

A STUDY OF THE DRYING MECHANISMS OF TRIFOLIUM REPENS L.
AND T. PRATENSE L.

by
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Short title

A STUDY OF THE DRYING MECHANISMS OF TRIFOLIUM

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ABSTRACT

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A STUDY OF THE DRYING MECHANISMS OF TRIFOLIUM REPENS L. AND T. PRATENSE L.

A gasometric apparatus was devised to continuously monitor rates of moisture efflux from laminae and petioles of Trifolium repens L. and T. pratense L.

The results showed that the drying of detached laminae occurred in four distinct periods: initial rate period (IRP), rapid fall period (RFP), slow fall period (SFP), and exponential decline period (EDP). Apparently, the rate-governing factors in these periods were stomata, stomatal closure, cuticle, and internal resistance to moisture transfer, respectively. Most of the moisture was removed during SFP, though the EDP lasted almost as long as the SFP. The instrumentation did not detect this pattern in the drying of petioles.

This study indicated the importance of internal resistance to moisture transfer in the drying of plant shoots.

SOMMAIRE

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A STUDY OF THE DRYING MECHANISMS OF TRIFOLIUM REPENS L. AND T. PRATENSE L.

On a construit un appareil gazométrique pour mesurer continuellement les pertes d'humidité des limbes et des pétioles de feuilles de Trifolium repens L. et de T. pratense L.

Les résultats montrent que le séchage des limbes détachés s'est produit en quatre phases distinctes: la phase du taux initial (PTI), la phase de perte rapide (PPR), la phase de perte lente (PPL) et la phase de déclin exponentiel (PDE). Il semble que les facteurs influençant le taux de séchage durant chaque phase respective aient été les stomates, la fermeture des stomates, la cuticule et la résistance interne au passage de l'eau. La majeure partie de l'humidité s'est échappée durant la phase PPL même si la phase PDE a duré plus longtemps que la précédente. On n'a pu retrouver le même schème de séchage dans les pétioles.

Les résultats de cette expérience ont démontré l'importance de la résistance interne au passage de l'eau dans le séchage des plantes.

to mom and dad

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GLOSSARY

a) Leaf

Lamina - leaf blade

Petiole - leaf stalk

Petiolate lamina* - lamina with petiole.

Detached lamina* - lamina without petiole

b) Moisture content

W_D^* - dry weight (oven dried at 80°C for 72 hrs)

W_F^* - final weight (weight of material at end of any drying experiment)

d.b. - dry basis (moisture content expressed as:

$$\frac{\text{weight of water}}{\text{dry weight}} \times 100)$$

RWC - relative water content (expressed as:

$$\frac{\text{weight of material} - \text{dry weight}}{\text{weight at saturation} - \text{dry weight}} \times 100)$$

ENC - equilibrium moisture content (moisture content of hygroscopic material in contact with air at a given relative humidity for an indefinite amount of time).

CMC - critical moisture content (moisture content at end of constant rate period, and start of falling rate period, q.v.).

GLOSSARY CONT'D

c) Rate periods

i) in physical model

CRP - constant rate period (drying in a manner comparable to that of an open-faced body of water)

FRP - falling rate period (drying at declining rates, when rate of internal moisture transfer is less than rate of evaporation from surface)

ii) in drying of red and white clover laminae

IRP* - initial rate period

RFP* - rapid fall period

SFP* - slow fall period

EDP* - exponential decline period

*Terms having specific meaning in this report.

I. INTRODUCTION

Conservation is a vital element in the efficient use of forage resources, especially where year round grazing is not possible. Efficient conservation methods should combine low unit storage costs as well as maximum nutrient preservation.

Hay and silage are the two most important forms of conserved forage. The production of both requires a period during which the cut material is allowed to lose moisture to the surrounding air. In its high moisture state in the field, this material is susceptible to nutrient and dry matter losses through respiration, leaching, bleaching, and leaf shattering. These losses have been estimated to total 30-50 percent of the original crop in much of the hay made in the United Kingdom (Watson and Nash 1960).

The reduction of nutrient losses is associated with maximizing the rate of moisture loss from the cut plants. Much effort has gone into developing mechanical and chemical treatments to achieve this. Nonetheless, the actual mechanism of moisture loss from cut plants remains comparatively obscure.

Basically the transfer of moisture away from wet material is subject to the control of a combination of physical conditions such as vapour pressure and energy gradients. The drying of whole plants, however, is uniquely affected by the presence of an existing water transport system. The interaction of these physical and biological factors renders the understanding of hay drying a particularly evasive and interdisciplinary problem.

II. REVIEW OF LITERATURE

2.1 Drying: Physical Perspective

The drying of solids is generally regarded as removal of water by evaporation - the process involving simultaneous mass and heat transfer (Fulford 1969). The mass transfer includes the movement of moisture within the material in liquid or vapour form and the movement of moisture in vapour form away from the surface of the material. Heat transfer occurs in the evaporation of the liquid water (Hall 1957).

The driving force of the drying process is the vapour pressure gradient between the wet material and the atmosphere. The atmospheric vapour pressure is a function of dry bulb temperature and humidity, while the vapour pressure of the material is the partial pressure of the water in the material.

The basic theory for the drying of solids, developed by the study of non-hygroscopic materials (e.g., Lewis 1921; Sherwood 1929), suggests that the drying of these materials occurs in two stages: the constant rate period and the falling rate period (Sherwood 1929; Henderson and Perry 1955; Hall 1957; etc.).

2.1.1 Constant rate period concept

The factors governing the constant rate period are well understood and described by the equation (Henderson and Perry 1955):

$$\frac{\delta W}{\delta \theta} = f_v A (P_s - P_a) = \frac{K_f A (t_a - t_s)}{h_{fg}} \quad \dots (1)$$

where:

- $\frac{\delta W}{\delta \theta}$ = drying rate, lb H₂O/hr
- f_v = vapour (mass) transfer coefficient, lb/(hr sq ft psi),
- A = water surface area, sq ft
- P_s = vapour pressure at t_s , lb/sq in
- P_a = vapour pressure in the air, lb/sq in
- K_f = thermal conductance of air film, Btu/(hr sq ft deg F)
- t_a = temperature of air, deg F
- t_s = water temperature, wet bulb, deg F
- h_{fg} = latent heat of vaporization, Btu/lb

As shown by the equation, it is the water and air conditions at the drying interface, not the nature of the solid, that determines the rate of drying.

2.1.2 Falling rate period concept

The falling rate period is generally of greater interest as most agricultural and food products dry in this period (Henderson and Perry 1955; Hall 1957; Saravacos and Charm 1962). It begins at the critical moisture content when the migration rate of water from the interior to the surface becomes less than the rate of evaporation from the surface. The drying rate is then governed by the migration rate which is determined by the properties of the material (Charm 1963).

Internal moisture transfer, particularly in complex hygroscopic biological materials, has been studied intensively.

Two fundamental approaches have been used, as reviewed by Fulford (1969):

2.1.2.1 Analytical approach

Attempts have been made to identify and quantify physical parameters in order to predict internal moisture (and heat) transfer rates and thus drying behaviour during the drying rate period. Several factors complicate this approach. Firstly, while as much as 80-90 percent of the moisture in foods (probably less in hay crops) exerts a vapour pressure nearly equal to that of pure water (Labuza 1960), the remaining 10-20 percent is bound with various degrees of tenacity, depending upon the form of binding (Kuprianoff 1958):

- 1) adsorption in a monomolecular film
- 2) adsorption in additional molecular layers
- 3) adsorption of condensed water, including dissolved solutes, by capillarity.

This bound water requires additional energy for its removal. Secondly, liquid-gas phase interchange may occur internally during moisture transfer. Thirdly, changes in physical properties of materials due to shrinkage, rupture, or crust formation accompany drying. Finally, the moisture may be transferred by several different mechanisms, depending on the nature of the material, type of bonding, moisture content, temperature, etc., as reviewed by Van Arsdel (1963):

- 1) liquid movement by capillary forces;
- 2) liquid diffusion due to concentration gradients;
- 3) surface diffusion of adsorbed water on pore surfaces;
- 4) vapour diffusion within pores due to partial pressure differences;
- 5) vapour flow due to pressure changes caused by shrinkage;
- 6) liquid flow caused by gravity.

Fulford (1969) reported two additional mechanisms:

- 7) movement as a direct result of temperature gradient;
- 8) liquid movement as a result of shift in vapour pressure gradients due to coupling of liquid and vapour transfer process.

2.1.2.2 Empirical approach

By contrast, in the empirical approach, only the overall drying behaviour of material samples is investigated and quantified. Lewis (1921) indicated that drying rate is proportional to the difference between average moisture content in materials at any time and equilibrium content. This can be expressed by the equation:

$$\frac{\delta M}{\delta \theta} = -K(M - M_e) \quad \dots (2)$$

where:

θ = time

M = average moisture content at time θ

M_e = equilibrium moisture content

K = drying constant

In this equation, K represents the overall heat and mass transfer properties of the material. The integrated form of this equation describes the relationship between "free moisture ratio" and time:

$$\frac{M - M_e}{M_o - M_e} = e^{-K\theta} \quad (3)$$

where

e = base of natural logarithms

o = original

$$\frac{M - M_e}{M_o - M_e} = \text{free moisture ratio}$$

giving also the relationship

$$\frac{\delta M}{\delta \theta} = -Ae^{-K\theta} \quad (4)$$

where

$-A$ = initial drying rate

These mathematical relationships can describe the thin layer drying of shelled corn (Hall and Rodrigues-Arias 1958), wheat kernels (Simmonds et al. 1953), and such high moisture products as formed poultry excreta (Midden et al. 1973) and vegetables and fruits (Saravacos and Charm 1962).

These equations have been applied to describe hay drying by many workers. Leshem et al. (1972) found equation (3) suitable for the drying of detached laminae of Dactylis glomerata at 28°C. Menzies and O'Callaghan (1971) successfully fitted it to their thin layer drying data for Italian and perennial ryegrass between 80 and 200°C but not above or below these temperatures. Morris (1972) used the

same equation to describe the drying of several grass species at 20°C including Lolium perenne, S23, Anthoxanthum odoratum, Agrostis stolonifera, Cynosurus cristatus, and Festuca ovina. Priepke and Bruhn (1970) found it appropriate for most of the falling rate phase of alfalfa plants drying at 97°F; Bagnall et al. (1970) found it appropriate for detached alfalfa stem segments at 80°F; and Whitney et al. (1969) applied it for the high temperature (300-1400°F) drying of alfalfa leaves.

Support for these equations has been widespread due to their root in mass transfer theory and their simplicity. Several authors have found a lack of fit when applying them to their data and have thus proposed alternative equations. For example, Paulsen and Thompson (1973) proposed the following polynomial expansion for the drying of grain sorghum:

$$\theta = A \ln \left(\frac{M - M_e}{M_o - M_e} \right) + B \left[\ln \left(\frac{M - M_e}{M_o - M_e} \right) \right]^2 \dots (5)$$

in which A and B are temperature dependent empirical constants having little physical significance. Rees (1974) proposed a truncated exponential series, similar to the above, for the drying of herbage.

$$M - M_e = ae^{-K_1\theta} + be^{-K_2\theta} \dots (6)$$

where $a + b = M_o - M_e$, while K_1 and K_2 are empirical constants.

Chen and Johnson (1969) proposed a rate law of the form

$$\frac{\delta M}{\delta \theta} = -K(M - M_e)^n \dots (7)$$

in which n , an empirical constant lacking in physical meaning, complicates the significance of K . Overhults et al. (1973) and White et al. (1973) used a similar 2 constant exponential equation to describe the drying of soybeans and white shelled corn, respectively. Bunn et al. (1972) proposed the following equation which they found described the drying of a variety of high moisture materials (e.g., tobacco, hay, peanuts, and manure) over a wide range of temperatures:

$$W = W_e + (W_o - W_e) \left(\frac{H}{\theta + H} \right) \quad \dots (8)$$

in which W = weight, and H represents the drying half life (i.e., the time when $\frac{W - W_e}{W_o - W_e} = \frac{1}{2}$) and thus the drying properties of the materials.

2.1.2.3 Multiple falling rate periods concept

The concept of a single falling rate period in hygroscopic materials has been challenged by many authors. Bravo and McGaw (1974) suggested three essentially linear falling rate periods in the drying of cocoa beans. Priepke and Bruhn (1970) found in addition to an exponential (rapid fall period), also a "first" period of rapid drying and a "last" period of slow drying for alfalfa. Their findings are similar to those of Menzies and O'Callaghan (1971), who suggested three exponential falling rate periods for the drying of ryegrass. Jason (1958) reported only two exponential falling rate periods for the drying of rectangular fish fillet, while Gorling (1958) found that the drying curve for potato slices was divided into three distinct regions by two "break-points."

These authors used information from analytical studies of the factors that regulate internal moisture transfer to explain the occurrence of numerous rate periods. No doubt, though, a great deal more work must still be done before the analytical and empirical approaches can be successfully unified.

2.2 Drying: Biological Perspective

The empirical study of drying, based on existing theories for non-living industrial material, has been gainfully conducted on plant parts having reached a dormant stage, such as seeds and woody tissue. This approach, however, is less successful for the drying of fresh leaves and stems, for which a fundamental understanding of anatomy and physiology is necessary. Hall (1957) reviewed several characteristics that render the drying of forage plants especially involved:

- 1) high initial moisture content
- 2) complex morphological and anatomical organization
- 3) complex chemical composition
- 4) high physiological activity

A considerable amount of research has been conducted on transpiration in living plants, even under conditions of moisture stress, but there has been comparatively little study of this process in desiccating plants. Warboys (1967) argued that transpiration continues after a plant has been severed "since there is little evidence to support the view that all physiological mechanisms come to an abrupt end once the water supply is removed". The decrease in drying rate

following cutting is due initially to the responses of the plants to moisture stress and subsequently to the gradual breakdown of the normal water transport/transpiration system in the dehydrating tissue. The course of this breakdown is not well understood.

2.2.1 The initial condition -
moisture transfer in
turgid plants

2.2.1.1 Vascular water flow
through plant shoots

Water transfer through plants, from the roots to the evaporating surfaces of the leaves, occurs in the liquid phase. Most of the liquid flow through the stem occurs in xylem elements along gradients of hydrostatic pressure. Vascular permeability has been estimated to be at least three orders of magnitude greater than that of any pathway external to it (Slatyer 1967), since moisture is able to travel not only along the highly cutinized cell walls of xylem vessels but also through their lumina. However, for normal flow to occur, continuous water columns must exist, as stated in the "cohesion theory of water ascent."

In the nodal regions, where leaves are attached to the stems, segments of the vascular system (called leaf traces) separate and extend through the petioles into the leaf blades, where they become known as veins. They branch and rebranch giving rise to so many tiny veins that few cells in the leaf are far removed from a vein.

2.2.1.2 Non-vascular water transport.

It is commonly believed that extrafascicular water transport occurs as mass flow across cell walls rather than through protoplasm or vacuoles, although Raney and Vaadia (1965) postulated a separate diffusion pathway which occurs more uniformly through the entire cell. It is not clear whether at low moisture contents mass flow or diffusion prevails or whether there is a transition from one mechanism to the other due to the retreat of evaporating surfaces during drying.

2.2.1.3 Movement of water through leaves

Two principal sites of evaporation are assumed to exist within a leaf; one located within the walls of mesophyll cells surrounding the extensive but tortuous network of intercellular spaces, and the other located within the walls of the epidermal cells.

The exact pathway of water from the veins to the leaf surfaces has not been entirely clarified. Williams (1950) suggested that the water is supplied to the epidermis directly from the veins. Wylie (1943) reported that bundle sheath extensions leading to both the upper and lower epidermis in mesomorphic plants form a pathway for water. Russel and Woolley (1961) reported that a significant proportion of the water diffuses through intercellular spaces as a vapour, but Kramer (1969) argued that this cannot be significant because of the slowness of vapour transport. Weatherly (1963) suggested movement through the mesophyll across cell walls.

It is now generally believed that moisture is supplied to the epidermis from leaf veins by liquid diffusion across cell walls, whereas water which evaporates from mesophyll cells; diffuses through intercellular spaces and exits leaves through stomatal pores.. Milthorpe (1959) summarized the components of leaf resistance to moisture transfer by the following equation:

$$R_L = d + \frac{1}{S_C + S_D / [1 + S_D (1/S_I + 1/S_W)]} \quad \dots (9)$$

where

R_L = total leaf resistance

S = conductance (reciprocal of resistance)

d = external resistance

C = cuticular

D = stomatal

I = substomatal cavities

W = cell wall

which for wheat simplified to

$$R = d + \frac{1}{S_C + 0.98 S_D} \quad \dots (10)$$

The relative magnitude of the resistances indicates the extent to which each restricts transpiration.

The resistance pathway in the leaf

a) External resistance

The external resistance is a function of the boundary layer, which is related to wind speed, leaf width and surface texture.

b) Cuticular resistance

The cuticular resistance, which comprises the combined resistances of epidermal cells, cutinised layer, cuticularised layer, and epicuticular wax layer, represents a major barrier to moisture loss (estimated at 10-40 sec/cm for most crop plants by Kramer, 1969). Neither the relative importance of each layer nor the location of the liquid/gas evaporating interface has as yet been determined, though Hall and Jones (1961) demonstrated the importance of epicuticular waxes in white clover. In drying, cuticular resistance is generally thought to be constant (e.g., Sepherd 1964), though Martin and Scott (1957) showed that the cuticles of grapes which had lost more than 20 percent of their original moisture, thickened and wrinkled, thus increasing their resistance to water transfer.

c) Stomatal resistance

Stomatal openings are the primary exits of water vapour from leaves. In physiologically active plants stomatal resistance is determined by stomatal aperture, which in turn is affected by numerous environmental and endogenous factors. Diffusion resistance through open stomata of crop plants ranges between 0.6 and 2.1 sec/cm (in Kramer 1969).

d) Intercellular resistance

The extensiveness of intercellular spaces results in internal surface area for evaporation in leaves being an order of magnitude greater than external area. The resistance to moisture transfer by

internal exposed cell walls, considered slight by Milthorpe and Spencer (1957) but significant by Shimshi (1963a) and Laouar (1974), is nonetheless slight in comparison with cuticular resistance. Its importance, which is normally significant only when stomata are open, may increase in response to dehydration because of changes in internal geometry (Kramer 1969).

e) Mesophyll resistance

Mesophyll resistance has generally been found negligible in turgid leaves (e.g., Gregory *et al.* 1950; Williams and Amer 1957; Milthorpe 1959), although it likely becomes significant during drying as evaporating surfaces retreat into cell walls, lengthening the diffusion pathway and lowering the vapour pressure (as in "incipient drying", Livingston and Brown 1912).

2.2.1.4 Water in cells (Slatyer 1967)

a) Forces holding moisture in cells

Although moisture is often thought of as existing in either bound or free form in plant material, a more correct view is that there is a continuum between these two extreme states. This continuum is frequently represented by sorption isotherms which relate equilibrium moisture content to vapour pressure deficit, or by implication, binding tenacity (e.g., Guthrie and Collins 1965). These binding forces differ between regions of cells and tissues.

b) Water in cell walls

The majority of moisture in cell walls is loosely held by surface tension within interfibrillar spaces of long chain cellulose and pectin molecule matrices, while less than 10 percent of total moisture (in wood, Stamm 1944) is tightly bound by monomolecular adsorption or by ionic bonds with methylated galacturonic acid side chains. The water content of cell walls in Avena coleoptiles averages about 50 percent (Preston* and Wardrope 1949).

c) Water in protoplasm

Most of the moisture which comprises up to 95 percent of protoplasm, exists in a relatively free state; while bound water is held by hydrophilic amino acid side chains on protein molecules and within their tertiary structural matrices. Some moisture is also bound to the plasmalemma and tonoplast.

d) Water in vacuoles

Vacuoles contain as much as 98 percent water, most of which is loosely held by osmotic forces, though some moisture may be bound to colloids.

e) Water in the vascular system

Most water in the vascular system exists as aqueous solution within lumina of vessel elements. Secondary thickening in vessel walls limits their capacity to hold moisture.

f) Water permeability of cells

The permeability of individual cells is determined primarily by the plasma membrane, although in cells secondarily cutinized and lignified, cell walls may also be important. Apparently, dehydration at first reduces membrane permeability to moisture, due to increased protoplasmic viscosity (Levitt et al. 1936) and then increases permeability due to plasmolysis (Myers 1951). Little is known of the effects of dehydration upon cell wall permeability.

2.2.2 Moisture transfer during drying

2.2.2.1 Water conducting system

Several experimenters have studied the effect of existing water conducting system in plants upon the removal of moisture during drying, in particular the role of leaves in the evaporation of stem moisture. Early work by Jones and Palmer (1933, 1934, 1936) and Jones (1939) indicated that intact shoots of alfalfa and Johnson grass plants with attached leaves dried faster than those with detached leaves. They reported further that Johnson grass maintained the difference for a longer time and attributed this to its larger midrib. Shepherd (1964) found that up to 24 percent of the total petiole moisture in white clover was lost via the laminae, this quantity frequently exceeding that residing initially in the petiole xylem. Pederson and Buchele (1960), however, found little difference in drying time between alfalfa plants with or without leaves, concluding that little axial but rather mostly radial water transfer occurred in the stems. Byers and Routley

(1966) reported that moisture moved through steamed alfalfa plants as long as both leaves and stems remained moist.

Bagnall et al. (1970) investigated the directional tendencies of moisture transfer in two-inch long alfalfa stem segments, during drying. They found that both the epidermis and cortex constituted important barriers to radial moisture flux; in fact, complete prevention of radial transfer reduced the drying rate constant (equation 3) by only 30 percent. They estimated that radial and axial diffusivities in these stem segments were in the order of 10^{-5} and 10^{-4} sq.ft./hr, respectively, while in epidermis diffusivity was roughly 10^{-8} sq.ft./hr. However, because they did not consider the effects of either capillary flow or diffusivity variation with moisture content, their estimates lack accuracy.

2.2.2.2 Stomatal control

The role of stomata in drying has been intensively studied. Open stomata offer the path of least resistance for moisture efflux from plants; for example, stomatal transpiration exceeds cuticular transpiration by a factor of 6.5 in Betula papyrifera leaves (Waisal et al. 1968).

Early reports by Hygen (1951, 1953) revealed that drying of detached leaves of many species occurred in three distinct phases: stomatal, stomatal closing, and cuticular. During the stomatal phase (which lasted 10-30 minutes) moisture loss rates declined exponentially due to increased internal resistance. The subsequent closing phase

lasted from 0.5 to 2-hours. Waisal et al. (1968) found a similar pattern for detached B. papyrifera leaves, though noting both a brief constant rate period of surface drying and a falling rate period within the stomatal phase. The stomata closed at a relative water content (RWC) of 70 percent after 18 minutes of drying. Laouar (1974) also found that the stomatal phase was associated with increased internal resistance. Gregory et al. (1950) found that stomata closed at 90 percent RWC. Several experimenters, including Gregory et al., Milthorpe (1959) and Williams and Amer (1957) found that internal resistance did not affect the transpiration rate until after stomata closed.

Other studies of the drying of whole plants have indicated that early fall in drying rate, usually up to three hours after cutting, is caused by stomatal closure (Jones and Palmer 1932, 1933, 1934; Jones 1939; Pederson and Buchele 1960; Shepherd 1964). Shepherd, however, noted that petiolar stomata in white clover closed only after about 70 percent of the petiole moisture had been removed.

Due to lack of proper techniques, the extent to which stomata close, or the role of stomatal leakage after closure has not been determined. Pederson and Buchele (1960) suggested that closure is complete, as did Shepherd (1964), though Jones and Palmer (1933) found that more than 40 percent of stomata remain partly open throughout drying. Whitney et al. (1969) showed that (in high temperature) drying rate can be appreciably affected by slight stomatal opening.

There have been several reports on the use of chemicals to promote drying by inhibiting stomatal closure. Waisal et al. (1968) found that the anti-transpirant phenylmercuric acetate prevented complete closure of laminar stomata. Stalfelt (1957) reported that sodium azide (NaN_3) can inhibit stomatal closure under conditions of moisture deficit, while Walker and Zelitch (1963) found that $5 \times 10^{-4} \text{M}$ NaN_3 was the only concentration that prevented closure in the dark. Mears and Roberts (1970) increased the overall drying rate of whole alfalfa shoots using this chemical, though Tullberg and Angus (1972) found it accelerated drying of leaves, but not whole plants.

Other chemicals have also been tried. Turner (1970) induced faster drying of alfalfa with the fungal toxin fusicoccin. Although this compound was known to effect stomatal opening in a wide range of species, the author was unable to show this. Morris (1972) accelerated the drying of leaves of Dactylis glomerata with this chemical. The hormone kinetin has also been used to open stomata in barley leaves (Livne and Vaadia 1965), though no drying studies have as yet been conducted.

III. OBJECTIVES

In view of the complex nature of the drying process in green plants, the present study was undertaken to clarify some biological and physical aspects in drying of fresh plants. Of particular interest was the manner in which internal control evolved during the course of drying. Aspects under investigation included the axial movement of moisture in petioles that enable the leaves to act as sinks or evaporators for petiole and stem moisture, the role of stomata, and factors which interfere with moisture transfer. In short, the objective was analysis of the generalized drying coefficient represented by "K" in equation (4).

IV. MATERIALS AND METHODS

4.1 Description of apparatus

4.1.1 Design criteria

Conventional drying studies have been based on gravimetric techniques. However, because of the dynamic and complex nature of the drying process in green plants, a system was needed that could directly measure the drying rates of the plants rather than their moisture content. The requirements for the system were considered to be:

- 1) The ability to measure desorption rates from both intact plants (transpiration) and excised plants (drying).
- 2) The ability to measure separately the desorption rates from individual plant parts such as leaves and petioles, without disrupting the integrity of the plant.
- 3) The ability to obtain measurements without handling or manipulating the plants.
- 4) Continuous recording.
- 5) Rapid response.
- 6) Sufficient resolution for measuring the vapour loss of single leaves.
- 7) Simplicity and reliability.

4.1.2 Logical design of the apparatus

A gasometric system, using "open" circulation (Sestak et al. 1971), was assembled to accommodate these criteria (see Figure 1).

The system involved the measurement of the increase of humidity in the air surrounding the plants by passing an air stream of known humidity at a constant, measured flow rate, through a chamber enclosing the plant and onto a vapour analyzer.

The system may be thought of as having four groups of components.

- 1) The air conditioning apparatus supplies air of steady state temperature and humidity to the environment room, in which the transpiration chambers are maintained.
- 2) The transpiration chamber encloses the plant or plant part to prevent escape of evolved vapour. The efflux rates are determined from the changes in vapour content of the ambient air surrounding the plant material within the chamber.
- 3) The gas analyzer measures vapour content of both control air and transpiration chamber air, thus estimating moisture contributed by plants.
- 4) The gas handling system maintains a flow of air through the transpiration chamber and channels the air to the gas analyzer for measurement.

4.1.3 Physical design

A. The air conditioning system

The entire gasometric apparatus, except the recording instruments, was located in a thermally insulated environment room (234 x 234 x 182 cm, inside dimensions; Figure 2). An Aminco-Aire unit (American Instrument Co., Silver Spring, Maryland; Figure 3) supplied the room with conditioned air, maintained at $21 \pm 1^{\circ}\text{C}$ and $45 \pm 4\%$ R.H. Dry and wet-bulb temperatures were continuously monitored by a Multi/Riter Recorder, model FMWDT6C (Texas Instruments Inc., Houston, Texas; Figures 2, 17) fitted with copper-constantan thermocouple wires.

For wet-bulb temperature measurements the thermocouple junction was encased in a solder-filled brass cylinder wrapped in a psychrometric wick. The wick dipped into a reservoir of distilled water and was subject to a fan forced draught at 1200 fpm. The air was directed away from the experimental area so as not to disturb the controlled environment.

B. Transpiration chambers (T)

Two types of transpiration chambers (T) were used, lamina chambers (Figures 5, 6 and 7) and petiole chambers (Figures 5 and 7).

A lamina chamber was constructed from a 10 x 1.5 cm plastic petri dish. The air inlet was a hole (0.6 cm in diameter) drilled into the lid near the edge. The outlet consisted of a hole, fitted with a tubing connector, near the edge of the bottom dish. The outlet was oriented distally to the inlet for maximum air exchange. A slit

(0.4 x 4.0 cm approx.) was also cut from edge to centre of the bottom dish. This slit enabled the sliding of an attached leaf into the chamber. A mastic compound, Apiezon Q (Apiezon Products Ltd., London, Eng.), was used to seal the top and bottom dish together and to caulk the slit around the petiole.

A petiole chamber was constructed from a plexiglass cylinder (12.5 x 1.6 cm O.D.) having walls 0.1 cm thick. The cylinder was slit into halves and hinged with plastic insulation tape. The air inlet was a hole (0.6 cm diameter) near an end in one of the halves. The outlet consisted of a hole of the same size, near the opposite end of the other half, fitted with a tubing connector. The unhinged side and the ends were sealed with Apiezon Q.

The lamina chambers were supported by flat jaw extension clamps, while the petiole chambers were held by three-prong extension clamps (Figure 5). The chambers contained no internal regulation of air circulation.

C. The gas handling system

The principal functions of the gas handling system were:

- 1) To maintain a constant measured flow of air into the transpiration chambers.
- 2) To transport air from the chambers into the gas analyzer for measurement.
- 3) To transport a reference air stream into the gas analyzer.
- 4) To enable the measurement of three air streams with the use of a single gas analyzer.

a) Transpiration chambers

The gasometric system was designed to compare the drying pattern of two sets of leaves or petioles (Samples I and II, Figure 1) receiving different treatments. Each set consisted of one, two, four, or eight transpiration chambers, for measuring a smaller or larger number of samples. Air was drawn into the chambers and through the apparatus by a vacuum pump. Although there was no device within the chambers to stir the air, its rapid turnover (at least 0.72 and 6.5 times/minute in the lamina and petiole chambers, respectively) assured efficient removal of vapour from the chambers.

b) The airline

Air was transported through the apparatus via 0.6 cm ID tygon tubing. It was found, with the aid of an air velocity meter, Model 55A1 (Flow Corp., Watertown, Mass.), that resistance to flow in the tubing is proportional to its length and curvature. Consequently, the connecting tubes used to collect the air from the chambers of each set into a single stream, were of equal length and kept free of constrictions, to assure equal flow from each chamber. However, the actual flow from each of the chambers could not be measured directly with available equipment.

The third (reference) air stream was drawn from the ambient air surrounding the chambers.

c) Flowmeters (f; Figures 8, 9)

Each of the three air streams was then channelled into a Tri-Flat Variable-Area flowmeter (Fischer and Porter Co., Warminster, Pennsylvania) consisting of a cylinder (FP-1/8-20-G-5) and a sapphire float (#1550). These rotameters enable simple and accurate measurement of air flow to a maximum of 960 CC (STP) per minute, although flow rates were maintained between 425 and 525 CC per minute. The slight flow resistance offered by the flowmeters resulted in negative pressures between the pump and the meters. This pressure was assumed equal for the three meters and therefore ignored in the calculations. The flow rates of the three air streams were equalized using the needle valves (N) located on top of the flowmeter housing.

d) Control box (Figures 10, 11 and 12)

Because the gas analyzer can measure only one air stream at a time, it is necessary to obtain successive measurements of the three air streams. The control box served to channel selectively the air streams either into the gas analyzer or through the bypass.

i) Electrical connection

The control box contained three 3-way solenoid valves (S; Ascoelectric Co., Brantford, Ont.) and a repeat cycle, 3-cam switch timer (T; Matrix, Toronto, Ont., Model No. D6314) with a Synchron motor (Model 313RC). Each solenoid valve was wired to one of the timer switches. Each switch was turned on in succession, for a five-minute period by the clock motor, thus activating its respective valve. This cycle was repeated every fifteen minutes.

ii) Pneumatic connection

Each solenoid valve has one inlet and two outlets. When the valves were energized the air flow was through outlet "A" (Figure 1), when de-energized through outlet "B". All "B" outlets led to the gas analyzer (Dph) while all "A" outlets led to the bypass. Since only one valve was activated at any time, only one of the air streams was channelled to the bypass. Each air stream thus passed through the analyzer for five of every fifteen minutes.

e) System air flow and regulation

The air stream passing through the analyzer also passed through an additional flowmeter (F_p), used as a continuous reference for the other flowmeters. Because this stream encountered more flow resistance than the bypass stream, two hosecocks (H_1) were used to equalize resistances in the lines, and hence maintain constant flow through the chambers throughout the measuring cycle.

The bypass and reference streams were then combined and channelled into damping jars (D; Figure 13), large volume flasks which smoothed out fluctuations in the air flow caused by the oscillating suction of the pump. The additional inlet before the pump, together with the hosecocks (H_2), served to regulate the overall air flow.

The pump (P; Figure 14) consisted of a high capacity peristaltic type pumphead (Masterflex, Chicago, Ill., model No. 7019) and a 1/3 horsepower utility motor (Canadian General Electric, Peterborough, Ont.). It provided fairly constant flow rates which had to be

readjusted every 24-48 hours, as the tygon tubing in the pump head fatigued.

D. The gas analyzing system

The gas analyzer (Figure 15) used was a dew point hygrometer (Cambridge Systems, Waltham, Mass.; model 880), which has a specified accuracy of 2°F nominal, resolution of 0.5°F nominal, and dew point response of $4^{\circ}\text{F sec}^{-1}$ maximally. The instrument was reliable, responsive and had fairly high resolution. Its accuracy, found to be the weakest attribute was tested before the start of experimentation by the procedure described in Appendix I. In addition, the measurements were verified continually during experiments using the dry and wet bulb temperatures.

The electrical output of the instrument was connected to a Heathkit Sento Recorder (R), model EU20B (Benton Harbor, Michigan; Figure 18), which was located outside the environment room.

4.1.4 Calculating of drying rates

The recorder output (millivolt units) (Figure 16) was non-linear and thus was converted to dew point temperature with a temperature vs percentage output chart. The dew point temperatures were converted to vapour densities with psychrometric tables. Drying rates were computed as follows:

$$\frac{\delta M}{\delta \theta} = \frac{(R_s - R_c) Q \alpha_T}{W_D} \quad \dots (11)$$

where

$\frac{\delta M}{\delta \theta}$ = drying rate (mg H₂O/gm W_D - min)

R_s = humidity ratio of sample stream (mg H₂O/mg air)

R_c = humidity ratio of reference stream (mg H₂O/mg air)

Q = flow rate (cc/min)

α_T = density of air at temperature T, assuming standard pressure (mg/cc)

W_D = oven dry weight (g)

Legend for Figure 1

T : Transpiration chamber
F_n : Sample flowmeter (n = 1, 2, or 3)
N : Needle valve
S_n : Solenoid valve (n = 1, 2, or 3)
T_m : Timer motor
S_w : Cam switch
D_{ph} : Dew point hygrometer
R : Recorder
F_R : Reference flow meter
H_n : Hosecock (n = 1, 2)
D : Damping jar (2 jars used)
P : Pump
A : Bypass outlet
B : To hygrometer outlet
—— : Pneumatic line
--- : Electrical line

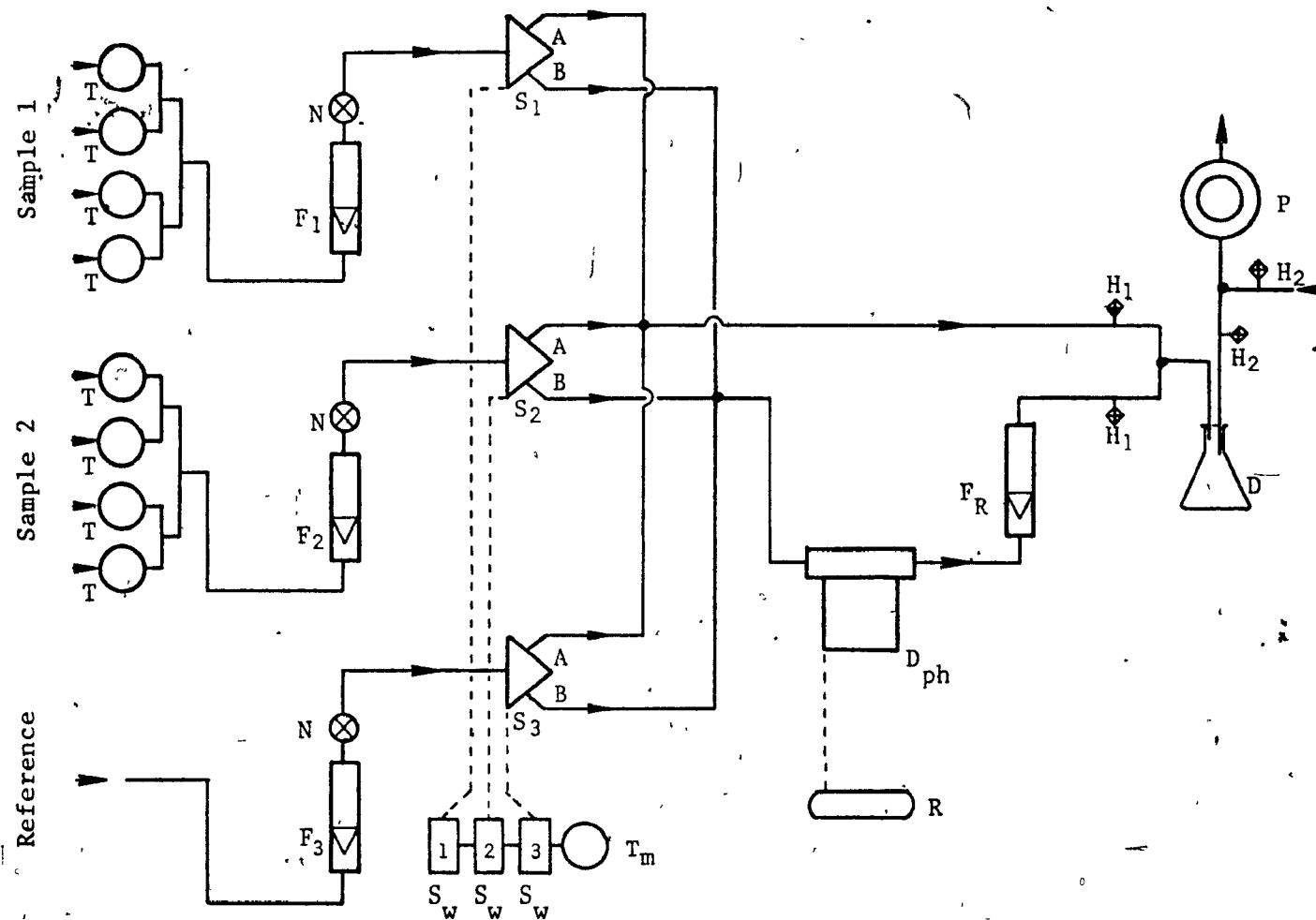


Figure 1. Gasometric apparatus, schematic. See legend.



Figure 2. Controlled environment room viewed from outside.

Figure 3. Aminco-Aire unit.

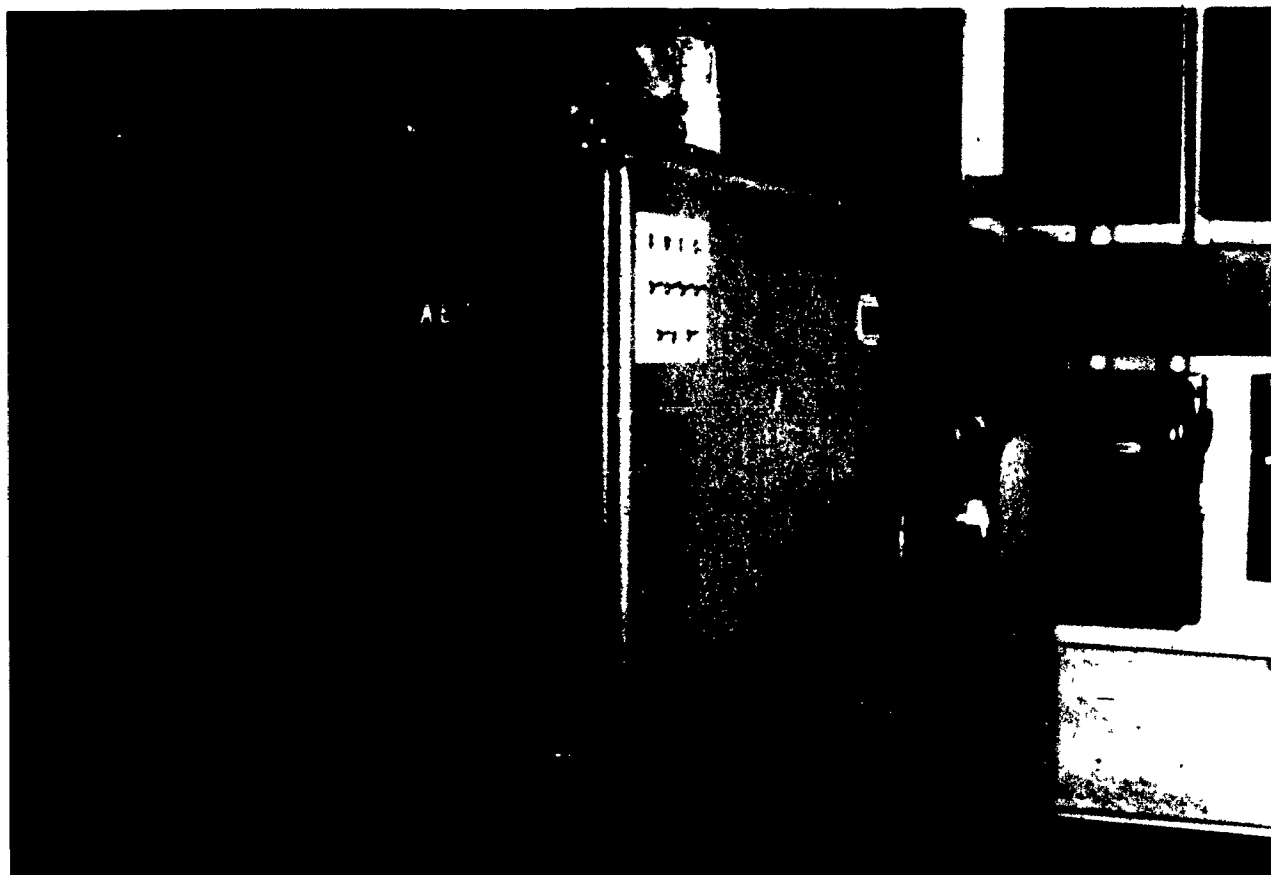




Figure 4. Gasometric apparatus in controlled environment room.

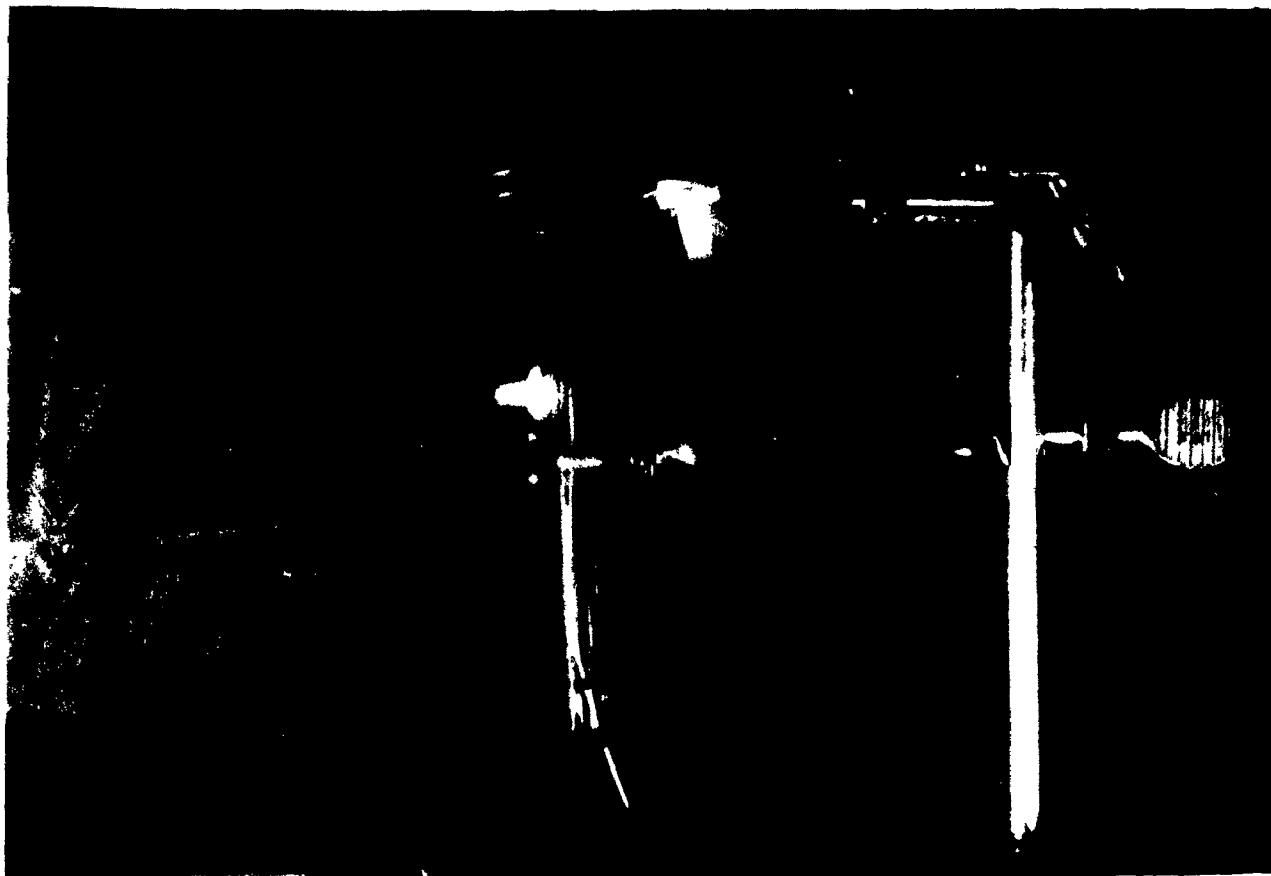


Figure 5. Leaf and petiole transpiration chambers.

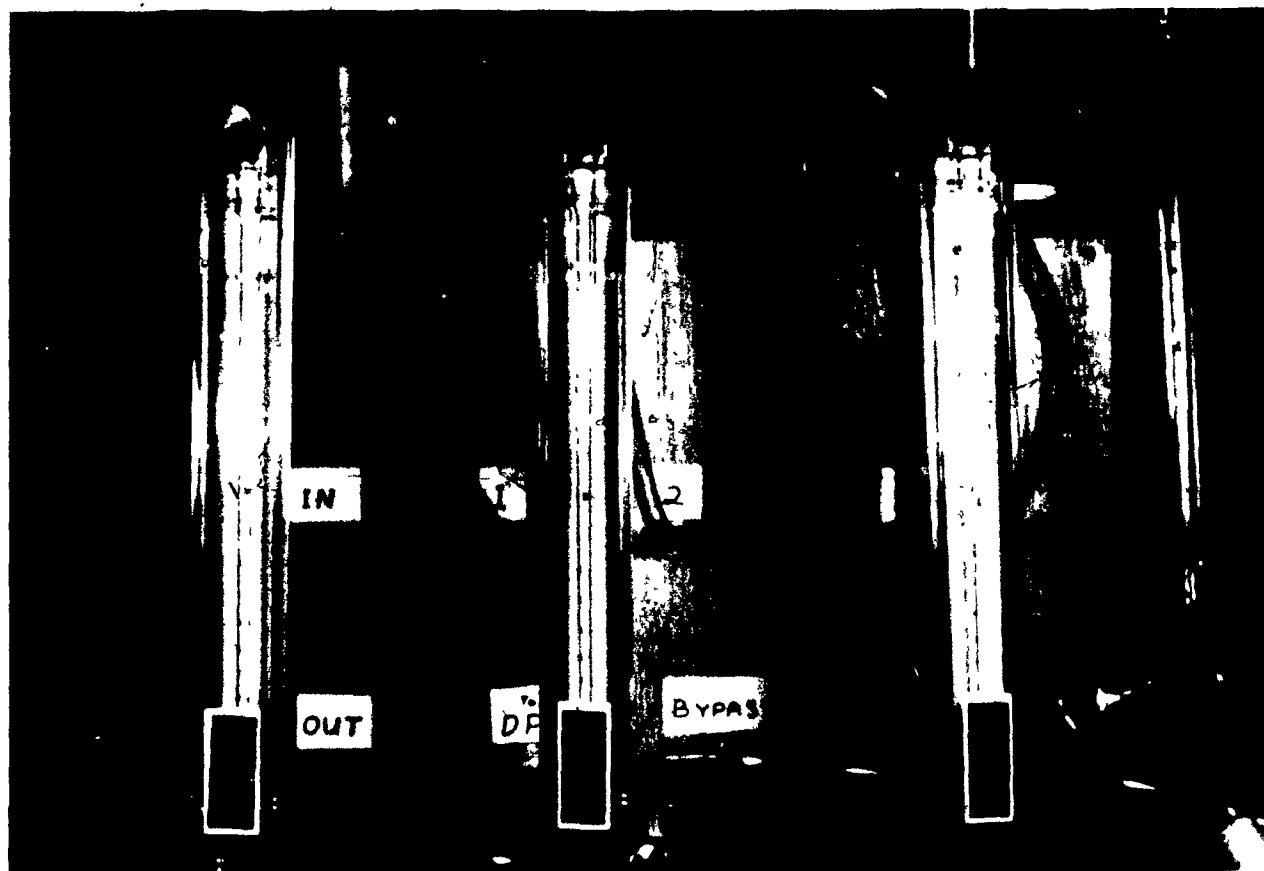
Figure 6. Leaf transpiration chamber.





Figure 7. Transpiration chambers (top) and tubing manifold (bottom).

Figure 8. Sample flow meters.



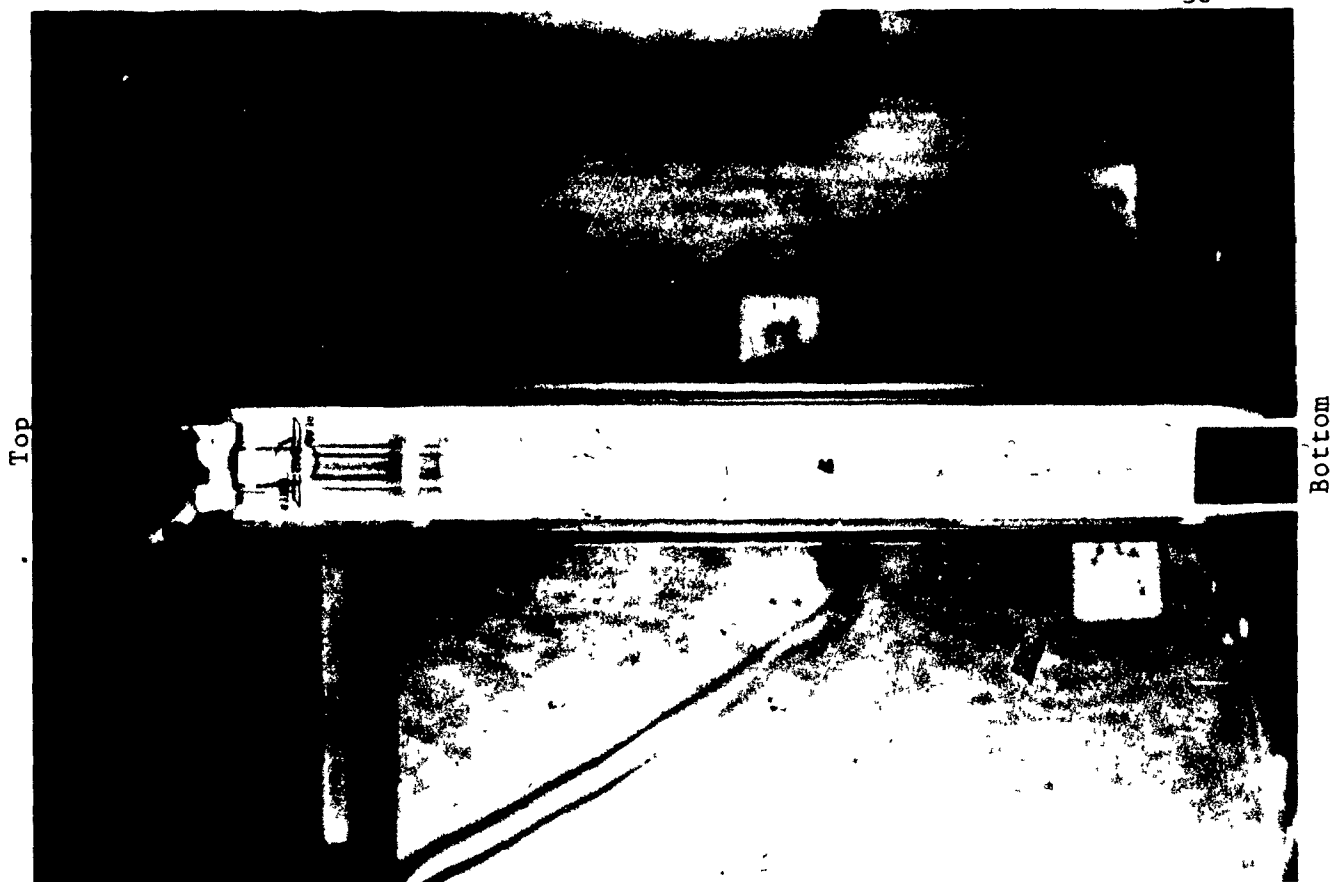


Figure 9. Flow meter (close-up), needle valve located on top.

Figure 10. Control box, having 3 inlets and 2 outlets.

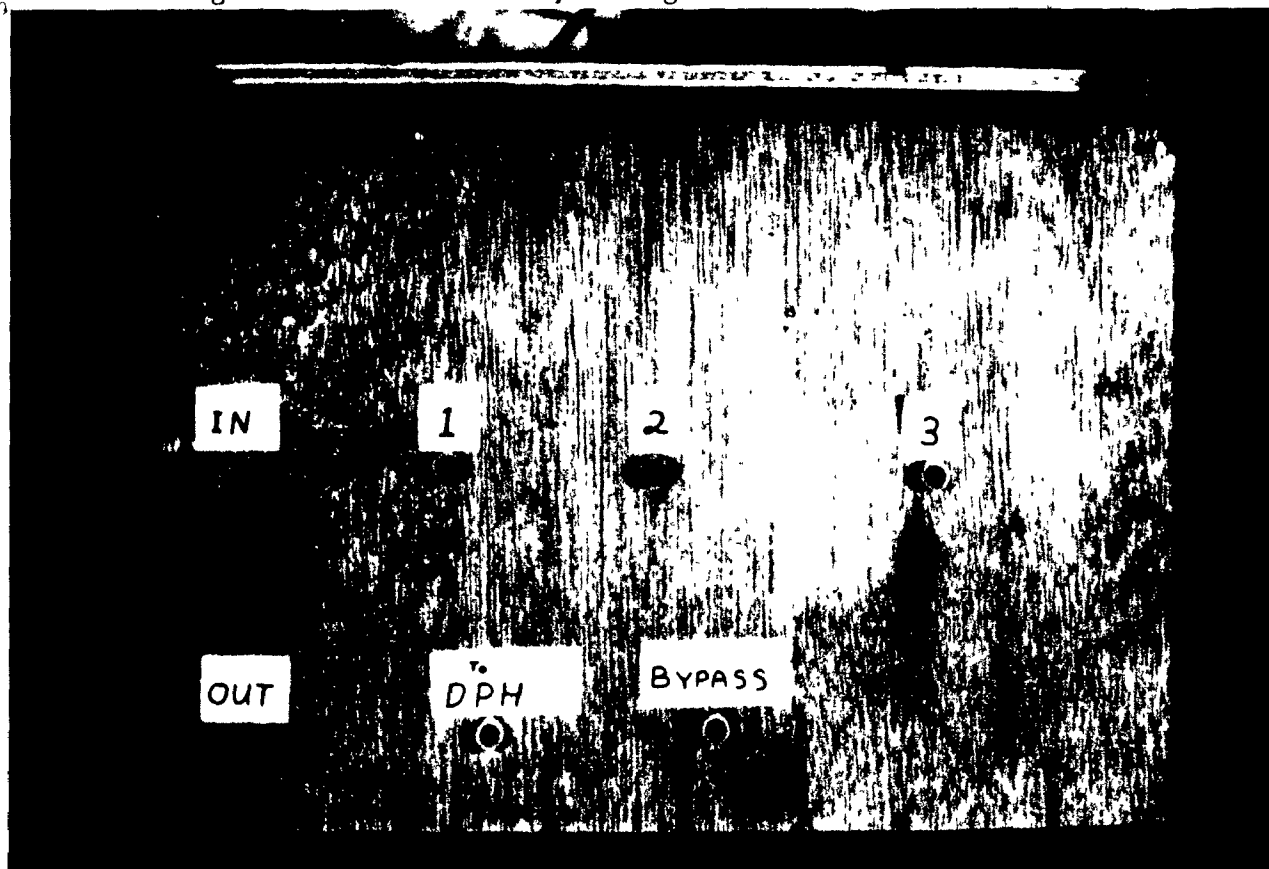
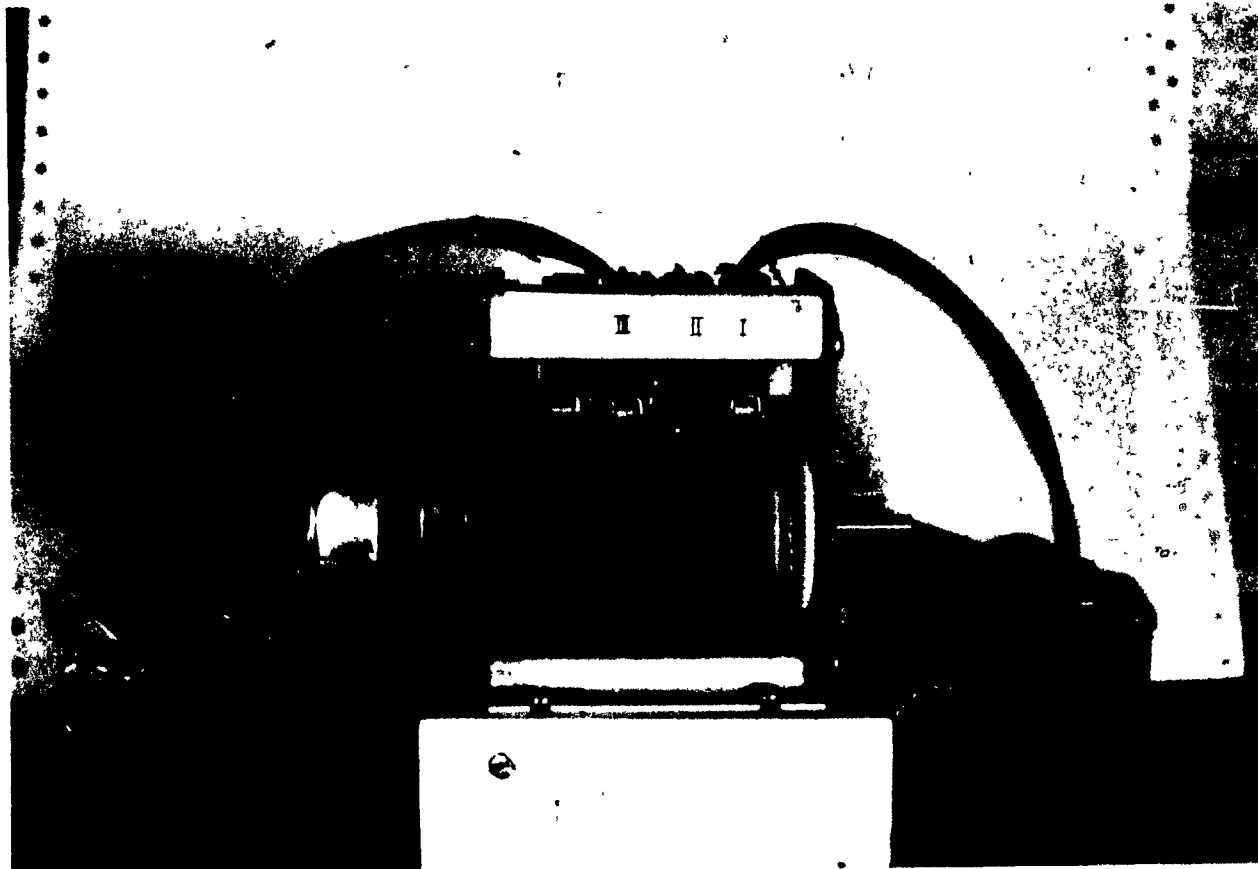




Figure 11. Inside control box; solenoid valves (center) and timer (above).

Figure 12. Timer, showing cam switches (#2 activated).



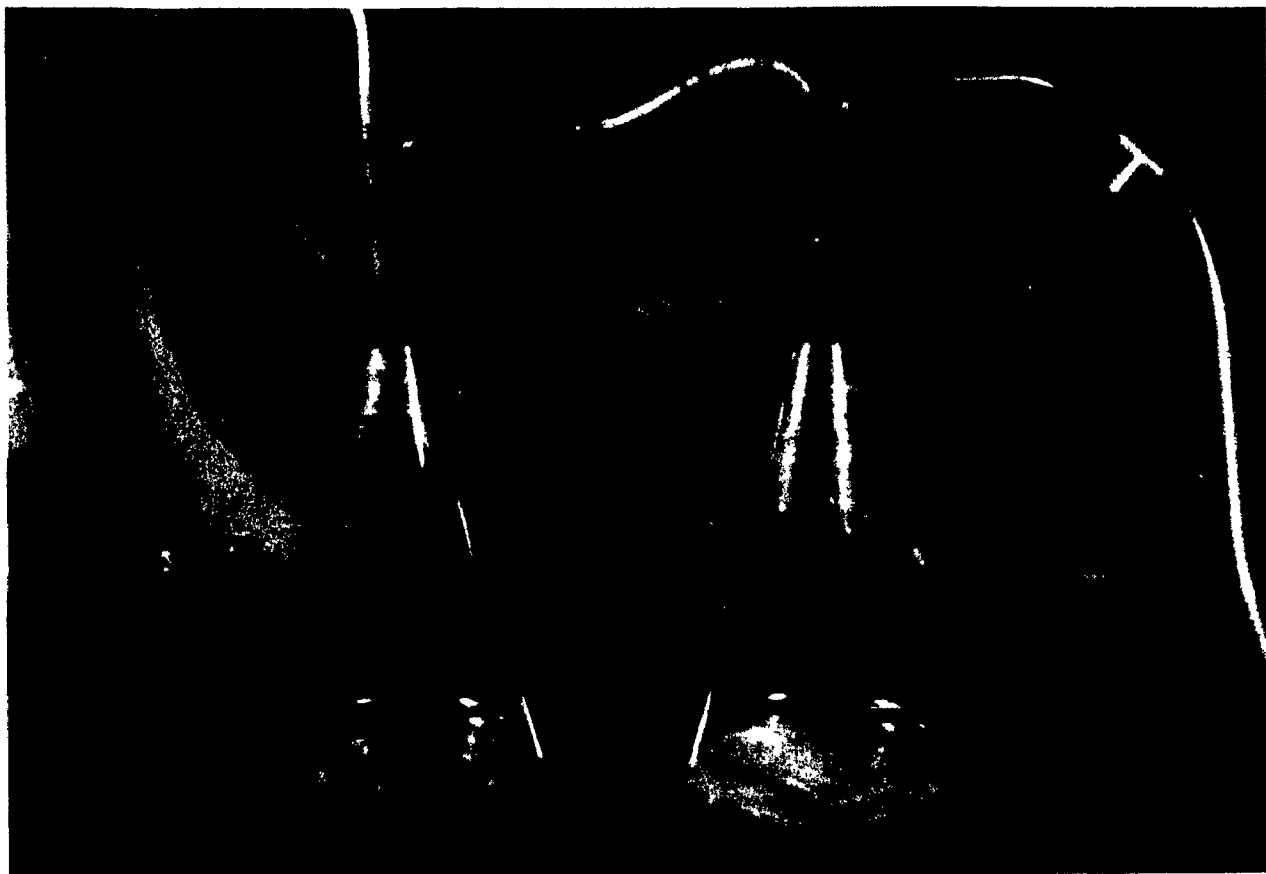
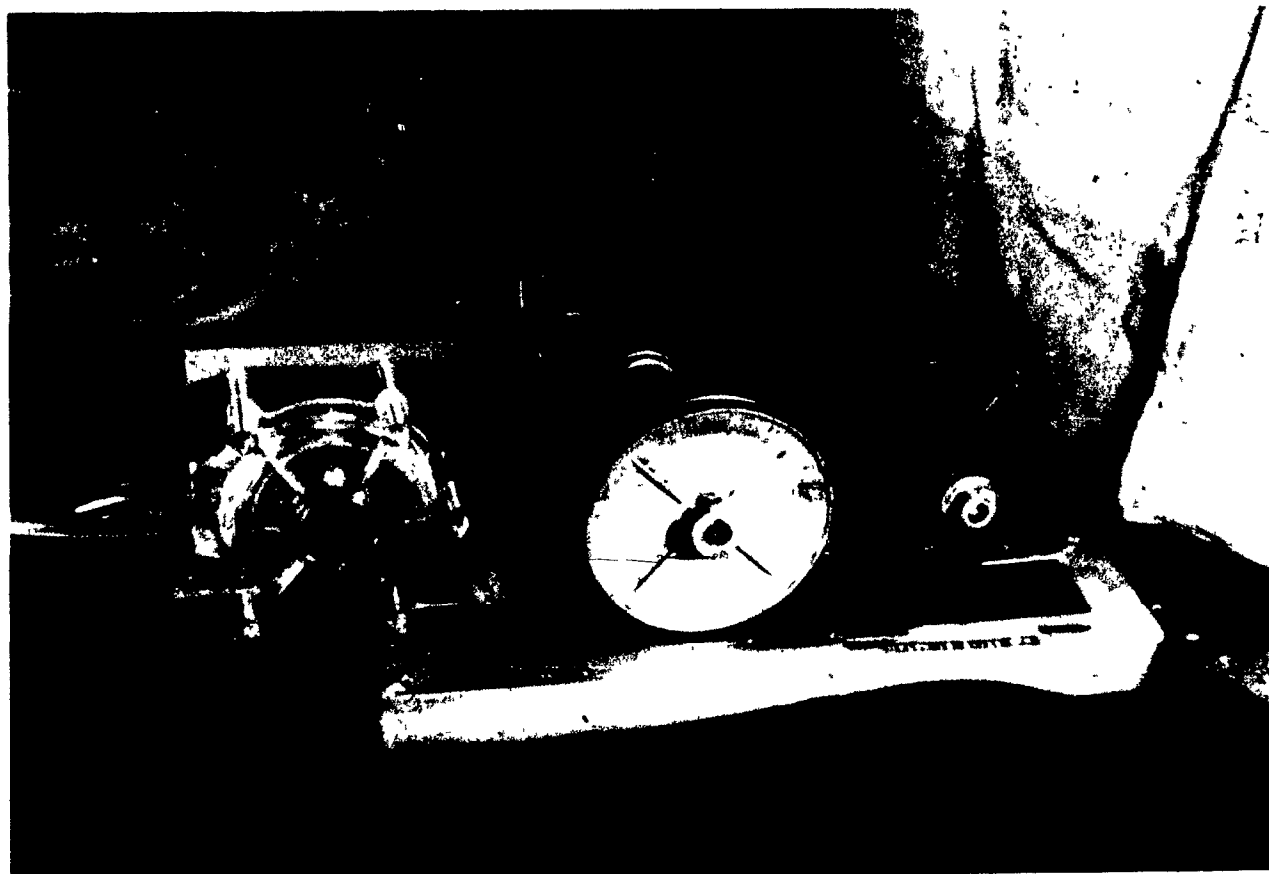


Figure 13. Damping jars.

Figure 14. Peristaltic pump.



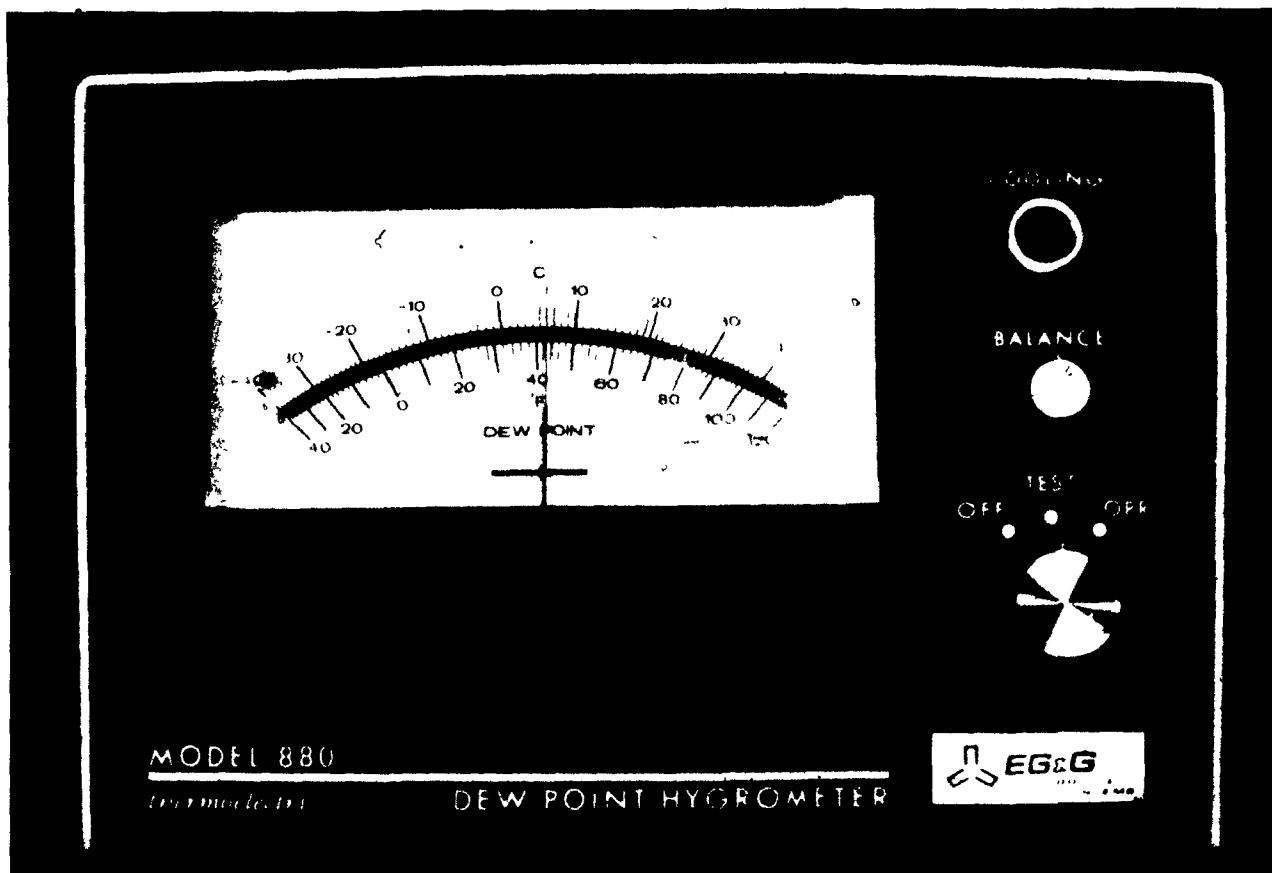
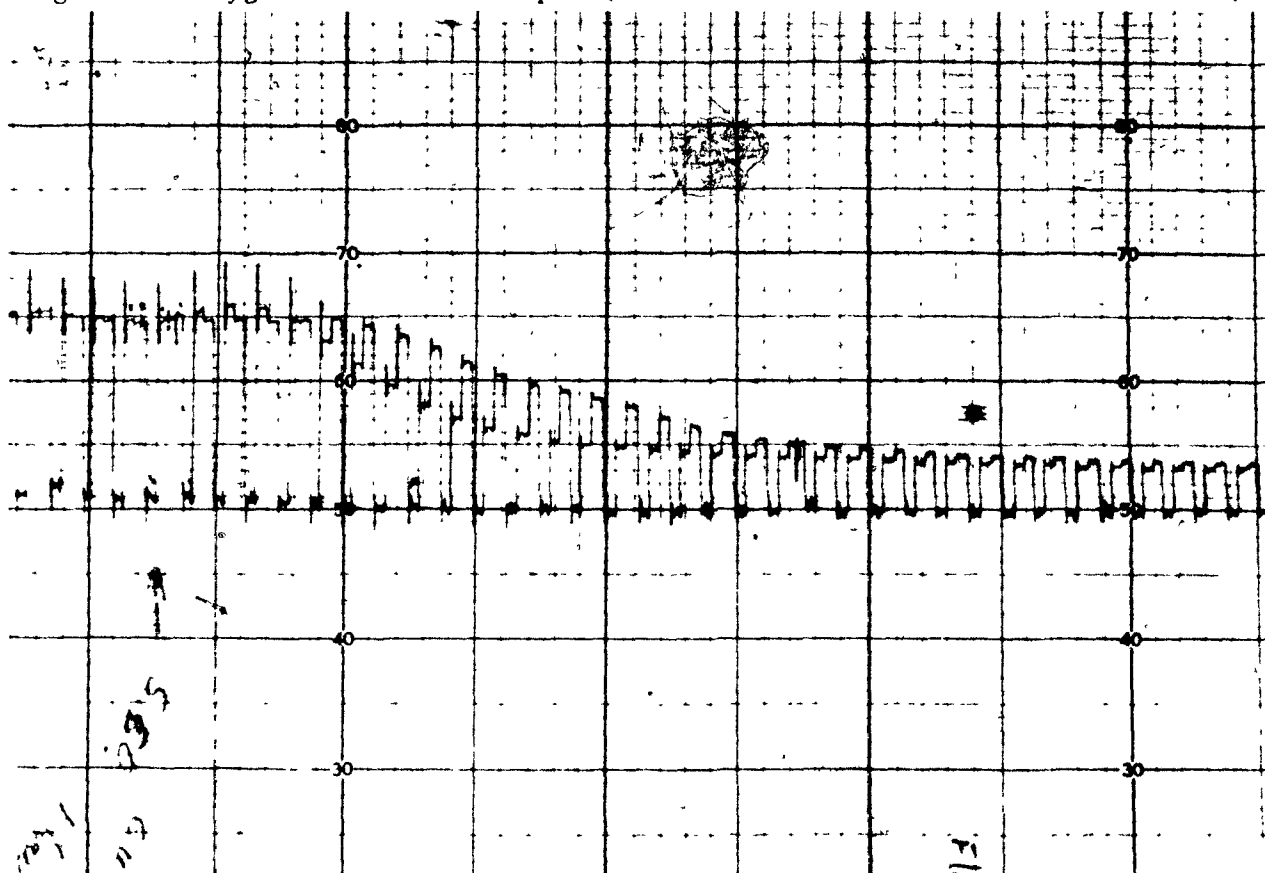


Figure 15. Dew point hygrometer.

Figure 16. Hygrometer chart output (one small division = 0.2 in. = 12 min.).



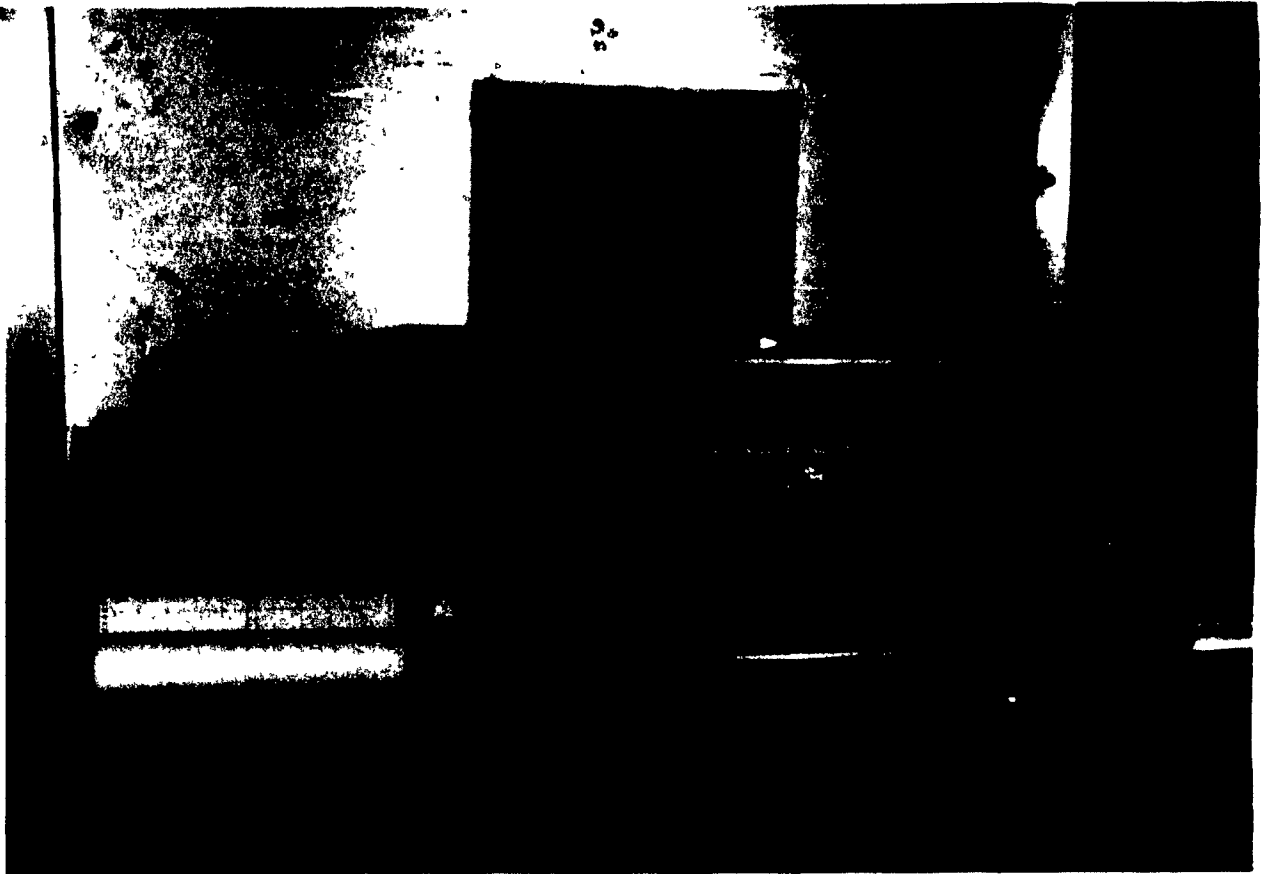
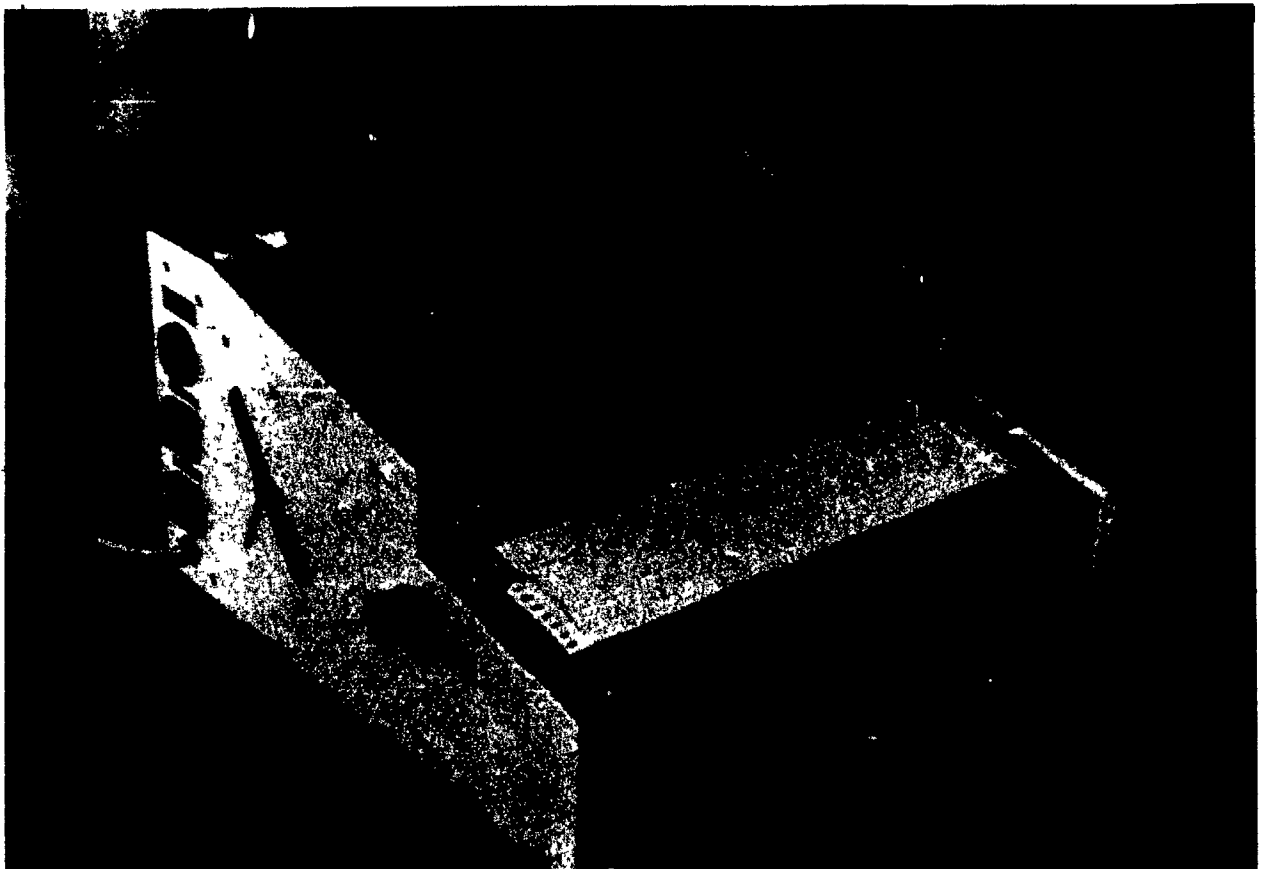


Figure 17. (L-R) Hygrometer and temperature recorders, ice point reference (used to calibrate temperature recorder).

Figure 18. Hygrometer recorder.



4.2 Evaluation of the Apparatus

Gasometric methods have been used frequently in transpiration studies (e.g., Beadle et al. 1974; Decker 1962; Mooney et al. 1971) but rarely in drying research. Butchbaker (1972) used a closed gasometric system to investigate moisture diffusion through surfaces of dehydrating biological products. Shepherd (1964) used an open system wherein the moisture evolved from detached white clover leaves was collected by hygroscopic chemicals which were then periodically weighed. The former system, having non steady state chamber conditions, required complicated analysis, while the latter did not provide for continuous and direct measurements of drying rates.

My apparatus combined the steady state environment of open systems, with instrumentation that continuously monitored rates of vapour flux. The system, however, did not permit direct measurement of moisture content; thus these quantities were calculated by integrating (graphically) the rate-time curve. When changes in moisture content estimated graphically were compared with weight loss measurements to test the system's accuracy, differences were found to be as great as 20-30 percent.

The calculation of the drying rate was based on several independently measured quantities (see equation 11), each of which contributed to overall error. The estimation of system error was based on the combination of probable errors according to the root-sum square (rss) formula (Scarborough 1955):

$$\Omega = \sqrt{\left(\frac{\partial Y}{\partial R_s} \omega R_s\right)^2 + \left(\frac{\partial Y}{\partial R_c} \omega R_c\right)^2 + \left(\frac{\partial Y}{\partial Q} \omega Q\right)^2 + \left(\frac{\partial Y}{\partial \alpha_T} \omega \alpha_T\right)^2 + \left(\frac{\partial Y}{\partial W_D} \omega W_D\right)^2} \quad \dots (12)$$

where

Ω = probable error of dependent variable, i.e., drying rate
(Mg H₂O/gm W_D - min).

ω = probable instrument error based on manufacturer's
specification

R_s = humidity ratio of sample stream $\left(\frac{\text{mg H}_2\text{O}}{\text{mg air}}\right)$

R_c = humidity ratio of control stream $\left(\frac{\text{mg H}_2\text{O}}{\text{mg air}}\right)$

Q = flow rate (cc/min).

α_T = density of air at temperature T, assuming standard.
pressure (mg/cc).

W_D = oven dry weight (gm).

The calculated probable error of the dependent variable (Ω) for the conditions in Table 1 (experiment 1, run 1, hour 4, control sample) was ± 1.59 or 37.1%.

Humidity ratio measurements, based on the specified hygrometer accuracy range of $\pm 2^\circ\text{F}$, contributed substantially to the probable error. Separate experiments (see Appendix I), however, indicated that hygrometer error was a unidirectional and almost constant bias, which was in part subtracted out in calculation of drying rates. A more reasonable error value of $\pm 1^\circ\text{F}$ considerably reduced Ω (± 0.93 or

21.7%). The percentage error of the system was sensitive to the magnitude of the drying rate, ranging from 7.7 to 62.5% for values from 23.5 to 1.04 mg H₂O/gm W_D - min.

In addition to instrumentation errors, other factors may have contributed to inaccuracy. These include:

- 1) leakage
- 2) non-standard pressures within flow meters and the hygrometer, caused by flow drag and meteorological phenomena
- 3) inefficient air circulation in chambers
- 4) unobserved fluctuations in flow rates

The system's accuracy could be improved with better equipment. Most importantly, for vapour determination, the Cambridge Systems hygrometer (model 110S-M) with a dew point accuracy of $\pm 0.54^{\circ}\text{F}$ (Beadle et al. 1974) can be used. In addition, chambers with fans for stirring the air can be employed. Further refinement is possible by including manometers for measuring air pressure in the system (as Shepherd 1964).

Sestak et al. (1971) suggested that the pump should be positioned between the chambers and the gas analyzer because greater accuracy and stability is possible with the analyzer positioned at the end of the gas sample line. This design requires a pump (membrane or diaphragm) that neither leaks nor contaminates the air. Furthermore, in combination, low pressure membrane regulators and flow regulators ensure constant air flow, irrespective of pressure at pump outlet.

The present study, however, was designed to reduce the need for exhaustive accuracy. The objective was the detection of differences in drying rates between samples and over time, whereas absolute quantities were of less interest. It was assumed that most of the system's error previously discussed influenced all samples approximately equally and remained unchanged through time. The comparative lack of hygrometer accuracy was of less importance than its high resolution (0.5°F). In addition the use of a reference flowmeter enabled continual calibration of the sample flow meters, assuring equal (if not exactly known) flow rates. And finally, repetition of the experiments, with randomization, further authenticated the results.

The system's error limited interpretation of data to relative rather than absolute magnitudes. Nonetheless in the context of the experimental objectives the system was judged to be efficient. Response time was less than 25 seconds, while equilibration time was usually well within the five minutes allotted. Repeated measurements of constant rates provided very similar results, while even slight changes (e.g., passive stomatal opening, Figures 21 and 28) were detected, attesting to the system's precision and resolution.

TABLE 1. Magnitudes and probable errors of variables used in calculating the probable error for the drying rate (Experiment 1, run 1, hour 4, control sample). See text for explanation.

Variable	Magnitude	Probable error	
$R_s \frac{\text{g H}_2\text{O}}{\text{g air}}$	7.50×10^{-3}	(2°F) 1.42	(1°F) 0.85
$R_c \frac{\text{g H}_2\text{O}}{\text{g air}}$	6.14×10^{-3}	(2°F) 0.72	(1°F) 0.38
Q cc/min	425	0.04	
α mg/cc	1.17	0.16	
W_D g	0.185	0.000043	
Ω mg H ₂ O/g W_D - min	4.29	1.59	0.93
% error		37.1%	21.7%

4.3 Plant Material Employed

Two forage species were chosen for this study. Trifolium repens L. var. Ladino was selected for its comparatively simple, uniform growth habit, its small number of large leaves, and because normally only the leaves and petioles of these plants are harvested. Because T. repens is not commonly a hay crop, an additional species, T. pratense L. var. Dollard, (known for its slow drying) was also used. These plants are less uniform structurally, and presented a problem in finding complete sets (2-16) of like leaves and petioles.

All plants were grown from seed in a greenhouse, and then transferred to a growth cabinet (21°C day and 19°C night temperatures, 12 hour photoperiod to inhibit flowering, 600 ft. candles illumination) where they remained for the entire experimental period in 6 inch pots containing a 1:1:1 (loam:peat:sand) soil mix. The plants were watered daily, fertilized weekly with water soluble 20-20-20 plus minor nutrients (0.3 gm per pot), and trimmed regularly.

4.4 Methods: General

Similar, fully expanded, leaves (avoiding old ones) were harvested for each experiment, each leaf consisting of a compound lamina; with leaflets each of 3-4 cm² area and petioles 10-15 cm in length. The number of leaves comprising each sample varied between experiments.

Immediately after leaves were excised, the bottom half inch

of the petioles was removed under-water, in order to eliminate air from the xylem. The petiole ends remained submerged while each lamina (or petiole) was inserted into a chamber. The chambers were then sealed and transpiration rates measured until they stabilized. If the sample rates differed substantially, some chambers were alternated between samples. Depending upon the experiment, either a preliminary treatment was then applied, or the drying experiment begun (by the removal of the moisture source).

The experimental conditions during drying, except where otherwise stated, were maintained at 21°C, 30 foot candles (cool white fluorescent bulbs), and 45% relative humidity (see section 4.1).

After each drying experiment, samples were weighed (final weight W_f), placed in an oven (80°C) for 72 hours and then reweighed (dry weight, W_d). Only final moisture contents were determined by weighing; all others were derived by integration of drying rate curves.

4.5 Methods: Description of Experiments

Experiment 1: The effect of stomatal closure, induced by sodium azide on drying rates of red clover (one or two laminae per sample).

The role of stomata in drying was tested using red clover laminae treated with sodium azide (5×10^{-3} M in 0.01 M sodium

tartrate buffer; as Zelitch 1961) to effect stomatal closure. After original laminar transpiration rates had stabilized, petioles of one sample were inserted in the sodium azide solution. Transpiration rates were permitted to re-stabilize (2-4 hours) before the petioles (and hence the source of moisture) were removed from all laminae.

Each sample consisted of just one or two laminae so that rate changes would appear more distinct. Additional lights (incandescent floods, 150 W), providing greater illumination (150 ft candles) and higher chamber temperatures (27°C), were used to promote stomatal opening and accelerate drying.

Experiment was repeated 4 times.

Experiment 2: Inhibition of stomatal closure with sodium azide during drying of red and white clover laminae (4 laminae per sample).

Weak solutions of sodium azide (10^{-3} , 5×10^{-4} , 2.5×10^{-4} M in 0.01 M sodium tartrate buffer) were applied to red and white clover laminae to inhibit stomatal closure during drying (as Stalfelt 1957; Walker and Zelitch 1963; Mears and Roberts 1970; Tullberg and Angus 1972).

After original transpiration rates of illuminated (as experiment 1) laminae had stabilized the chambers of one sample were re-opened, and the laminae sprayed by or immersed in the

solution of sodium azide (with wetting agent). Chambers were then resealed and the petioles removed either immediately or after transpiration rates had re-stabilized.

Other tests were conducted in which the sodium azide solution was imbibed by the petioles, as in experiment 1.

Each trial was repeated at least twice.

Experiment 3: Effect of rubbing white clover laminae on drying (4 laminae per sample)

After initial transpiration rates had stabilized, the chambers of one sample were re-opened, and the laminae gently rubbed by five uniform strokes (per leaflet surface), with a piece of soft flannel, to remove epicuticular waxes as Hall and Jones (1961). The chambers were resealed, transpiration rates allowed to re-stabilize, then petioles removed from all laminae.

Experiment was repeated 3 times.

Experiment 4: The effect of piercing on the drying of white clover laminae (4 laminae per sample)

The effect of overcoming cuticular resistance by piercing laminae (similar to Gregory *et al.* 1950) was tested. The procedure was similar to experiment 3, except that each leaflet, instead of being rubbed, was pierced 10 times (1-2 mm slits) with the corner of a razor blade.

Experiment was repeated 3 times.

Experiment 5: The role of stomata in drying; using light and dark treated white clover laminae (8 laminae per sample)

Laminae transpired in their chambers for a 24 hour period, at which time one set of laminae was subject to its usual photoperiod, though with only 30 ft-candles illumination, (control chambers) while the other was kept entirely in the dark (covered chambers). At the end of this period, petioles from both samples were removed. Dark treated stomata were partially open because of endogenous rhythms.

Experiment was repeated 3 times.

Experiment 6: The role of stomata in the drying of detached white clover petioles, using light and dark treatments. (2 petioles per chamber; 16 petioles per sample)

The procedure was similar to that of experiment 5. Fifteen cm long petioles were used in 12 cm petiole chambers so that the ends protruded; one end was immersed in water while the other supported the laminae. The laminae were detached from both samples at the same time that the water source was removed. The cut petiole ends were located outside the chambers thus evaporation from them was not measured.

Experiment was repeated twice.

Experiment 7: Effect of laminae on evaporation rate from white clover petiole surfaces during drying (2 petioles per chamber; 16 petioles per sample)

Petioles at least 15 cm long were used as in experiment 6. Petiolar transpiration rates were measured until they stabilized, whereupon laminae were removed from only one set of petioles while moisture source was removed from both.

Experiment was repeated 3 times.

Experiment 8: Removal of petiole moisture by white clover laminae (8 laminae per sample)

To investigate whether laminae aid in removing petiole moisture, the drying rates of detached and intact (petiolate) laminae were compared. After the initial laminar transpiration rates had stabilized, petioles and moisture source were removed from one set of laminae, while only the moisture source was removed from the other set (these laminae retained their 10 cm long petioles).

Experiment was repeated 5 times.

Experiment 9: Effect of laminae on removing petiole moisture after stomatal closure, in white clover (8 laminae per sample)

This experiment was conducted to investigate whether petiole moisture continued to move into laminae after stomatal closure. Procedure followed was similar to that of experiment 8, except that petioles were removed from one set of laminae, only after 6 hours of drying, the other set remaining intact throughout.

Experiment was repeated 4 times.

Experiment 10: Effect of laminae on removing petiole
moisture after 20 hours of drying, in white clover (8 laminae per
sample)

Procedure followed was similar to that of experiment 9,
except that petioles were removed from one set of laminae, only
after 20 hours of drying.

V. RESULTS AND DISCUSSION

5.1 The Drying Curve

5.1.1 Results

The drying of detached red and white clover laminae occurred in four distinguishable phases (Figs. 25 and 26, p. 69, 70) and therefore cannot be described by the conventional logarithmic equations (e.g., equations 2-4, section 2.1.2.2)..

In order to simplify the drying pattern the effects of stomata were minimized by promoting their closure with sodium azide (experiment 1, Fig. 19). For red clover laminae treated this way the initial fifteen minutes of drying, during which pre-cutting transpiration rates were maintained, was designated as initial rate period (IRP). This period was succeeded by rapidly declining drying rates, designated as rapid fall period (RFP), which continued to moisture content of ca 364% dry basis (d.b.). Thereafter a prolonged (6-7 hr.) almost steady-state rate, designated as slow fall period (SFP) prevailed, until the onset at moisture content of ca 105-70% d.b., of exponential decline period (EDP) which continued until moisture content reached equilibrium.

The data for the drying curve of sodium azide treated red clover laminae were fitted to the logarithmic drying equation 4,

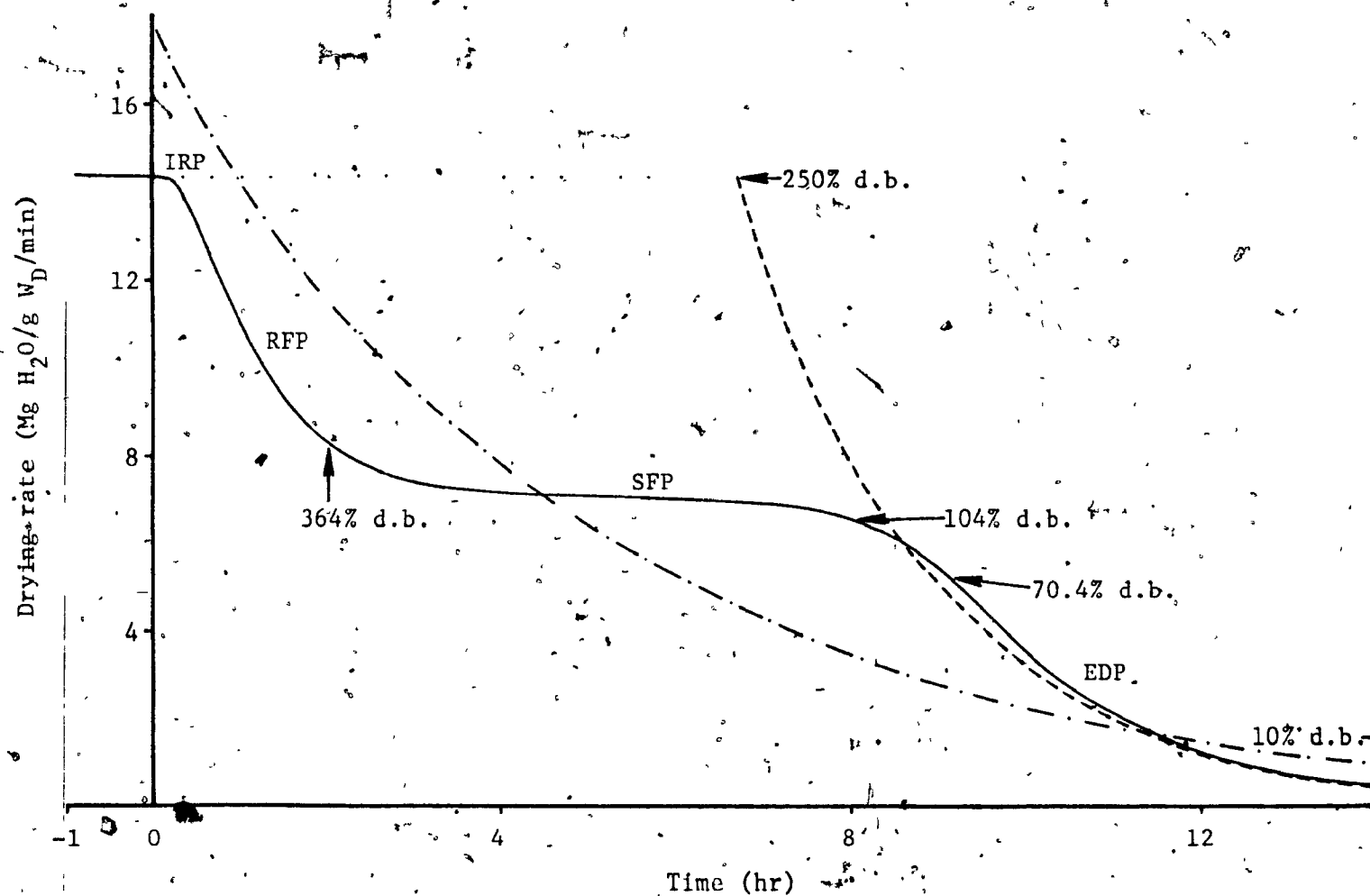


Figure 19. Drying curve for detached red clover laminae, pre-treated with sodium azide to effect stomatal closure. Derived from Figure 25. (see text for explanation)

- Drying curve
- .- Drying curve data fitted to equation 4
- EDP fitted to equation 4

(section 2.1.2.2) using the least squares method. The poor fit was demonstratively shown (Fig. 19).

5.1.2 Discussion

5.1.2.1 The Multiple Rate Period Concept

Although there are many reports of single drying rate periods (eg. Leshem et al. 1972; Morris 1972), several studies (eg. Priepke and Bruhn 1970; Von Bargaen 1961) support the findings of multiple rate periods in drying. These drying periods have been attributed to both physical and biological factors. For example investigators have suggested that these rate periods in food drying are associated with the manner in which water is bound and the mode of moisture transfer in tissue (Gorling 1958; Jason 1958, Saravacos and Charm 1962; see section 5.1.2.4). Studies of early drying of detached laminae, however, revealed the superimposition of physiological control on physical plant/water relations; hence the stomatal, stomatal closing, and cuticular phases reported by Hygen (1951, 1953). However, drying rate periods for intact shoots of alfalfa (eg. Priepke and Bruhn 1970) appear to be somewhat less distinct, probably because of the unsynchronized drying of the shoot parts.

5.1.2.2 The Slow Fall Period (SFP)

The drying of most agricultural products occurs during the

falling rate period (Hall 1957; Henderson and Perry 1955; see section 2.1.2). Nonetheless, the predominant rate period in experiment 1 (Fig. 19) was the slow fall period (SFP), which exhibited fairly constant drying rates. During the SFP drying rate declined from 8.1-6.7 mg H_2O /gm D_w /hr (ie. a 17% decrease) while the moisture content diminished from 360% to 104% d.b. (ie. a 71% decrease), suggesting that moisture content was not a principal rate governing factor during this period. These results agree with Pederson and Buchele's (1960) findings that a nearly constant evaporation rate for alfalfa leaves began after three hours of drying, (at 56.4% R.W.C.) and lasted until equilibrium moisture content was reached. Their data, converted by graphical differentiation, is shown in Fig. 20. They suggested that this constant rate was due to the thinness of the leaves and to evaporation taking place only through the cuticle and possible wounds.

The importance of the cuticle in this period was investigated in experiment 3, in which the laminae were rubbed lightly with soft flannel to remove epicuticular waxes (Hall and Jones 1961; Leshem *et al.* 1972). This treatment markedly increased drying rates during SFP, caused an earlier onset of EDP, and left the other rate periods comparatively unchanged (Fig. 21). Hall and Jones (1961) obtained similar results for the drying of lightly brushed, Moroccan red clover leaves.

In experiment 4, overcoming cuticular interference by piercing

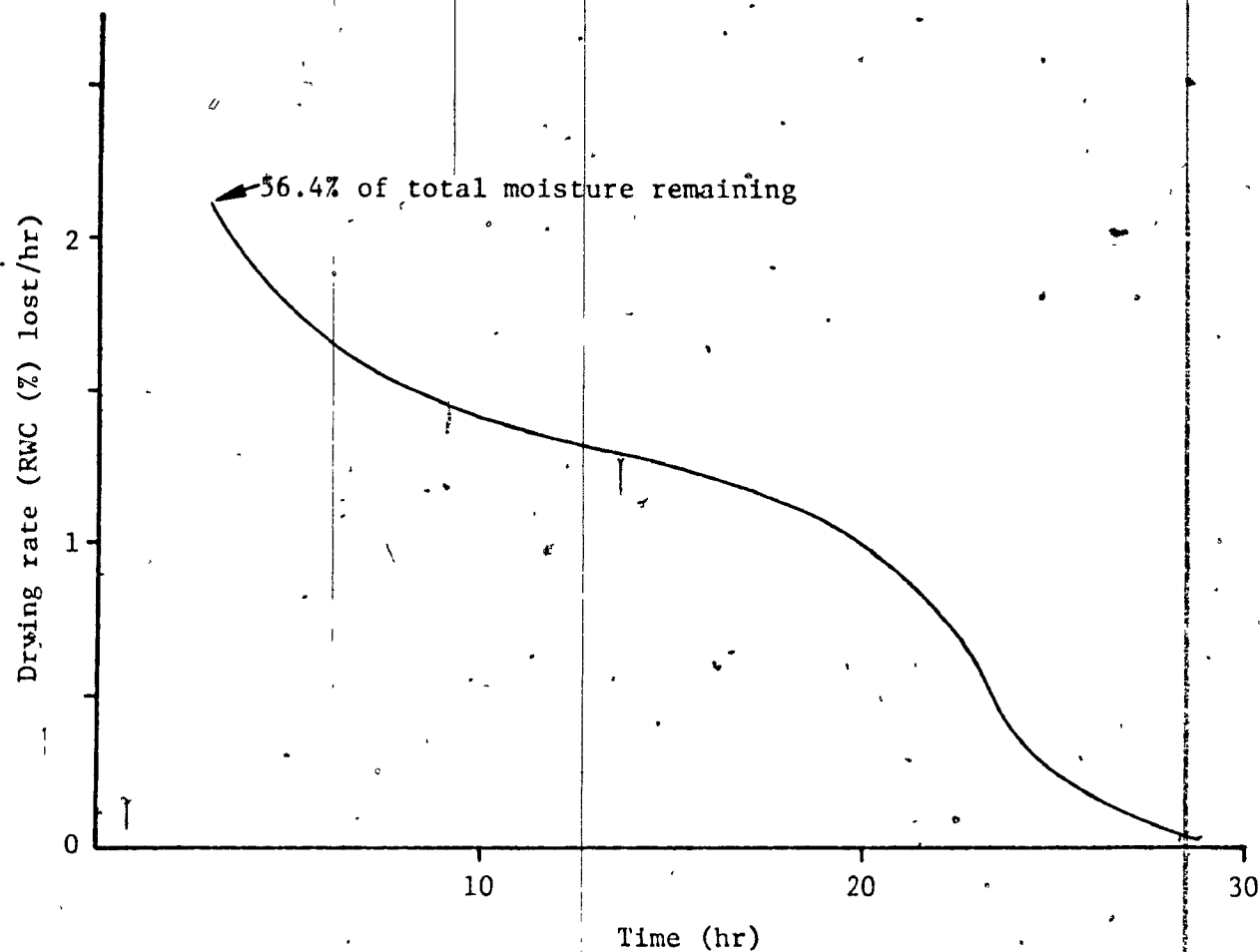


Figure 20. Drying curve for alfalfa leaves, from Pederson and Buchele (1960); (original data were transformed graphically).

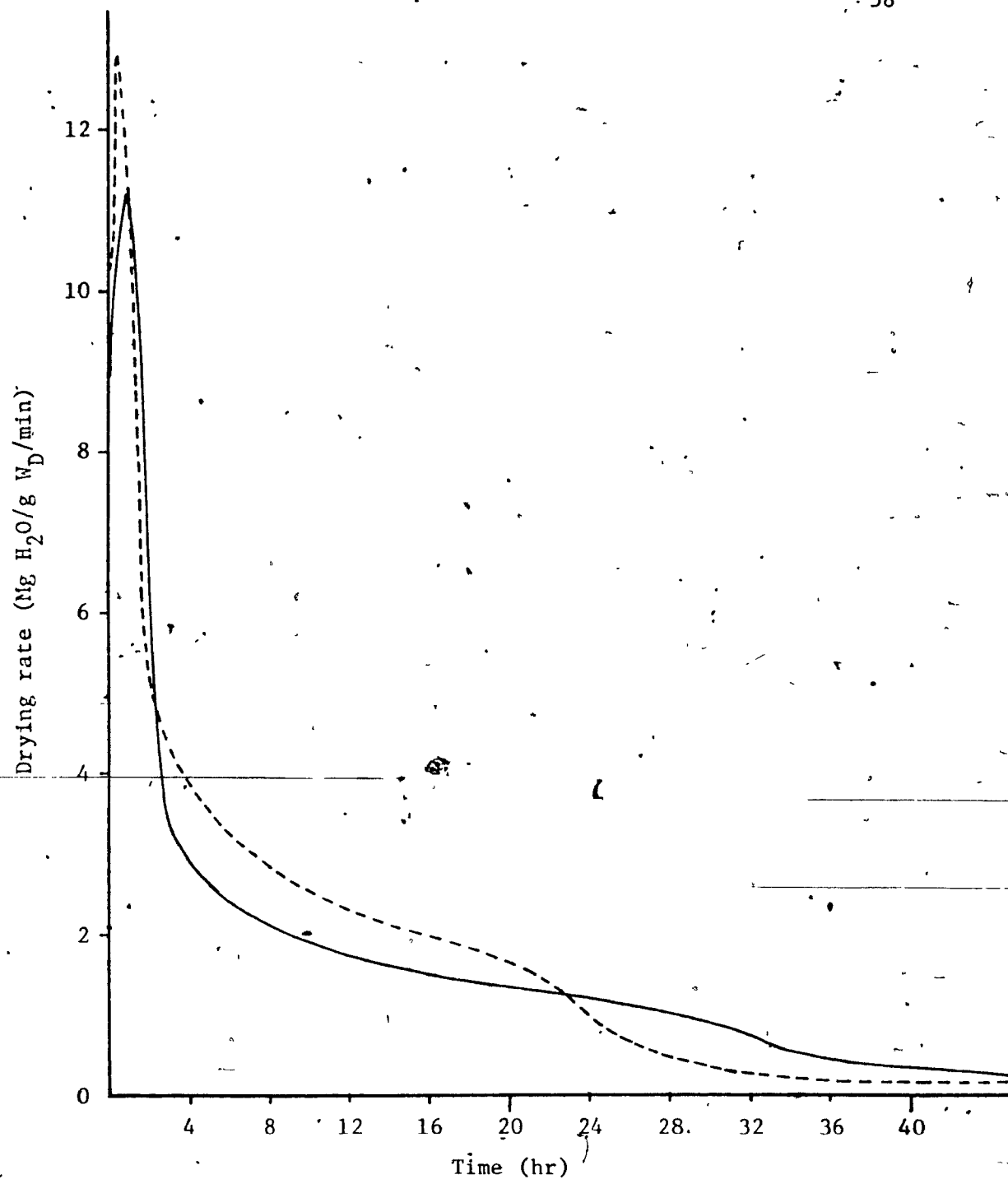


Figure 21. Drying curve for white clover laminae, experiment 3.

— Control laminae ($W_F = 36\%$ d.b.)
- - - Rubbed laminae ($W_F = 19\%$ d.b.)

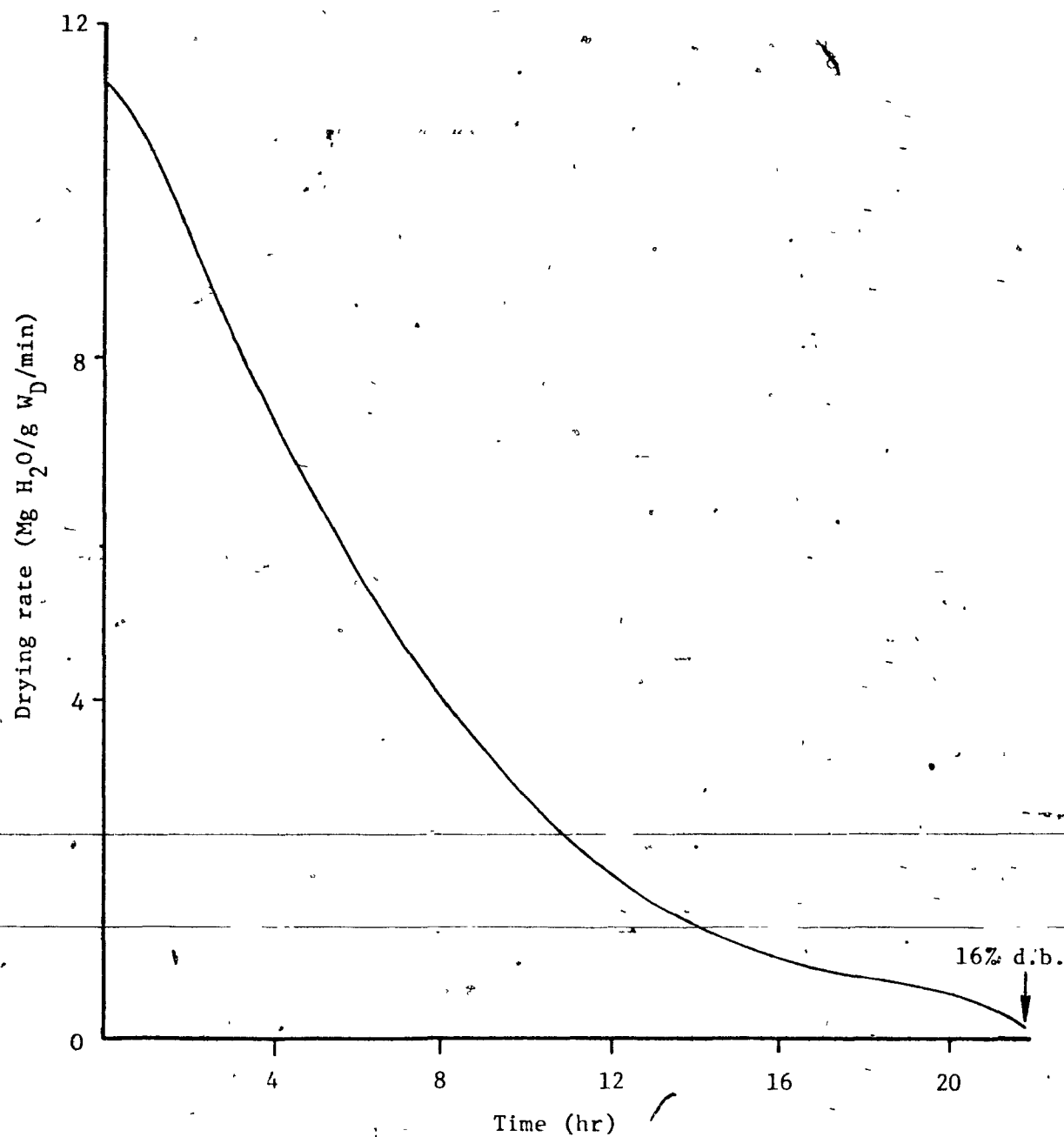


Figure 22. Drying curve for pierced white clover laminae, experiment 4.

of leaves (as Gregory et al. 1950) resulted in the complete disappearance of SFP (Fig. 22), further suggesting the importance of the cuticle in this period. Furthermore, Hygen (1951, 1953) found that in leaves, cuticular control became important after stomatal closure (designated cuticular phase), at which time there was a slight dependence of drying rate upon moisture content. Similar so-called cuticular phases were reported by Waisal et al. (1968), and Williams and Amer (1957).

All these findings suggest that because of slow evaporation (in SFP) while the cuticular control prevails, surface moisture is adequately replenished despite decreasing water content in the leaf--until moisture depletion becomes too pronounced. Reducing cuticular resistance (Figs. 21 and 22), means that internal control, and thus probably average moisture content, becomes proportionately more important. In respect to interfacial regulation of drying rate, especially its independence of moisture content, the SFP resembles the constant rate period of physical models. They differ, however, in that the SFP is characterized by the predominance of cuticular resistance over boundary layer resistance, and vapour pressure gradient at the surface, and the diffusivity of vapour in air--all of which are fundamentally important in rate regulation during the constant rate period.

5.1.2.3 Critical Moisture Content (CMC)

It was suggested above that EFP was entered when the rate of moisture transfer from the interior to the surface became less

than the evaporation rate. Therefore the transition from SFP to EFP occurs at the critical moisture content (according to definition, section 2.1.2).

The values for this critical moisture content in both red and white clover laminae are presented in Table 2 by intervals, not discrete values, because of difficulty in locating a precise point of transition. Despite variability in results due to both sampling and instrumentation errors, the critical moisture content ranges can be viewed with a high degree of certainty.

Information in the literature concerning the critical moisture content appears to be limited and contradictory. Estimates of the CMC for alfalfa ranged from 360 to 468% d.b., depending upon maturity, harvest date, and number of previous cuts (Von Pargen 1961). Hygen (1951), however, postulated that critical moisture content of leaves of many species was actually greater than their initial moisture content. Gregory *et al.* (1950) found critical moisture content to be approximately 90% R.W.C. in Pelargonium leaves. Williams and Amer (1957) disputed Hygen's while supporting Gregory's findings. Milthorpe and Spencer (1957) found little relationship between transpiration rate and water content in wheat leaves down to 70% R.W.C. Further work by Milthorpe (1959), based on tissue water potential analysis, suggested that in a moderate environment transpiration declined by as little as 4% as a result of internal resistance from full turgidity to severe wilting. He does not

TABLE 2. Estimates of the moisture content at the start of the EDP.

Experiment	No. of runs	Lower Estimate % d.b.	Higher Estimate % d.b.	Average % d.b.
I White Clover				
A control	3	86.4	110.9	99.9
B control	3	83.9	105.3	93.5
Range 40.0 - 111% d.b.				
II Red Clover				
C (Exp. 1 NaN_3)	3	70.4	104.2	85.2
D (Exp. 1 control)	3	65.9	98.9	81.9
E control	8	49.7	79.7	66.7
F control	6			75.7
Range 41.4 - 152% d.b.				

indicate the moisture content at which internal resistance is likely to become influential (ie. CMC).

Estimates of the critical moisture content for other materials are also confusing. Saravacos and Charm (1962) reported values for vegetable and fruit slabs ranging from 350-500% and 550-770% d.b. respectively. They explain that the high values for foods relative to inorganic materials (Perry 1950) results from their colloidal and hydrophylic nature. Interestingly Simmonds et al. (1953) reported critical moisture content values for wheat kernels (69-85% d.b.) that were much closer to Perry's values for non-hygroscopic materials.

Menzies and O'Callaghan (1971) used the term critical moisture content to identify transition from one falling rate period to another, finding two such points on the moderate temperature drying curve of grasses; at 350% and 450% d.b. Their term therefore appears to correspond more closely to Gorling's (1958) "break points" and Priepke and Bruhn's (1970) "end points", which also marked transitions within the falling rate period, than to the critical moisture content, defined as terminating a constant rate period.

It seems that the equivocation in the literature maybe due in part to the direct application of a physical concept of critical moisture content to a biological system without sufficient study or redefinition. Although critical moisture contents of different

materials may not be directly comparable, much information may be obtained by studying these values in individual products.

5.1.2.4 Exponential Decline Period (EDP)

It can be seen from Fig. 19 that remaining 'free' moisture in detached laminae evaporated at continuously declining rates, until tissue moisture content reached equilibrium. The time-rate relationship for this region of the drying curve for the sodium azide treated laminae in experiment 1 (Fig. 19) was well represented by equation 4 (section 2.1.2.2).

The exponential decline period occurred for detached laminae of both red and white clover irrespective of treatment, though the period was more pronounced for fast drying laminae (see Figs. 21, 22, 23). Apparently, initial aperture of stomata did not significantly affect this period in red clover laminae (Fig. 25). Removal of epicuticular waxes (Fig. 21) ~~resulted in earlier onset of EDP,~~ but analysis of the curves for treated and untreated leaves (Fig. 23) showed little treatment effect. The drying of pierced leaves (Figs. 22 and 24) occurred almost entirely in the EDP, and thus resembled drying of non-hygroscopic materials. Apparently factors other than the nature of leaf surfaces were operative during EDP.

Assuming static surface characteristics during drying (i.e. unaltered cuticular and boundary layer resistances, Shepherd 1964), the diminishing rates were likely the result of increasing internal

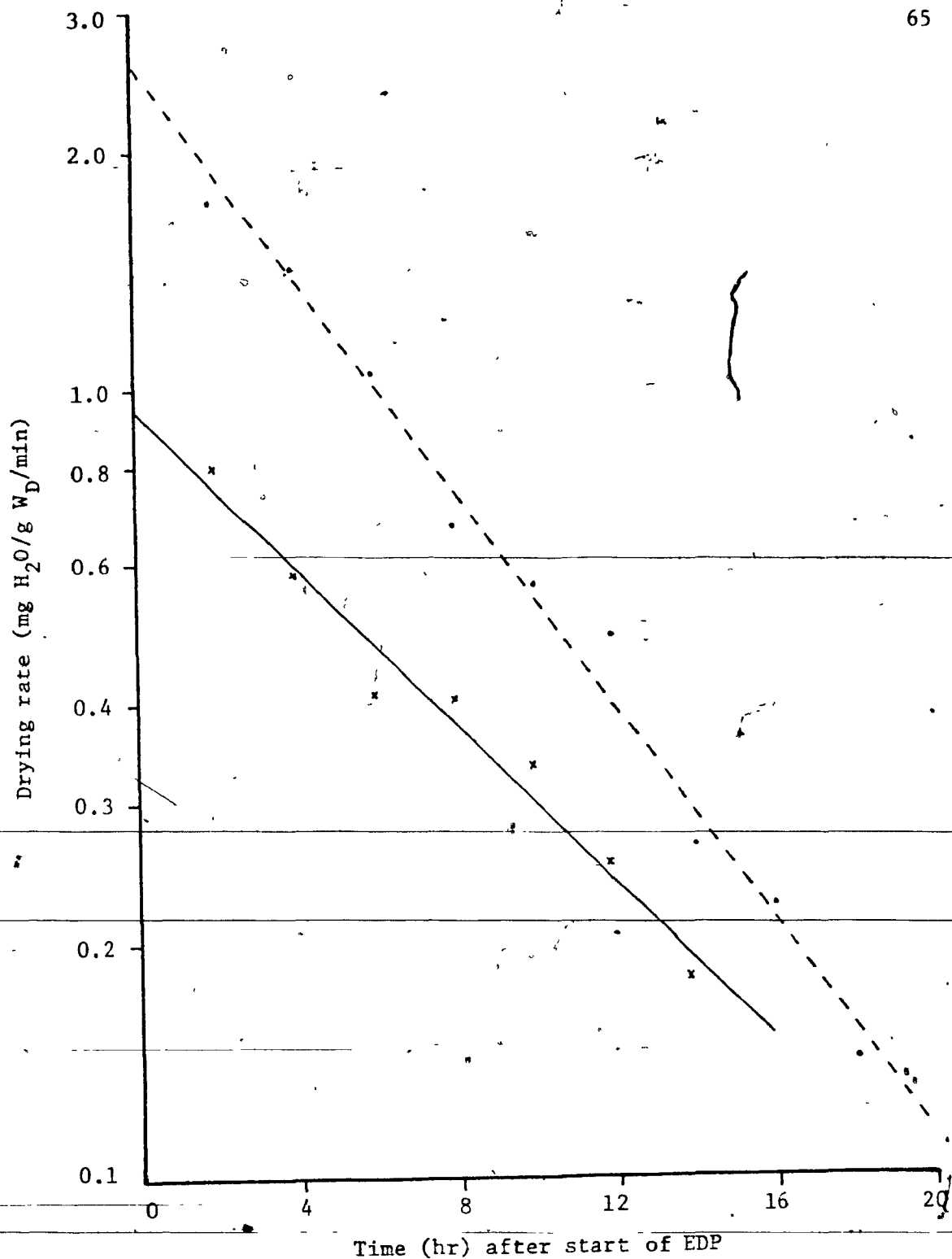


Figure 23. Semilog plots of EDP's, experiment 3 (from Fig.21)

x control laminae

• rubbed laminae

— regression line (K = -0.23)

---- regression line (K = -0.31)

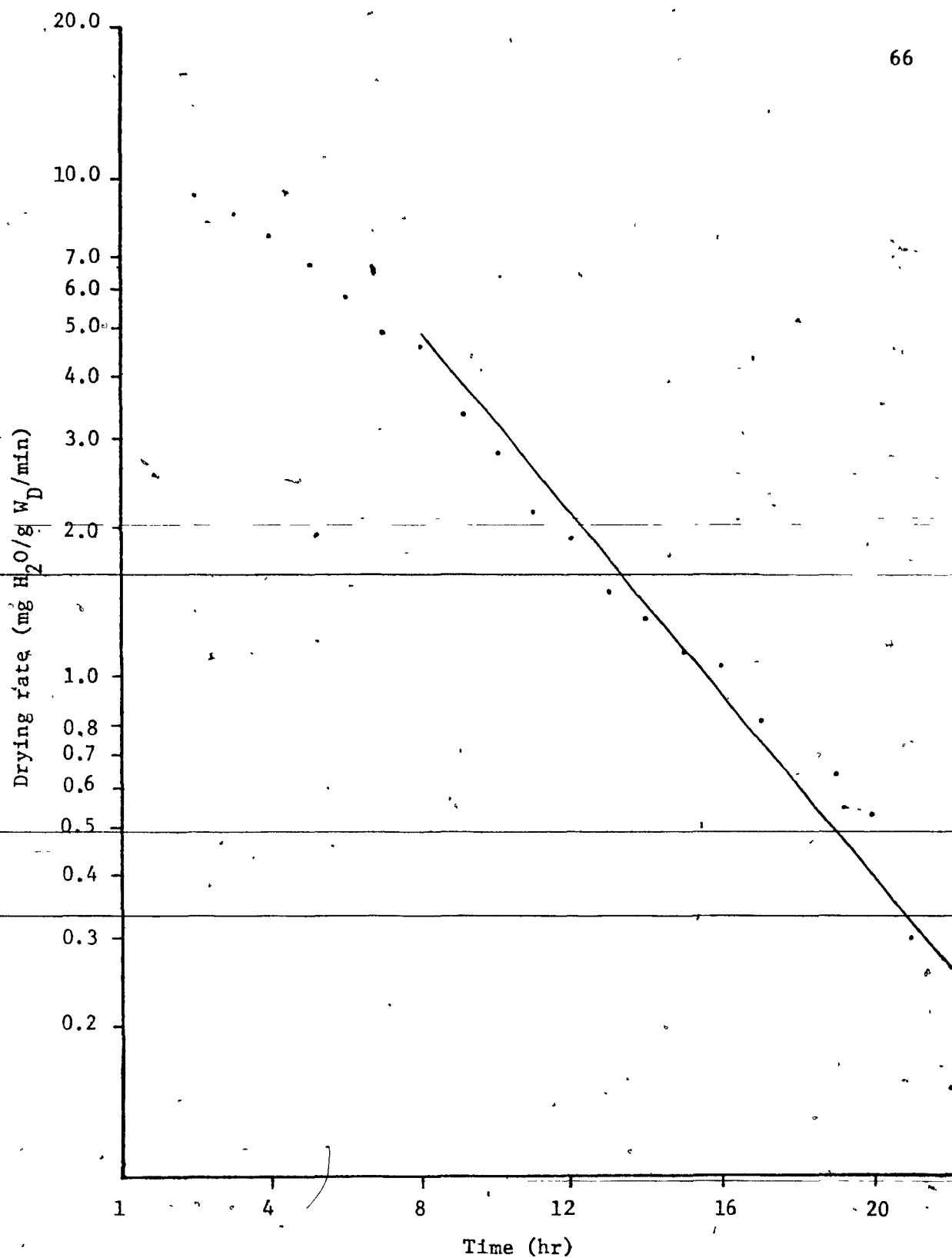


Figure 24. Semilog plot of Figure 22 (drying of pierced laminae).

— regression line ($K = -0.20$)

resistance to moisture transfer.

The reduced mobility of water at low moisture contents in hygroscopic materials appears to be related to both mode of moisture transport and bonding of water molecules. Gorling (1958) suggested that in vegetable products the migration of water initially takes place only by capillarity, whereas subsequently evaporation occurs within the porous vegetable material and at least part of the transport is in the vapour phase. Saravacos and Charm (1962) however found predominance of diffusion in moisture transfer throughout drying in fruits and vegetables. They attributed reduced drying rates to higher average energy of activation (or latent heat of evaporation) for the remaining moisture. Jason (1958) surmised that the transition from one drying phase to another in fish muscle was associated with uncovering of monomolecular inner layers of water after removal of multimolecular outer layers. Crank (1958) further suggested that the last traces of moisture are generally removed under conditions of low concentration gradients and consequently low diffusion coefficients.

These studies suggest that internal resistances operative at low moisture content are not necessarily the same as those at higher contents. Extrapolation of the EDP (Fig. 19) showed that if no internal resistive forces other than those present during this period existed earlier on, then the critical moisture content (assuming initial surface resistance) would occur at approximately

250% d.b. or 50% R.W.C. Since this estimate is low in comparison with data reported in the literature, (see previous section), it therefore seems likely that other internal forces are operative in the early stages, but are masked by the high cuticular interference. They may account for the slight rate decrease of the slow fall period.

5.2 Biological Aspects of Drying

5.2.1 Stomatal Control

A number of experiments were conducted to clarify the role of stomata in drying.

a. The drying pattern of excised red and white clover laminae, having initially open stomata, was investigated (experiment 1 and 2). The results (Figs. 25 and 26) revealed a sudden though slight increase in laminar transpiration rate after petiole removal. The increase ended abruptly with a very rapid decline in the transpiration rate. This initial rate increase was unexpected based on previous drying studies which showed either constant or falling rates after cutting (see section 2.2.2.2). Meidner and Mansfield (1963), however, noted that sudden mesophyll water deficits reduce the turgor of the epidermal and subsidiary cells before that of the guard cells, causing stomata to open further for a short time (a matter of minutes) until the guard cells lose turgor and effect stomatal closure. This phenomenon is known as "passive stomatal opening" and represents evidence for stomatal control early in drying.

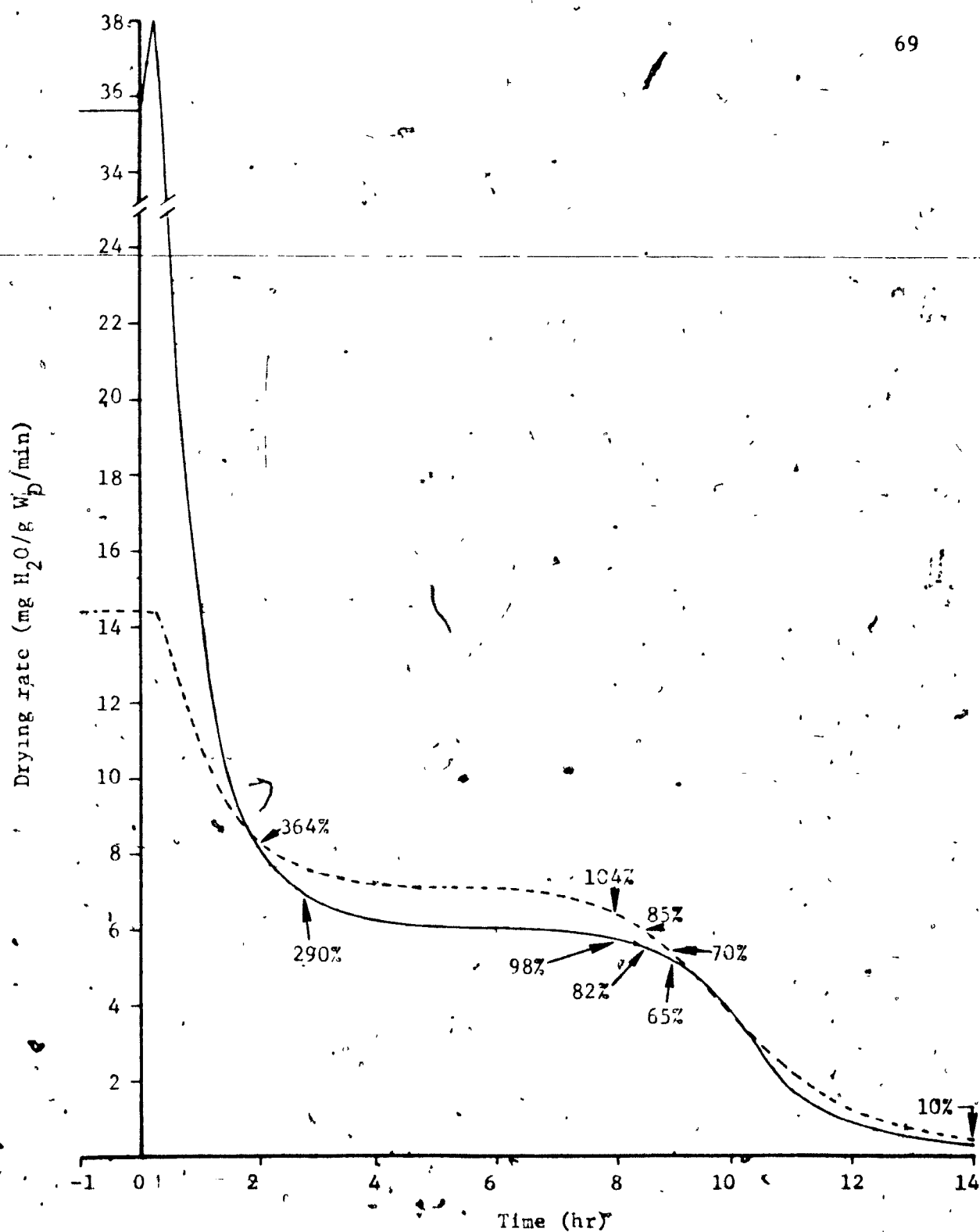


Figure 25. The effect of stomatal closure, induced by sodium azide, on drying rates of red clover, experiment 1.

--- sodium azide treated — control
(percentages in dry basis (d.b.))

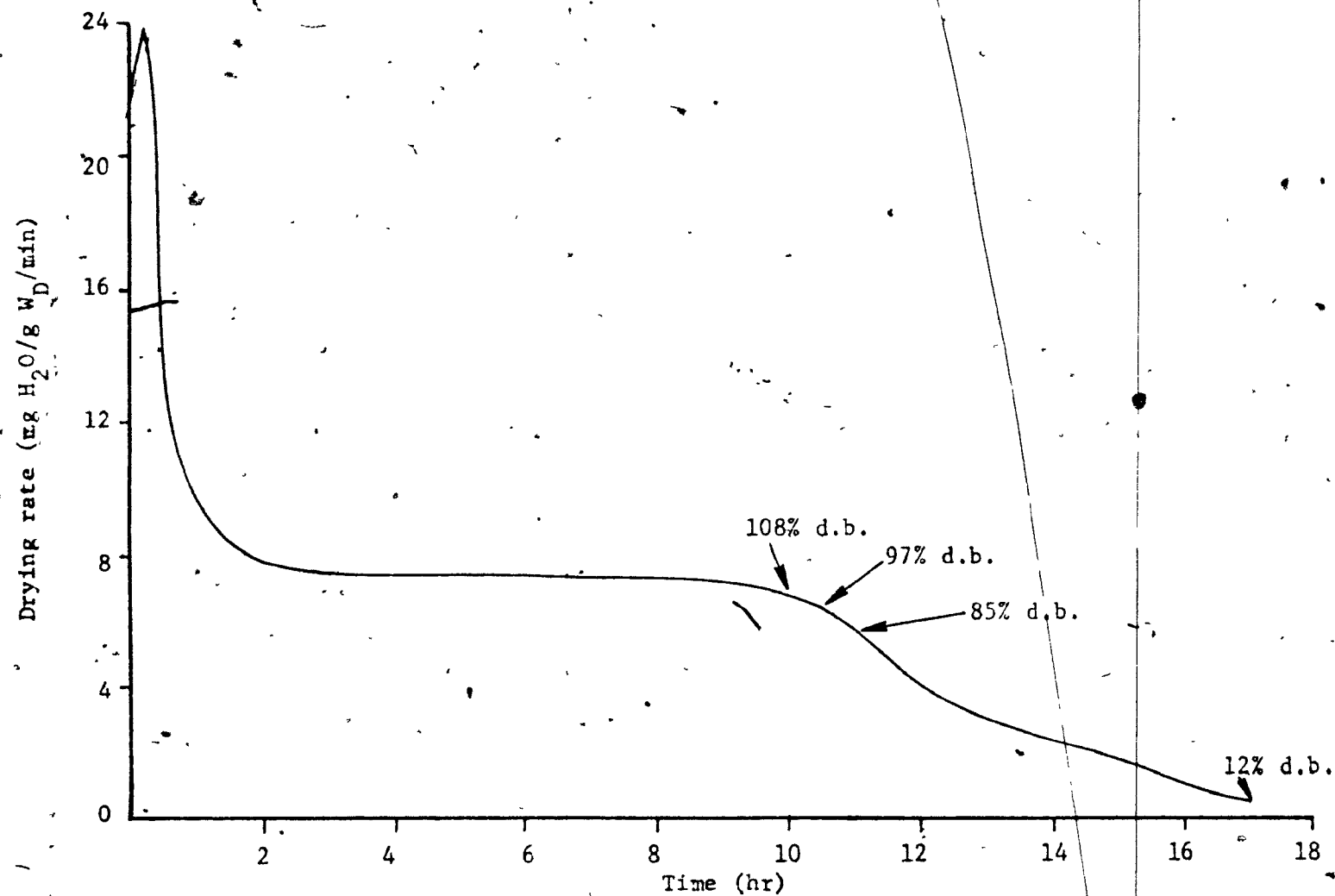


Figure 26. Drying curve for detached white clover laminae, experiment 2.
(untreated laminae)

The subsequent decline in the drying rate may be under both stomatal and mesophyll influence. Silicone impressions (as Zelitch 1961) taken of the red and white clover laminae after two hours of drying revealed almost total stomatal closure. Most researchers agree that stomata close soon after cutting, usually within three hours (Jones and Palmer 1932; Pederson and Buchele 1960) and sometimes within minutes (Waisal *et al.*, 1968) in a moderate environment. Laouar (1974), however, suspected that resistance to moisture transfer develops in sub-stomatal chambers before stomatal closing, and Hygen (1951) also postulated internal resistance during the "stomatal" phase. Gregory *et al.* (1950), Williams and Amer (1957) and Milthorpe (1959) found no internal impedance before stomatal closure. Waisal *et al.* (1968) reported that within the stomatal phase there is a constant rate period exhibiting no internal resistance, and a subsequent period during which the resistance develops. Williams and Amer (1957) suggested that the length of time that stomata stay open, which depends on their previous and current physiological status, determines whether internal resistance to moisture transfer will develop. A fixed rate of internal moisture transfer may limit transpiration at high surface conductance, but not at reduced conductance (i.e. after stomatal closure).

b. The foregoing pattern of transpiration was compared with that for laminae pretreated with sodium azide (concentration of 5×10^{-3} M) to close stomata (experiment 1). Cuticular and stomatal

TABLE 3. Stomatal and cuticular transpiration rates by laminae of Trifolium pratense and Betula papyrifera.
See text for explanation.

	Control		Treated		Change in transpiration rate	
	Red Clover	<u>B. papyrifera</u> *	Red Clover (NaN ₃)	<u>B. papyrifera</u> (P M A)	Red Clover	<u>B. papyrifera</u>
Stomatal Transpiration mg H ₂ O/gm DM/min	29.4	36.7 (2.8) ⁺	7.3	18.6 (1.7)	-75.2%	-49.3%
Cuticular Transpiration mg H ₂ O/gm DM/min	6.20	5.7 (1.1)	7.1	8.9 (1.4)	+14.5%	+56.1%
<u>Cuticular</u> Transpiration <u>Stomatal</u>	21.1%	15.5%	97.0%	47.8%		

* B. papyrifera data after Waisal et al. 1968. (Experimental conditions: temperature 25°C; relative humidity = 40%; light intensity = 1400 ft. candles; air velocity = 3460 m/hr.)

⁺ Numbers in brackets represent stomatal aperture in micron units (μ).

transpiration rates* for treated and untreated leaves of red clover (Fig. 25) are presented in Table 3, alongside similar data for Betula papyrifera leaves treated with the anti-transpirant phenylmercuric acetate, PMA (after Waisal et al. 1968). Sodium azide reduced stomatal transpiration by 75% to a rate comparable with the cuticular rate. Thus sodium azide did not completely close all stomata. Results obtained by Waisal et al. (1968) also indicated continued stomatal transpiration after application of PMA, while surface impressions confirmed incomplete stomatal closure. Consequently, the ensuing rate decline in treated leaves, at least in part, resulted from further stomatal closure. Waisal et al. (1968) observed that stomata closed earlier, and at lower moisture contents, in PMA treated leaves than those in control leaves, a pattern confirmed by my results for sodium azide treated leaves (Fig. 25).

The results in Table 3 indicate that the sodium azide treatment in effect increased cuticular transpiration by 14.5%. The higher moisture content of the treated leaves was probably not responsible for higher cuticular transpiration rates as these rates are not greatly affected by moisture content (see section 5.1.2.2). Waisal et al. (1968), finding a similar response in PMA treated leaves,

*Cuticular transpiration rate is defined (as Hygen 1951, 1953) as the rate during the "cuticular phase" (slow fall period) while stomatal transpiration rate is the initial rate less the cuticular rate.

attributed this increase to the failure of some stomata to close, and verified this with microscopic examination. They suggested that this failure was due to a process of structural fixation in either the protoplast or cell wall of the guard cells.

The ultimate drying time of the leaves was essentially unaffected by the initial stomatal aperture (Fig. 25). The higher initial rates of the untreated leaves were offset in part by the lower cuticular rates. Although the onset of the EDP was at a somewhat lower moisture content in the untreated leaves, the interdependence of rate and moisture content, being the same for both samples, equalized the overall drying times.

c. Sodium azide was applied at low concentrations (10^{-3} , 5×10^{-4} , 2.5×10^{-4} ; experiment 2) to red and white clover laminae to inhibit stomatal closure, as previously done for leaves of Vicia faba (Stalfelt 1957), Nicotiana tabacum (Walker and Zelitch 1963), and Medicago sativa (Cears and Roberts 1970; Tullberg and Angus 1972). Sodium azide was applied by immersion, spray (a wetting agent added), and imbibition through petioles. There was no increase in transpiration or drying rates in either species.

d. The effect of stomata on drying rate of white clover laminae was also examined using light and dark treated laminae (experiment 5, Fig. 27). Light was supplied by cool white fluorescent bulbs emitting only 30 ft. candles (to minimize radiative heating), while the dark treated leaves were kept in darkened transpiration

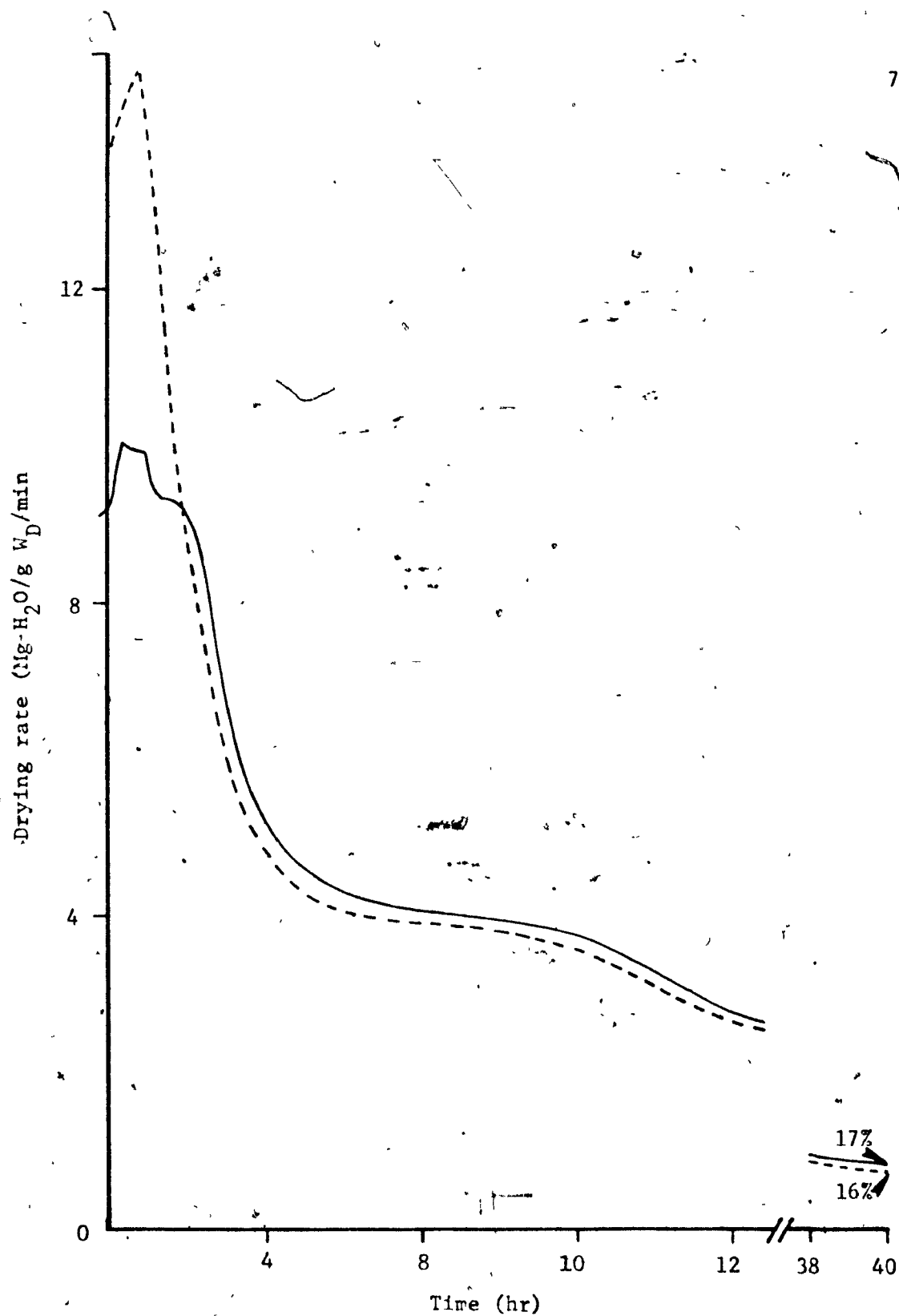


Figure 27. Drying curves for light and dark treated laminae of white clover (experiment 5).

— dark treated
--- light treated

chambers. The stomata of treated leaves were not fully closed at time of cutting because of endogenous rhythms. Stomata of laminae from both treatments showed rapid closure, briefly preceded by passive opening, after which differences in the drying rates, or overall drying time, became minimal. This further demonstrates the transiency of stomatal control in drying.

In a separate experiment (6), the petioles exhibited no discernible response to light.

e. The importance of the stomatal pathway early in drying is also suggested by experiment 3 (Fig. 27) in which removal of epicuticular waxes had slight overall effect while stomata were open, whereas epicuticular removal had a marked influence during the subsequent cuticular phase.

f. The drying pattern of detached white clover petioles was studied (experiment 7). The results (Fig. 30, p. 82) indicated, instead of either constant or increased rates, the immediate onset of a rapid fall period after cutting. The initial rapid decline was probably associated with both rapid moisture loss from the cut petiole ends and with closure of stomata, although Shepherd (1964) reported that stomatal closure does not occur in white clover petioles until after removal of the majority of water. The rate decline became more gradual after 10 hours of drying, appearing then to follow the exponential decay (equation 4) drying pattern (Fig. 31, p. 84).

Petiolar drying rates were found to be comparable with laminar rates (0.45x and 1.3x laminar rates at one hour and 7 hours after cutting, respectively), when contrasted on a dry weight basis. The very high moisture content of the petioles makes a comparison between the two, on this basis, meaningless. In fact, petiole drying is so much lower than laminar (on moisture content basis) that despite the usage of 16 petioles (12 cm in length) of white clover per sample, the vapour flux was barely within the measuring sensitivity of the apparatus. Consequently, data of petiole rates are less accurate and more scattered than laminar rates (Fig. 30).

5.2.2 Transfer of Petiole Moisture to the Lamina

a. The loss of petiole moisture via the lamina, in particular the duration of axial tendency of moisture transfer, was investigated. Experiments entailed comparison of drying rates of detached laminae to those of laminae with intact petioles (petiolate).

In the first experiment (experiment 8, Fig. 28) petioles were removed from one set of laminae at the outset of drying. The drying curves show that whereas the detached laminae exhibited the drying pattern discussed previously (section 5.2.1,a) the petiolate laminae maintained their original transpiration rates for about 1.5 hours while exhibiting no passive opening. The reservoir of moisture in the petioles apparently prevented the sudden development of a water deficit in the mesophyll. In detached laminae this deficit

resulted in passive opening of stomata. The existence and abrupt end of the constant rate in the petiolate laminae, suggests that at first the very mobile moisture residing in the xylem supplies the laminae, and when this is exhausted a water deficit develops in the leaves which ultimately closes the stomata.

The more gradual drying rate decline of the petiolate laminae probably reflects less abrupt and synchronized stomatal closure, whereas the higher cuticular (SFP) rates of these laminae may be due to stomatal leakage and/or higher moisture content. After 18 hours of drying the moisture content of petiolate laminae was 122% higher, and transpiration rate 27% higher, than that of laminae without petioles, suggesting a tendency for more even drying of laminae and petioles when they remain attached.

b. A study (experiment 9) was conducted to investigate whether the axial movement of moisture continued after stomatal closure, and hence to discover whether these two biological aspects of drying, both related to the presence of highly mobile moisture, are associated. In this experiment, both sets of laminae retained their petioles for the first 6 hours of drying, whereafter the petioles of one set were removed. The drying curves (Fig. 29) show little difference in drying rates of the two samples for the following 10-12 hours, a gradually increasing difference for the next 4 hours, and a rapidly growing difference as soon as the exponential decline period was reached by the detached laminae (moisture content

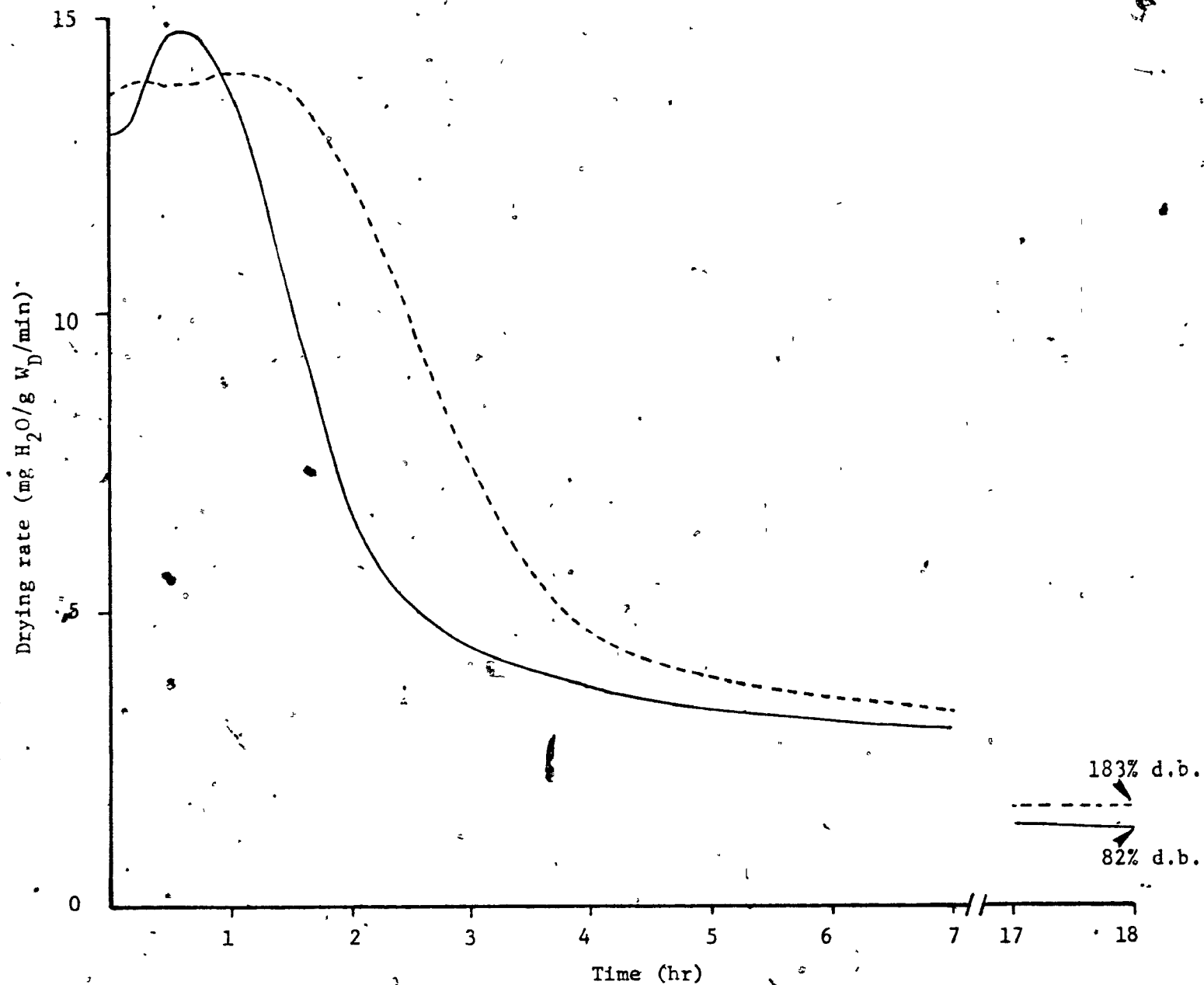


Figure 28. Drying curves for petiolate and detached laminae of white clover.

— petiolate laminae

--- detached laminae

of 75% d.b.). The drying of petiolate laminae had no exponential decline period during the entire duration of the experiment.

The final moisture contents after 38 hours of drying were 96.2 and 13.5% for petiolate and detached laminae respectively; and in addition, 117% d.b. more moisture was lost by petiolate laminae. Altogether, in this experiment about 200% d.b. of petiole moisture was removed by the laminae after the first 6 hours of drying.

c. A similar experiment (10) showed only a very slight transfer of moisture to the laminae after 20 hours of drying.

d. The effect of laminae upon the direct evaporation from petiole surfaces was tested (experiment 7) by determining the moisture loss from 2 sets of petioles, one retaining its laminae the other lacking them. Petioles with laminae attached (Fig. 30) had a more rapid drop in transpiration rate than those without laminae, indicating the importance of laminae in removing petiole moisture. However, after 100 hours of drying, moisture contents of the two sets of petioles were quite similar, though above storageable levels. This suggests, as Pederson and Buchele (1960) have indicated (see section 2.2.2.1), that over the entire course of drying the role of laminae in removing petiole moisture may be unimportant.

Apparently petiolar transpiration is a function of moisture content (section 5.2.1.f), suggesting that drying is inhibited not only by the cuticular layer, but also by the internal process of radial moisture transfer, especially through the cortex (section

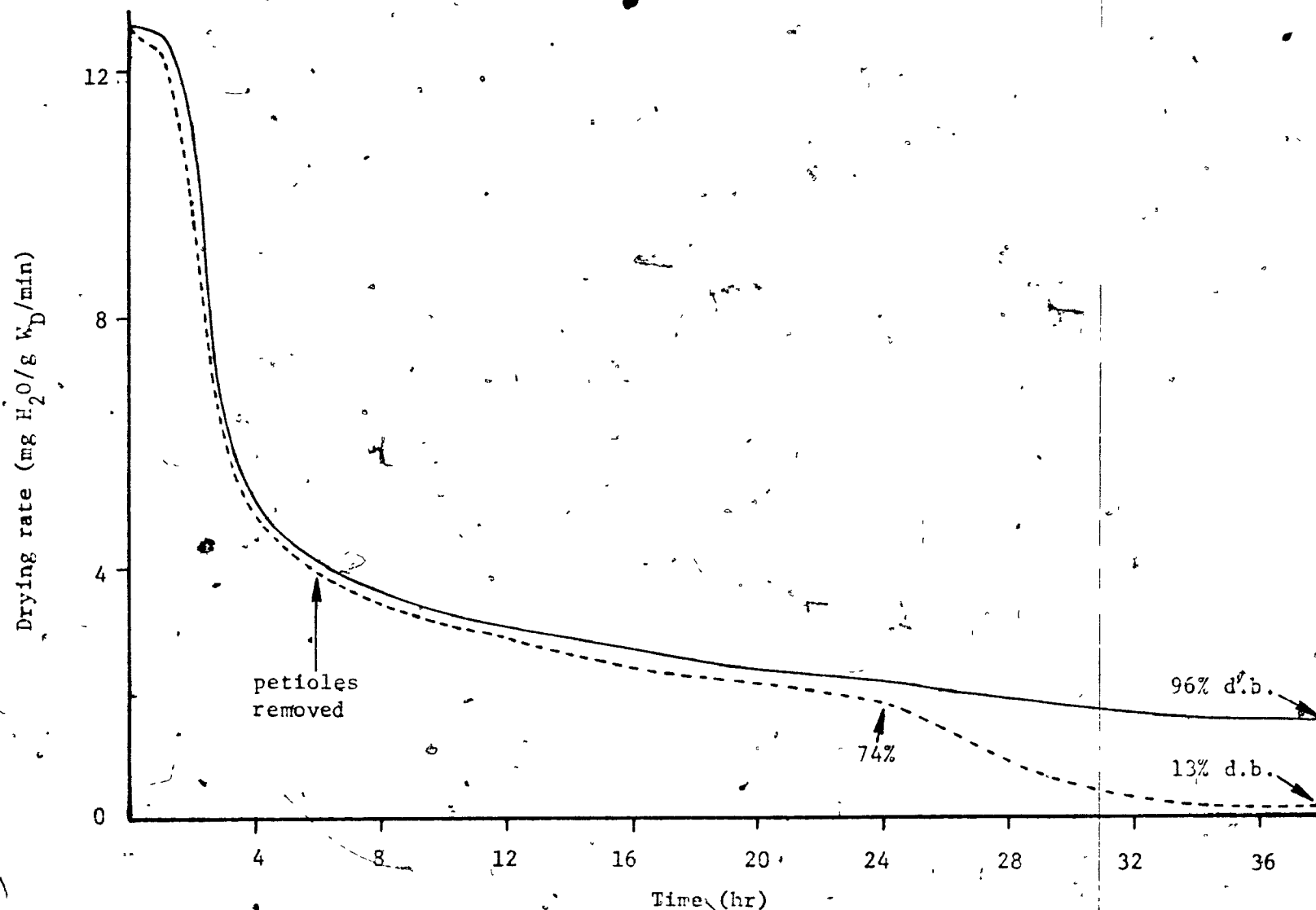


Figure 29. Drying curves of petiolate and detached (after 6 hours of drying) laminae of white clover.

— petiolate laminae

---- detached laminae

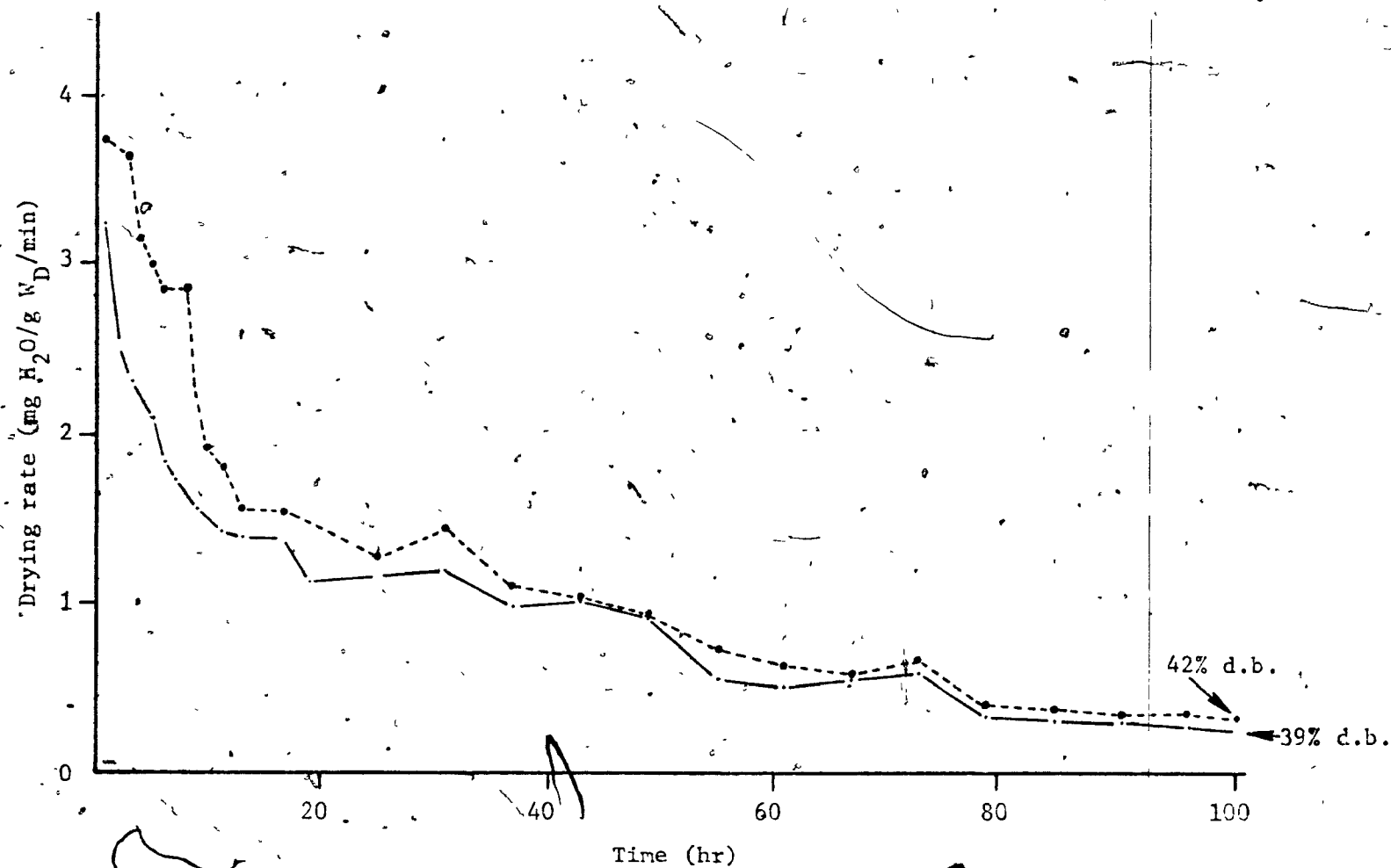


Figure 30. Evaporation rates from petioles with and without their laminae.

- petioles with laminae
- petioles without laminae

2.2.2.1; Bagnal et al. 1970), which may be moisture dependent (section 2.2.1.2). Thus the geometry of the petiole and the thickness of the cortex may be important rate governing factors, in addition to the cuticle.

Further study should be conducted to establish the importance of leaves in removing stem moisture.

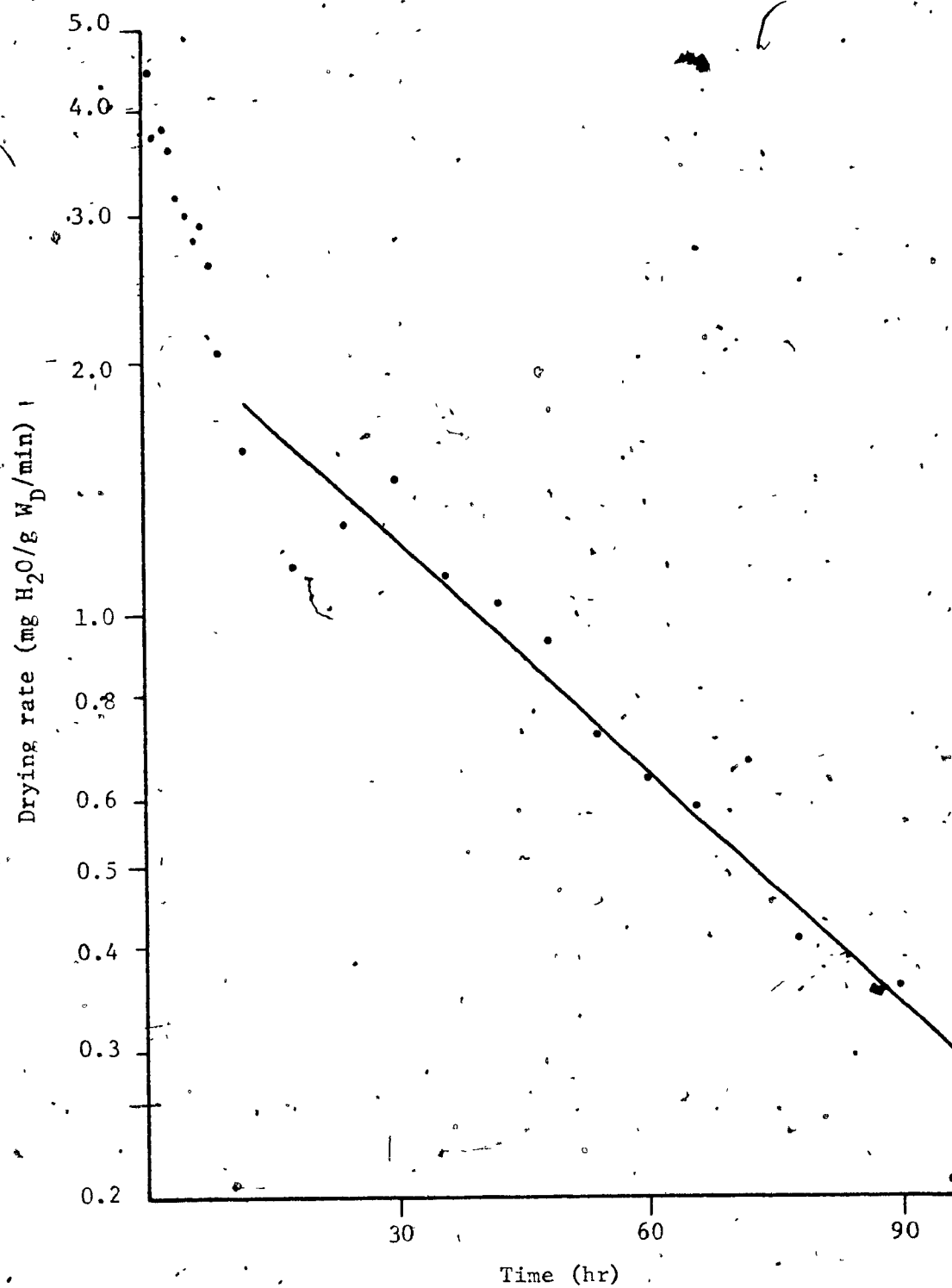


Figure 31. Evaporation rates from petioles without laminae (derived from Figure 30).

— regression line ($K = -0.020$)

VI. CONCLUSIONS

A gasometric apparatus was devised to study the drying of white and red clover plants. The apparatus monitored the drying patterns of laminae and petioles that were either attached or separate.

Apparently drying in thin layers is controlled by atmospheric conditions, as well as surface and internal plant characteristics. Because these factors vary in importance during drying, the drying mechanism of plants is complex.

Shepherd (1964) and Leshem et al. (1972) showed that atmospheric conditions, such as air velocity and vapour pressure deficit, control drying only in the early stages, especially while stomata are open; while the present study has indicated a transition from surface (stomatal and cuticular) to internal control in the drying of laminae. Moisture transfer through stomata lasts briefly, therefore cuticular resistance to moisture transfer is important through much of the drying period. Cuticular control (cuticular phase or SFP) ends at moisture contents well above safe storage levels when internal resistance becomes relatively great (in EDP).

The importance of cuticle has been stressed in many hay drying studies (eg. Byers and Routley 1966), probably because it

is easy to demonstrate that its disruption results in accelerated drying; however, *the significance of internal resistance to moisture transfer in forage drying as demonstrated in my study*, has not been widely recognized. In much of food drying, because of the thickness of the food morsels and the absence of skins, internal resistance is more obviously important and has been studied by many workers. Increase in internal resistance during drying has been attributed to mode of moisture transfer and form of water binding (eg. Jason 1958; Saravacos and Charm 1962; see section 5.1.2.4). In forage plants, however, there is little indication of the mode of moisture transfer in the latter stages of drying; it is not known, for example, whether moisture transfers at this time as a liquid or vapour, or even whether it moves predominantly axially as has often been reported (eg. Jones and Palmer 1933) or radially as suggested by this study (see section 5.2.2,d). Further research, using tritiated water, may indicate the pathway of moisture transfer throughout the different stages of drying.

The tenacity with which moisture is bound in tissues is shown by sorption isotherms, which may be simplistically represented by single equilibrium moisture content (EMC) values. Though EMC, has received little attention as a factor which regulates drying, Rees (1974) attributed the faster drying of (finely chopped) the S23 cultivar of Lolium perenne (relative to Sabel) to its lower EMC. Furthermore Guthrie and Collins (1965) showed that the

growing environment influences sorptive capacity (EMC) of plants. Therefore, there appears to be scope for research in this area; both for the selection of cultivars which have low EMC, and for management practices to promote low EMC.

The results of Person and Sorenson (1970), that alfalfa dries faster than brome grass at high, but slower at low moisture contents, supports our findings that drying is governed by different factors as it progresses. Therefore, the search for improved lines or management practices should include a study of both surface and internal properties which would favour drying.

VII. SUGGESTIONS FOR FURTHER RESEARCH.

The present study was limited in that only two species were investigated. Other forage species should be examined to determine whether they exhibit a similar drying pattern.

For white and red clover, internal resistance, in addition to cuticular resistance, is apparently important in impeding drying, especially in its latter stages. In view of this, three avenues of research may be followed in order to improve drying characteristics of forage plants.

- 1) Basic research on water pathways within plants, especially during the latter stages of drying, possibly using tritiated water.
- 2) Applied agronomic research to improve the drying characteristics of plants. This may include the search for genetic lines having low EMC and permeable cuticles, or for management practices that would favour these properties.
- 3) Engineering research in post harvest treatments that would overcome barriers to moisture loss that could not be minimized agronomically.

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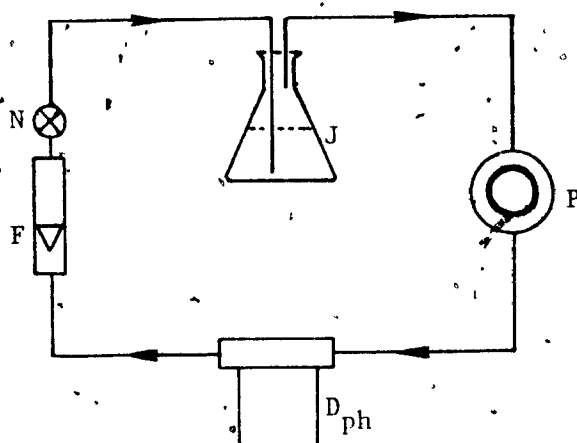
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APPENDIX I

CALIBRATION OF THE DEW POINT HYGROMETER

In order to calibrate the dew point hygrometer, dew point measurements were compared with equilibrium dew point values for air above water or saline solutions.



A closed air circuit (see diagram above) was assembled, which included a peristaltic pump (P), dew point hygrometer (D_{ph}), flowmeter (F), needle valve (N), and six-liter flask (J). The apparatus was located in the controlled environment room (Fig. 2) where temperature was maintained at 68°F. Separate trials were conducted in which air was bubbled through either distilled water, or saturated solutions of sodium chloride or calcium chloride, in the flask. The air was pumped through the circuit until stable dew point measurements were obtained. The dew point measurements for the 3 liquids were compared with

standard values (Hall 1957):

Liquid	Dew point temperatures (°F)		Error
	Standard (from Hall 1957)	Dph measurement	
distilled water	68.0	66.1	1.9
sodium chloride	59.7	58.0	1.7
calcium chloride	38.3	36.7	1.6

The results indicate that the hygrometer readings were consistently less than 2°F below standard values.