17th century onward. Malpighii (1675) suggested that leaves produce (“concoct and prepare”) the food of plants and from leaves this food passes to all parts of the plant. Similarly, Claude Perrault in his “Essais de Physique” (Perrault 1680) defended the hypothesis that the root act as the mouth of the plant and that the leaves serve to prepare the food arriving with the sap from the root so that it can be used in the rest of the plant. John Ray in “History Plantarum” (Ray 1686) concurs with this, however adds in “The wisdom of God” (Ray 1691 in Lazenby 1995) that “not only that which ascends from the Root, but that which they take in from without, from the Dew, moist Air, and Rain.”. He also thought that light could play a role in this preparation of the plant sap. At this time, most authors (Malpighi, Perrault, Mariotte, Ray) knew about the circulation of sap, up as well as down, and that leaves served somehow to transform the upcoming sap into food for the plant.

In 1770 Lavoisier published “Sur la nature de l'eau” (“On the nature of water”, translation by the author) and reviewed the literature on the possibility of water changing into earths to nourish plants. Lavoisier cited the Van Helmont experiment and later works which tested Van Helmont’s idea by growing plants in water (e.g. Boyle, however he did not cite Woodward). He was critical of the idea that it could be a transformation of water that would constitute plant material. This was based mainly on experiments by himself and others, showing even distilled water would contain traces of “soil”. However, he also defended the idea, based mainly on Charles Bonnet's observations, that leaves absorb vapours from the atmosphere that contribute to plant growth.

Helmont had coined the term “gaz” in the mid 17th century and had been able to distinguish different gazes from air (Egerton 2004a). It was only in the middle of the 18th century that gases were studied in the laboratory and several observations by different researchers would finally lead to an understanding of respiration and photosynthesis (Tomic, Cussenot, and Dreyer 2005). Richard Bradley seems to be one of the first to clearly state (in letters from 1721 to 1724) that plant nourishment can be drawn from the air. Hales (1727) agreed with this theory, which was not yet widely accepted (Morton 1981), and suggested that light might be involved, which helped to pave the way for the discovery of photosynthesis. Charles Bonnet (1754) made an important observation, i.e. branches with leaves that were submerged under water would produce air bubbles on their surfaces when sunlight shone on them. He further observed that this was not the case in degassed water, and also that bubbles would appear more rapidly when he saturated the water with air. This further suggested that light was involved. Black (1756) was able to identify carbon dioxide (which he called ‘fixed air’) using a lime water precipitation test. He demonstrated that this ‘fixed air’ did

not support animal life or a candle flame (Egerton 2008). Tomic, Cussenot, and Dreyer (2005) present nicely the steps leading up to the term photosynthesis. This began with Priestley (1775) demonstrating that the air given off by animals and by plants were not the same, Ingen-Housz (1779) observed the important role of light, and the dispute between Senebier and Ingen-Housz from 1783 to 1789, resolved more clearly the functions of carbon dioxide emission (respiration) and absorption (photosynthesis). Based on these results and his own, very detailed observations, De Saussures reported in 1804 that the carbon necessary for plant growth is absorbed mainly by green leaves from atmospheric carbon dioxide and he estimated that the largest part of the accumulated dry matter of plants is made of this carbon. **Thus, the dispute of what the plant matter is made of and began in antique Greece, was resolved at the end of the 18th century.**

II) How much water do plants need to grow ?

The late 18th century was the beginning of applied agricultural science and the rise of plant physiology (Morton 1981). Work continued on transpiration and stomata, with a large number of experiments, reviewed by (Burgerstein 1887; 1889). Unger published in 1862 a major review article covering such subjects as: the relationship of transpiration to temperature and humidity; daily cycles, including night; differences in adaxial and abaxial leaf surfaces; the impact on transpiration of type, number, size and distribution of stomata; the structure of the epidermis (cell layers, cuticle, hairs, and wax); development of the mesophyll; size of intercellular spaces and cell turgor; and the impact of plant transpiration on the atmosphere (Unger 1862). Scientists started to reflect on the interaction of plants, or more specifically their leaves, with their environment, and experimentation included the responses of stomata to light quantity (Moldenhawer 1812) and quality (Daubeny 1836). Based on inconsistent observations by e.g. Banks, Moldenhawer and Amici, advances were also made on the functioning of stomata (Mohl 1856). However, progress was mainly based on a comment in von Schleiden (1849), that the state of the stomata would be the result of the water in or outflow of the pore-cells (called "Schliesszellen") and he showed experimentally that stomata close when the pore-cells lose water. As knowledge of transpiration, stomatal opening and their dependence on environmental variables increased, new questions arose about the water consumption of plants.

Another milestone along the way to understanding the transpiration of plants in the 19th century was the publication by Sir John Bennet Lawes (1850) "Experimental investigation into the amount of water given off by plants during their growth; especially in relation to the fixation and source of their various constituents". He described experiments on wheat, barley, beans, peas, and clover using differently fertilised soils. He observed increased evapotranspiration with higher temperatures during the growing season, and asked whether "this increased passage of water through the plants,

carrying with it in its course many important materials of growth from the soil, and probably also influencing the changes in the leaves of these, as well as of those derived from the atmosphere, will not be accompanied with an equivalently increased growth and development of the substance of the plant.”. This was followed by an important discussion of the influence of temperature on evaporation and growth as well as the resultant ratio. He discussed in the introduction "the relationship of the water given off to the matter fixed in the plants", he gave his results in this ratio and in the inverse ratio, and applied these ratios to different scientific questions. The first ratio (transpired water divided by plant matter is the inverse of today's TE) was used to interpret his results in terms of water use compared to field available water and the latter's ratio (plant matter divided by transpired water, equivalent to today's TE), **was used to discuss his results in terms of functional differences among species**. From the observed functional differences, he concluded that there was "some definite relationship between the passage of water through the plants and the fixation in it of some of its constituents.". He was, thereby, introducing a new question about the link between dry matter accumulation and transpiration, which will be treated in the next chapter.

Toward the end of the 19th century, research interest started to include agricultural questions of water use. Marié-Davy (1869) measured transpiration (standardized by leaf surface) of over 30 plant species, including eight tree or shrub species as well as herbaceous and agricultural plants. He estimated transpiration per soil area, thereby establishing that a prairie would transpire more than trees. von Höhnell (1879) estimated long term transpiration of branches 15 tree species (standardized on leaf surface or leaf dry weight). He used this data of branch transpiration to upscale to whole trees and concluded that compared to agricultural plants, the amount of rain seemed sufficient for tree growth. Hellriegel (1871) had already similarly concluded for cereals in the Mark Brandenburg (Germany) region that rainfall would not be sufficient, as had Marié-Davy (1874) for wheat in the Paris (France) region. In parallel with these more quantitative interrogations about water use, from the mid 19th century, scientists started to ask more functional questions about the relationship between transpiration and dry matter accumulation, in a context of vigorous growth of botanical sciences and the complex relation between organisms and their environment (Morton 1981).

III) Are transpiration and dry matter accumulation linked

Lawes (1850) had already reflected on a functional relationship between water flux and plant matter accumulation. In the following years there were several publications on the transpiration of trees, and although no transpiration efficiency was estimated, the understanding of tree transpiration advanced. Many comparative studies were published. Lawes (1851) on "Comparative evaporating properties of evergreen and deciduous trees" considering twelve different tree species. He provided measurements of the variation in transpiration with temperature and hygrometry data. With these he

concluded that, « evaporation is not a mere index of temperature but that it depends on vitality influenced by heat, light and other causes ». In the late 19th century several researchers estimated and compared values of the ratio of transpiration and dry matter accumulation for different plants (Burgerstein 1887). With the growing evidence of variation in this ratio, scientists started to reflect on the relationship between transpiration and dry matter accumulation, aided by the development of new measurement techniques. **A major question was if there would be a tight coupling between transpiration and dry matter accumulation, resulting in a constant transpiration efficiency, or if variation could be observed.**

Dehérain (1869) studied evaporation and the decomposition of carbonic acid in leaves of wheat and barley. Using an ingenious apparatus, he was probably the first to directly measure evaporation of water in parallel with carbonic acid decomposition. He studied the effect of variously coloured light, and although he did not calculate the ratio between evaporation and carbonic acid decomposition, he did conclude that light of different colours had a similar effect on carbonic acid decomposition and on water evaporation from the leaves. His final conclusion was that “it is likely that there is existing between the two main functions of plants, evaporation and carbonic acid decomposition, a link, of which we need to determine its nature” (translation from the original French by the author). Several other scientists also commented on the relationship between transpiration and dry matter production. Fittbogen (1871) supposed, similarly to Lawes (1850) before him, but with more experimental evidence, that there should be a positive relationship between transpiration and production of dry matter. Dietrich (1872) supposed that this relationship would be linear, whereas Tschaplowitz (1878) introduced the idea that there should be an optimum transpiration at the maximum production of matter. Therefore, when the transpiration would increase over this optimum, this would lead to a decrease in assimilation rate. He was one of the first to suggest a non linear relationship between transpiration and assimilation. Sorauer in “Studies on evaporation” (1880) defended the hypothesis that transpiration was not only a physical phenomenon but was also physiological. He stated that “It is not possible as yet to study the plant internal processes which regulate the transpiration, however it is possible to quantify the relationship between dry-matter and transpiration” (translation from German by the author), suggesting thereby **TE as a means to advance the understanding of plant internal processes.** Sorauer was probably at the cutting edge of science of his time. He pointed out specifically that variability among plants of one species was due to genetics (German, “erbliche Anlagen”) a startling and even daring assertion for his time. He asserted that for comparative studies, genetic variability needed to be minimized. To achieve this he used, when possible, seeds from the same mother-plant, grown in the same environmental conditions and a large number of repetitions. Using these protocols, he was probably one of the first to estimate TE on tree seedlings, showing that there

was within species diversity in transpiration and growth, but that their ratio was more constant. He concluded from experiments on pear and apple trees that the pear trees used less water for the same biomass growth. He was able to go one step further and demonstrate that this difference was due to less transpiration per leaf area. By comparing different woody and herbaceous plants with different growth types, he postulated that when plants had a small leaf area combined with high transpiration, they had either a very strong growth increment, a higher dry matter percentage, or a larger root system. Overall he observed relationships between dry matter production and transpiration; he concluded that there must be some **regulation of the transpiration per unit leaf area by the co-occurring dry matter production.**

Hellriegel (1883) argued that one cannot estimate a constant ratio between transpiration and production as there were factors which influence each independently. He also commented that it might make sense to estimate mean values of transpiration for various agricultural plants, as this would be for practical and scientific value. He thought that the most logical standardisation would be by the mass of the dry matter produced during the same time period. He called this "relative Verdunstungsgrösse" which can be translated into English as "relative transpiration". He was probably one of the first to give a name to the ratio between, whole plant transpiration and dry matter production. He proposed a theory that for a long-term drought, plants would acclimate their morphology to decrease their "relative transpiration". He provided additional experimental evidence that barley had decreased in relative transpiration over as many as seven levels of soil water deficit, relative to field capacity. Using his own observations, he proposed that when calculating a mean "**relative transpiration**" for a single species, variation of transpiration should be minimised and that plants should be tested together only under optimal conditions. Hellriegel also concluded from his own observations that the reason for a species' preference for certain soil water conditions was not only to be found in their relative transpiration ratio. Hellriegel was thus probably one of the first scientists to point out that **the relationship between drought adaptation and "relative transpiration" might not be straight forward.**

Understanding how biomass and water loss were connected was studied by Iljin (1916) on a newly detailed level. He measured simultaneously water loss and carbon dioxide decomposition and reported his data as grams water lost per cc of carbon dioxide decomposed. He concluded from studying more than 20 plant species, that "...it is generally agreed that the rates of water loss and of CO₂ assimilation are directly proportionate to stomatal aperture, and that consequently there exists a close connection between these two processes".

At the end of the 19th century the ratio of transpiration versus dry matter accumulation was recognized as an important plant process, which **varied among and within species in a complex interaction of each component with the other and with environmental factors.**

IV) How do plants differ in water requirement and how do they respond to variations in environmental factors ?

In the late 19th century several researchers estimated and compared values of the ratio of transpiration and dry matter accumulation for a range of cultivated plants (Fittbogen 1871; Dietrich 1872; Farsky 1877, cited in Burgerstein 1887), giving evidence of the growing interest of agricultural scientists. The number of studies of transpiration efficiency greatly increased, thereby driving a new standardisation in terminology. King (1889) studied the inverse of transpiration efficiency and described it as “the amount of water required for a ton of dry matter”, and promulgated this terminology by using it in the titles of his publications between (1892 and 1895). Similarly Leather (1910) published « Water requirements of the crops of India », in which he defined the “**Transpiration ratio**” as “the water transpired to the weight of dry plant produced”. The shift from a purely descriptive use of “water requirement” to a clearly defined one was provided by Kearney and Shantz (1911) as “... the degree to which a plant is economical in its use of water is expressed in its water requirement, or the total quantity of water which it expends in producing a pound of dry matter”. This term “**water requirement**”, is the inverse of the modern transpiration efficiency, and was used by a rapidly increasing number of publications which were published on the water use of crops in the early 20th century. Montgomery (1911) may have been the first to use the term for a plant trait in “Methods of determining the water requirements of crops”. In the now well known studies on “The water requirement of plants. I. Investigations in the Great Plains in 1910 and 1911.”, Briggs and Shantz (1913a) measured the water requirement for 21 crop and weed species, sometimes for different varieties of the same crop and under controlled and field conditions. In the same year they reviewed the available literature on water requirement (Briggs and Shantz 1913b). They discussed in detail studies from 29 different authors, many of which had only published once or twice on this subject. A few researchers were notable for their number of publications on the water requirement of crop plants : King with 6 publications between 1889 and 1905, and Von Seelhorst with 9 publications between 1899 and 1907. The difference among species and the impact of environmental factors on water requirement was one of the main questions raised. Briggs and Shantz (1913b) compiled most of the comparative studies, increasing their data set to 31 different crop species. The largest contributions came from Hellriegel (1883; 10 species) and Leather (1911; 15 species). Kiesselbach (1916) also reviewed 59 publications “ which had studied transpiration in relation to crop yield, based upon plants grown beyond the seedling stage” between 1850 – 1915. There were regular publications of original work from 1870s onwards, with more than per year from 1890 onwards. **These reviews and the increasing amount of newly published work per year, are evidence of the growing interest in the “water requirement” of plants as a trait of increasing importance in agricultural sciences.**

With regard to species differences in water requirement among crops, Schröder (1895) found two groups, among seven cereals, which differed in water requirement by a factor of two. Millet, sorghum and maize were known to be drought resistant, and showed a lower water requirement than the remaining plants. These differences were confirmed by Kolkunov (1905; cited in Maximov 1929), Briggs and Shantz (1914), Briggs and Shantz (1917) and Shantz (1927). Millet, sorghum and maize are now known to use the C4 carbon pathway of photosynthesis.

With regard to external environmental influences on the plants, Briggs and Shantz (1913b) distinguished between soil, atmosphere and plant factors. Soil factors which were investigated were soil moisture content, soil type, cultivation, soil volume, soil temperature, effect of fertilizers in soil or water cultures and effect of previous crops. Weather factors considered were air temperature and humidity, shade and carbon dioxide content. Other factors studied in direct relationship to the plants were parasite attacks, relative leaf area, cutting frequency, defoliation, planting density, and the age of plants.

A critique of the term “water requirement” was not long in coming. Dachnowski (1914) wrote, “It is assumed by many writers that a definite and quantitative relation exists between transpiration and growth, and that hence the ratio of the weight of water absorbed and transpired by a plant during its growth to the green or dry substance produced is an adequate and simple measure of growth.”, followed by an argument why this is **not** be the case.

V) Why do plants differ in transpiration efficiency ?

The adaptations of plants to dry environments was an important ecological topic at the beginning of the 20th century, as the discipline of “**physiological ecology**” (Iljin 1916; Moore 1924) began to develop. Iljin (1916) studied more than 20 different plant species *in situ* from different ecological locations, e.g., wet bottom soils and variously-facing slopes of ravines with different aspects. Iljin proposed that “the water requirements of the different species should be very different, and consequently the amounts of water available should differently affect their processes of life.” Using his observations he was able to show that “... in no case was the water loss per unit of decomposed CO₂ found to be equal to or more in xerophytes than in mesophytes”, thus suggesting a higher transpiration efficiency. He argued that mesophytes would have to close stomata “... in dry places in order to reduce evaporation, thus diminishing the rate of assimilation as well, whereas in the case of xerophytes, which are adapted to extreme conditions of existence, assimilation in similar circumstances proceeds actively” and then tried to confirm his hypothesis by transplanting mesophytes from wetter sites to the drier environment of xerophytes. Iljin showed experimentally that in all cases, a higher water requirement was measured for mesophytes transferred to a drier site compared to their original site and compared to xerophytes at the dry site. He interpreted his

observations as « **plants growing in dry places are adapted to a more economical consumption of water.** » He held this to be true for among- and within-species variation.

A milestone in forest “physiological ecology” was Bates’ (1923) study of the physiological requirements of Rocky Mountain trees. Bates wrote that for foresters, knowledge of demands of tree seedlings for moisture, light, heat and soil fertility was important for planning reforestation. He started a large investigation of six forest tree species, combining field studies to describe ecosystems, with experiments in controlled environments in order to determine species differences in relative transpiration and other water-flow related traits. Bates concluded from the comparison among species, **that trees of low water requirement would be trees that have a superior control over their water supply.** He was however critical of a direct relationship between water requirement and drought resistance in trees. Moore (1924) comments that in correlating physiological measurements with the habitat characterisation of the species, Bates «... has opened new fields to forest investigations ». He also stressed that the result were counter-intuitive in that the most xerophytic species had the highest water requirement, whereas the most mesophytic species had the lowest water requirement.

A similar discrepancy was observed by Maximov (1929) in the chapter “Efficiency of transpiration” in his book “The Plant in relation to water”. Maximov preferred “efficiency of transpiration” to “water requirement”, arguing that the former would be more logically correct, because the determining processes (transpiration) should be in the denominator, which also would have the effect that “... an increase in the figure denoting the value of the ratio actually corresponds to an increase of the efficiency per unit of water used”.

In his book, Maximov (1929) described experiments done at Tiflis Botanic garden by Maximov and Alexandrov (1917), where they studied local xerophytes for three years. They found xerophytes with a high efficiency of transpiration, particularly drought-resistant annuals. They also found that plants with a low efficiency of transpiration, particularly appeared to be the most typical semi-arid xerophytes. The mesophytes all displayed a medium efficiency. Maximov noted from other observations on the same plants that the "... majority of xerophytes with a low efficiency of water expenditure possess very extensive root systems, far exceeding in length the sub-aerial portions of the plant". He also observed that these plants showed a strong transpiration, and that this transpiration might constitute the "pump" which could draw water through such an extensive root system. He also observed that "members of the group of annual xerophytes with a high efficiency of transpiration are characterized by a relatively large leaf surface, which develops very rapidly". He argued that this would confer a high intensity of assimilation. From these observations he concluded a "lack of direct proportionality between efficiency of transpiration and the degree of drought resistance", but also that "**the magnitude of the efficiency of transpiration affords one of the**

most satisfactory tests of the ecological status of a plant". Maximov applied the ecological classification developed by Kearney and Shantz (1911), which they had based on plants of the arid and semi-arid regions of North-America : (1) drought-escaping with an annual growth cycle restricted to favourable conditions, (2) drought-evading, delay by various means the exhaustion of soil moisture, (3) drought-enduring, can wilt or dry but remains alive and (4) drought-resisting, can store a water supply. It should be noted that the ecological definitions behind these concepts have changed with time and are used slightly differently today. Shantz (1927) argued that many of the drought-evading plants had a low water requirement and Maximov noted that this group included the highly efficient xerophytes with a large leaf area. Maximov also observed that xerophytes from the third group (drought enduring) could show a very low efficiency of transpiration and belonged to the group of xerophytes with large root systems. Without concluding directly, he suggested a **relationship between the transpiration efficiency of a xerophyte and its ecological strategy** when facing limited soil water content. These studies by Maximov are among the most complete concerning the relationship between a plants' resistance to drought and their transpiration efficiency, reflecting the **interest of scientists in ecological questions of plant functioning, especially in relation to drought.**

Although work on crop plants advanced greatly in the early 20th century, results were scarcer for tree species. Raber (1937) concluded his book on "Water utilization by trees, with special reference to the economic forest species of the north temperate zone", with detailed discussion of available data for forest trees. He commented that "much more work on the water requirements of trees of all ages and under varying site conditions is needed". And he continued that "In view of the importance of planting drought-resistant species in regions where the water supply is below the optimum for most tree species, it is extremely urgent to know more about what qualities make for drought resistance and what species possess these qualities to the greater degree.". These conclusions by Raber show that **from the beginning of the 20th century, the estimation of transpiration efficiency had taken an important place in ecological studies on forest tree species, however not without some critical thoughts on the subject.**

VI) What is the functional importance of transpiration ?

Already in the 1870s and 1880s, the role of stomata in the diffusion of carbon dioxide into the leaf (during the day) and out of the leaf (during the night) was discussed in the scientific literature, as shown by the extensive literature review by Blackman (1895) (see also III above). Especially the functional importance of transpiration was an open question. There were **two opposing lines of thought**. As summarised by Iljin (1916), **one defended the line of inquiry that transpiration was important only in the process of transporting mineral salts from roots to leaves; the other held**

that the opening of stomata was necessary for absorbing the carbonic acid from the atmosphere, which leads to a loss of water and is described as an “inevitable evil”. Iljin (1916) preferred the second line of investigation, and attributed a major role to the stomatal aperture, which controlled both the absorption of carbonic acid from the atmosphere and the loss of water. He concluded that in “physiologico-ecological” investigations assimilation should be studied together with transpiration. Methodological advances (Eggle and Ernst 1949) as well as the development of the theories about the diffusion of gases, were applied to plants (Brown and Escombe 1900). These not only intensified research on the leaf-level relationship between assimilation and transpiration, but also allowed to study plant functioning in more detail. The major step forward, was the construction of an infrared gas analyser (URAS : in German “Ultrarotabsorptionsschreiber”, IRGA, Infrared Gas Analyser) by Lehrer and Luft in 1938 (Luft 1943) at a laboratory of BASF, IG Farbenindustrie. Normally used in industry and mining, Eggle and Ernst (1949) may have been the first to describe the use of the URAS for plant physiological measurements. By 1959, the URAS was routinely used for measuring stomatal resistance or transpiration in parallel and simultaneously with CO₂ assimilation, on the same leaf (Rüsch 1959). This was a great improvement on previous methods and led rapidly to a set of equations for calculating assimilation and stomatal conductance (Gaastra 1959).

Scarth (1927) argued that there would be little advantage for a plant to have a high rate of transpiration, but stressed the «... advantage of maintaining the fullest diffusive capacity of the stomata and the highest possible pressure of CO₂ in the intercellular spaces ». He concluded that the principal function of stomata «... is to regulate that very factor which is presumed to regulate them, viz. the concentration of CO₂ in the leaf or, respectively, in the guard cells ». Maskell (1928) tested this hypothesis experimentally and concluded that the rate of uptake of carbon dioxide was determined by variations in stomatal resistance and by resistances within the leaf. **The suggestion of a strong link between the leaf internal carbon dioxide concentration and leaf level WUE represented a large advance in the theoretical understanding of WUE.**

Penman and Schofield (1951) proposed, perhaps, the first theoretical link between leaf level **transpiration ratio** (leaf transpiration divided by assimilation) and the ratio of the coefficients of diffusion of water vapour and carbon dioxide in air, and the water vapour and carbon dioxide air-to-leaf pressure gradients. Gaastra (1959) suggested that the leaf internal conductance to carbon dioxide is a pivotal point of the ratio of assimilation to transpiration and of the water economy of crop plants. Bierhuizen and Slatyer (1965) showed that the **transpiration ratio could be predicted** from water vapour and carbon dioxide gradients over a range of light intensities, temperatures and relative humidities. These studies were the first to suggest that **whole plant transpiration efficiency might be regulated in part by leaf functioning and is, therefore, predictable.** They

opened new possibilities for plant improvement of drought resistance.

VII) How can the transpiration ratio be improved ?

Because water is increasingly scarce in a warming world, Rüschi (1959) queried whether the luxury of highly transpiring tree species could be justified. He argued for selective breeding of tree species varieties with low transpiration-to-assimilation ratio T/A by means of minimising transpiration while maximising assimilation. Also Polster, Weise, and Neuwirth (1960) assessed the potential suitability of tree species to sites by their dry matter production and transpiration ratio. Troughton (1969) and Cowan and Troughton (1971) suggested that genetic selection of plant varieties could be used to improve the transpiration ratio by decreasing leaf internal resistance to carbon dioxide diffusion. Cowan and Farquhar (1977) built on this theme by proposing that **stomata might optimise carbon gain to water lost by varying the conductances to diffusion and thereby maximising the ratio of the mean assimilation rate to mean rate of evaporation in a fluctuating environment**. Approaches which target photosynthesis, stomatal opening, leaf internal resistance to carbon dioxide diffusion or stomatal optimization in order to improve plants performance have since been followed in plant breeding and have largely been reviewed elsewhere (e.g. Condon et al. 2004; Cregg 2004; Vadez et al. 2014).

VIII) Intrinsic water use efficiency and carbon stable isotopes

Another milestone towards contemporary research on water use efficiency was the use of stomatal conductance to water vapour by Farquhar and Rashke (1978) rather than transpiration and to calculate water use efficiency as assimilation divided by stomatal conductance. This definition allowed an estimation of water use efficiency resulting only from plant functioning, without a direct impact from leaf-to-air vapour pressure difference and was named by Meinzer, Ingamells, and Crisosto (1991) « **intrinsic water use efficiency** » (W_i). Knowledge of W_i facilitated the search for a genetic basis of within species variation, e.g. Brendel et al. (2002), Condon et al. (2002) and Chen et al. (2011).

Development of the **stable carbon isotope method for estimating W_i resulted in a widely applicable screening method, and a large increase of publications around plant water use efficiency**. Based on the two-step fractionation model (atmospheric CO_2 – leaf internal CO_2 – plant carbon) proposed by Park and Epstein (1960), various models explaining the difference in carbon isotope composition between atmospheric CO_2 and plant carbon were developed in the late 1970's and early 1980's, e.g. Grinsted (1977), Schmidt and Winkler (1979), Vogel (1980). Vogel's model contained many theoretical aspects which, however, lacked experimental understanding. In parallel, Farquhar (1980) developed a similar model, but resulted in a simple, elegant mathematical model

relating plant natural abundance carbon isotope discrimination, relative to atmosphere, to the ratio of leaf internal to atmospheric CO₂ concentration. This was, in turn, related to W_i . Experimental evidence showed that carbon isotope measurements, in wheat, reflected long-term water use efficiency (Farquhar, O'Leary, and Berry 1982) as well as whole plant transpiration efficiency (Farquhar and Richards 1984). They concluded that carbon isotope discrimination may provide an effective means to assess and improve WUE of water-limited crops. Strong correlations between whole plant TE and stable carbon isotope measurements of plant organic material were shown in a host of papers to be. Some of these papers were (1) for crops and other annuals (Hubick, Farquhar, and Shorter 1986, Ehleringer et al. 1990, Virgona et al. 1990); (2) for trees (Zhang and Marshall 1994, Picon, Guehl and Aussenac 1996, Roupsard, Joly and Dreyer 1998). The isotopic method has spread rapidly as a general estimator of WUE and continues to be used widely in screening programmes for plant improvement as well as in ecological research, e.g., Rundel, Ehleringer, and Nagy (1989) and notably used in tree rings (McCarroll and Loader 2004).

IX) Conclusions

Water use efficiency is probably one of the oldest plant traits to stimulate across the centuries the interest of philosophers, theologians, Middle Age savants, and natural philosophers to modern plant scientists across different disciplines (plant physiology, ecophysiology, ecology, genetics, agronomy). The interest began as a purely philosophical one, progressed to thought experiments, toward an interest in plant functioning and its relationship to the environment. Already in the early Renaissance an experimentation was proposed, in a time when botany consisted mainly of naming plants (Morton 1981). It is then also an early example of an actually performed experimentation, the famous willow experiment by Van Helmont (1662) as well as of early "in laboratory" experimentation on plants (hydroponics experiments by Woodward in 1699). The decision what makes plants grow, between water or soil, kept natural philosophers busy up to the end of the 18th century, when the assimilation of CO₂ was discovered and the question finally solved.

Early in the 19th century, the interest turned to the amount of water that plants would need to grow, in the context of a developing research on agricultural practices (Morton 1981). Biomass was used to standardize the water losses which allowed comparisons among species (crops as well as trees) and a beginning study of the impact of different environmental variables.

At the end of the 19th century, knowledge on the functional aspects of CO₂ assimilation and the control of transpiration by stomata had sufficiently advanced, so that scientists started to reflect on the relationship between dry matter accumulation and transpiration. Was transpiration only a physical process or was there a physiological control? Was transpiration regulated by the dry matter production? Or does the stomatal opening determine the rate of CO₂ assimilation? Similarly to

photosynthesis (Nickelsen 2007), research on water use efficiency followed a path from the whole plant to molecular mechanisms.

At the turn of the 20th century, the study of species differences became more intensive (especially for crops) as well as the study impact of soil and climatic variables on the water requirement with a clear aim of improving agricultural practices, as show early examples from the United States Department of Agriculture (Briggs and Shantz 1913a, Briggs and Shantz 1914). At the beginning of the 20th century, observations of large differences in water requirement among plant species resulted rapidly the question “why” this was the case. As the discipline of “physiological ecology” developed, “water requirement” was inverted into an “efficiency”, reflecting an evolution from standardizing transpiration to a trait in its own right. This introduced ecological questions about the adaptation of plants to dry environments and its relation to transpiration efficiency. Further, a stronger interest in within species variations became apparent and counter intuitive results stimulated the discussion about ecological strategies. Methodological and theoretical advances in the mid 20th century showed the central role of stomata in the control of the transpiration as well as the assimilation of CO₂. The phrase “inevitable evil” for transpiration was coined, but also the idea that stomata might optimize water losses, and thus the objective that transpiration efficiency might be improved by breeding. Studies on all levels of water use efficiency increased exponentially in the 20th century, especially with the development of measurements of stable carbon isotopes in plant organic matter as an estimator of leaf level water use efficiency in the second half of the century. In parallel, modelling approaches were developed to scale from leaf level WUE to whole plant TE, e.g., Cernusak et al. (2007) and to the field or canopy, e.g. Tanner and Sinclair (1983).

At least from the beginning of the 20th century onwards, also critical views on the relationship between water requirement and its relation to growth mostly in terms of yield, were published (Dachnowski 1914). Viets (1962) asked “Is maximum water use efficiency desirable?”, especially in terms of crop production. Sinclair, Tanner, and Bennett (1984) considered different options for improving water use efficiency, however concurs that most of these have important limitations or drawbacks. This discussion is ongoing, as can be seen by the article published by Blum (2009): “Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress”. Still, many publications ask the question of how water use efficiency relates to the improvement of productivity of crops in water-limited environments (Araus et al. 2002; Passioura and Angus 2010), with some success stories of selecting for higher WUE (Condon et al. 2002) and positive notes on space on improvement, especially using molecular approaches (Chen, Chang, and Anyia 2011; Tuberosa 2012). Exploration and application of transpiration efficiency, at the whole plant level, and it derivatives at other levels are still a very active research field across nearly all levels of botanical research : concerning very rapid processes

at the leaf level (Violet-Chabrand et al. 2016), up-to-date genetic and genomic approaches for breeding (Dharmappa et al. 2019; Torre et al. 2019), studying local adaptation of plants to their environment in a population genetic context (Eckert et al. 2015) or an ecological context (Pellizzari et al. 2016), water use efficiency from the plant to the ecosystem (Medlyn et al. 2017; Tallec et al. 2013), estimated at the population level (Rötzer et al. 2013; Dekker et al. 2016) or modelling up to the global earth level (Cernusak et al. 2019), just to name a few. Thus the first curiosity of greek philosophers has motivated scientists through history, with many exciting discoveries still to come.

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