not only changes in the main components that are important: not only should earthworms and grass grubs be studied as well as sheep, but weeds are involved in the system as well as grass and clover.

CONCLUSIONS

a. For studies of pasture production and its utilisation the ecosystem is the natural unit of study.

b. A particularly significant expression of the ecosystem is found in ecosystem processes.

c. However, the nature of the soils and the species of plants and animals present in the ecosystem are also important.

d. So are the changes that take place in the numbers and species of organisms present.

e. These three, the ecosystem itself, the dynamics of its populations and the rates of its various processes provide a conceptual framework which allows the whole system to be kept in view while detailed studies are carried out.

f. The compenents and processes may be measured quantitatively and it is possible to take into account not only natural changes but also changes introduced by man.

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STRUCTURE OF VEGETATION IN RELATION TO ENERGY EXCHANGE

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New Zealand has a proud ecological history. Particularly as far as our vegetation is concerned, ecology has gone through phases similar to those in most countries of the world. The pioneers described the general patterns of the communities and set in perspective the picture for the country as a whole. Then came more detailed description of particular situations, and the introduction of quantitative measurement techniques. The latter allowed standardised definition of what is present at a site and measurement of differences between sites. The result has been a generally satisfactory answer to the question of "what species are present and what trends are occurring"?

Next came the question of why certain species are present and why the trends are occurring. It is with the treatment of these questions of "why" that vegetation ecology, and probably many other branches of ecology as well, has become notable for its imaginative speculation and for the low quota of hard facts on which those speculations are based. Remembering Kelvin's dictum that an issue does not become science until you can measure it, we have here a reason for the relative decline in the status of plant ecology, within the scientific community within the last 30 years.

The essential feature to which attention is drawn now is that the tools to reverse that situation have been forged within the last decade. The challenge to ecologists is to make effective use of them and thus restore ecology's position as a guiding science, with its role of integrating the findings of the more specific disciplines.

Techniques for controlling climate within rooms and cabinets give an essential tool for translating knowledge of physiological processes into the quantitative terms required for definition of their importance in various field situations and with various species. At the same time the techniques of micro-meteorological physics are being successfully used to give understanding and quantitative definition of the energy exchange between the atmosphere and the vegetation. These two aspects, the physiology of the plants and the pattern of energy exchange at the vegetation-atmosphere interface between them, determine the ecological results. In large measure the energy exchange patterns have direct impact on all aspects of the ecosystem in an area, whereas the plants, the animals and the micro-organisms each have their set of physiological features adapting themselves to particular ecosystems. Accordingly, most emphasis in subsequent comments will be given to energy exchange patterns.

In calm weather the main energy inflow to the vegetation surface comes from radiation from the sun—so called "short wave" radiation, and radiation from the atmosphere—so called "long wave" thermal radiation. Energy outflow is more varied. There is the reflection of short wave radiation by vegetation and soil, the emission to the atmosphere of long wave thermal radiation generated by the effective temperature of the vegetation or soil surface, the conduction of heat from the leaf and soil surfaces to the surrounding air, and finally the evaporation of water from leaves and soil. The quantities of energy used for heating and cooling of the soil and for photosynthesis are usually sufficiently small, i.e. 0—2% of the totals, to be neglected when assessing the size of the main components of the energy balance.

The quantities of energy involved are large. For instance, the average amount of solar energy received daily is equivalent to over 10,000 kilowatts of electricity per acre. By comparison the use of electrical energy by the city of Palmerston North averages about 60 kilowatts per acre per day.

TABLE 1. *Example of energy exchange balance at the vegeation-atmosphere inferface.*

Calories/sq.cm./min.

INWARD		OUTWARD	
Short-wave solar radiation	1.00	Reflection of short-wave radiation	0.25
Long-wave thermal sky radiation	0.44	Long-wave thermal radiation from vegetation surface	0.58
		Sensible heat, i.e. heated air in conduction and convection	0.19
		Latent heat of evaporation	0.40
		Soil heating and photosynthesis	0.02
TOTAL	1.44	TOTAL	1.44

There are considerable seasonal, and of course day-to-day and diurnal, variations in the quantity of energy coming in from the two main sources. Within the latitudinal range of New Zealand the average amount of solar radiation per month varies about three-fold in the North and six-fold in the South between December and June. Its annual average is about 350 calories/sq.cm./day at Auckland and 300 at Invercargill. The incoming long wave thermal radiation has been empirically found to be proportional to about 75% of the black body radiation corresponding to the air temperature at 4 ft.

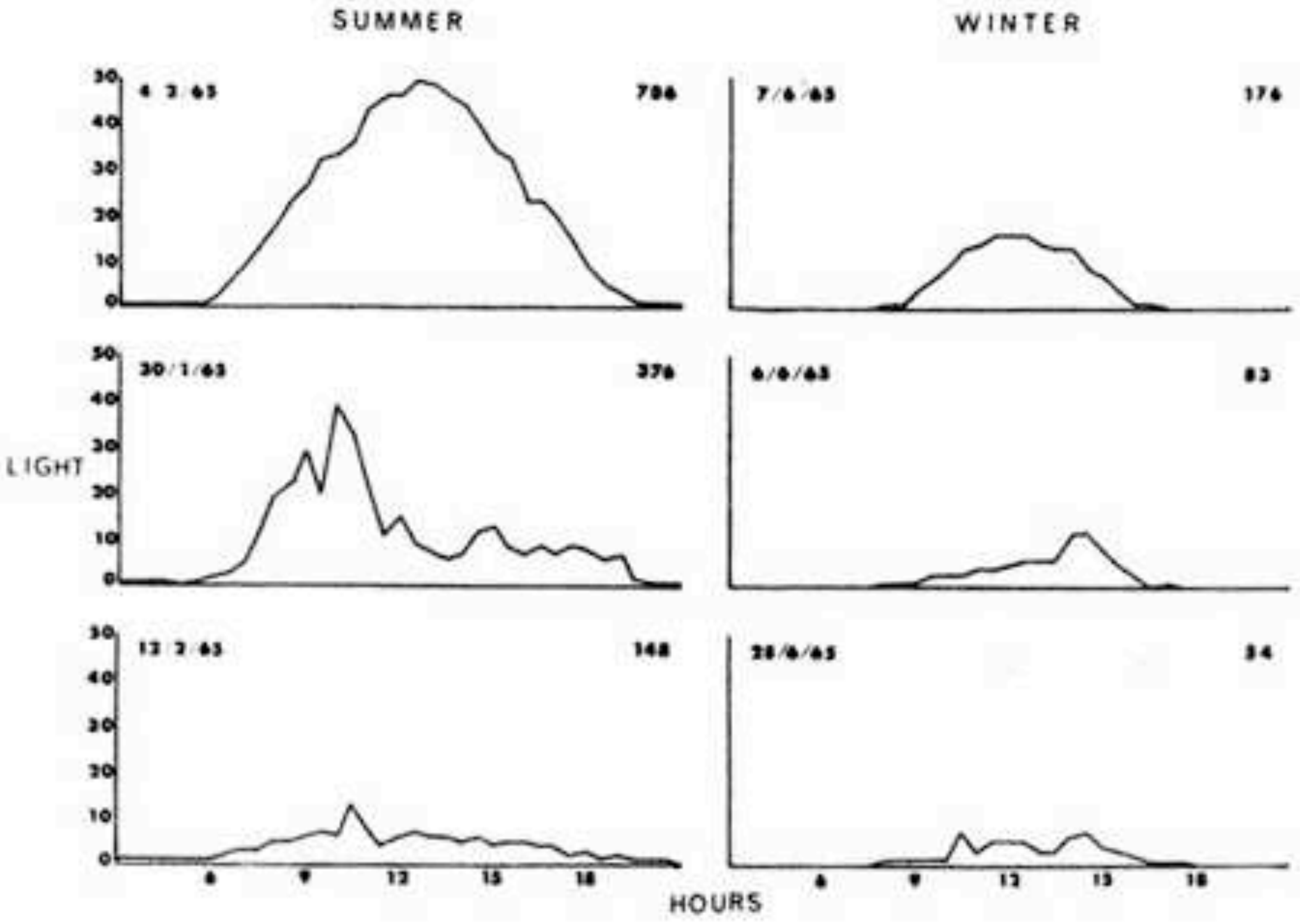


FIGURE 1. *Examples of variation in daily solar radiation at Palmerston North. Values in arbitrary units.*

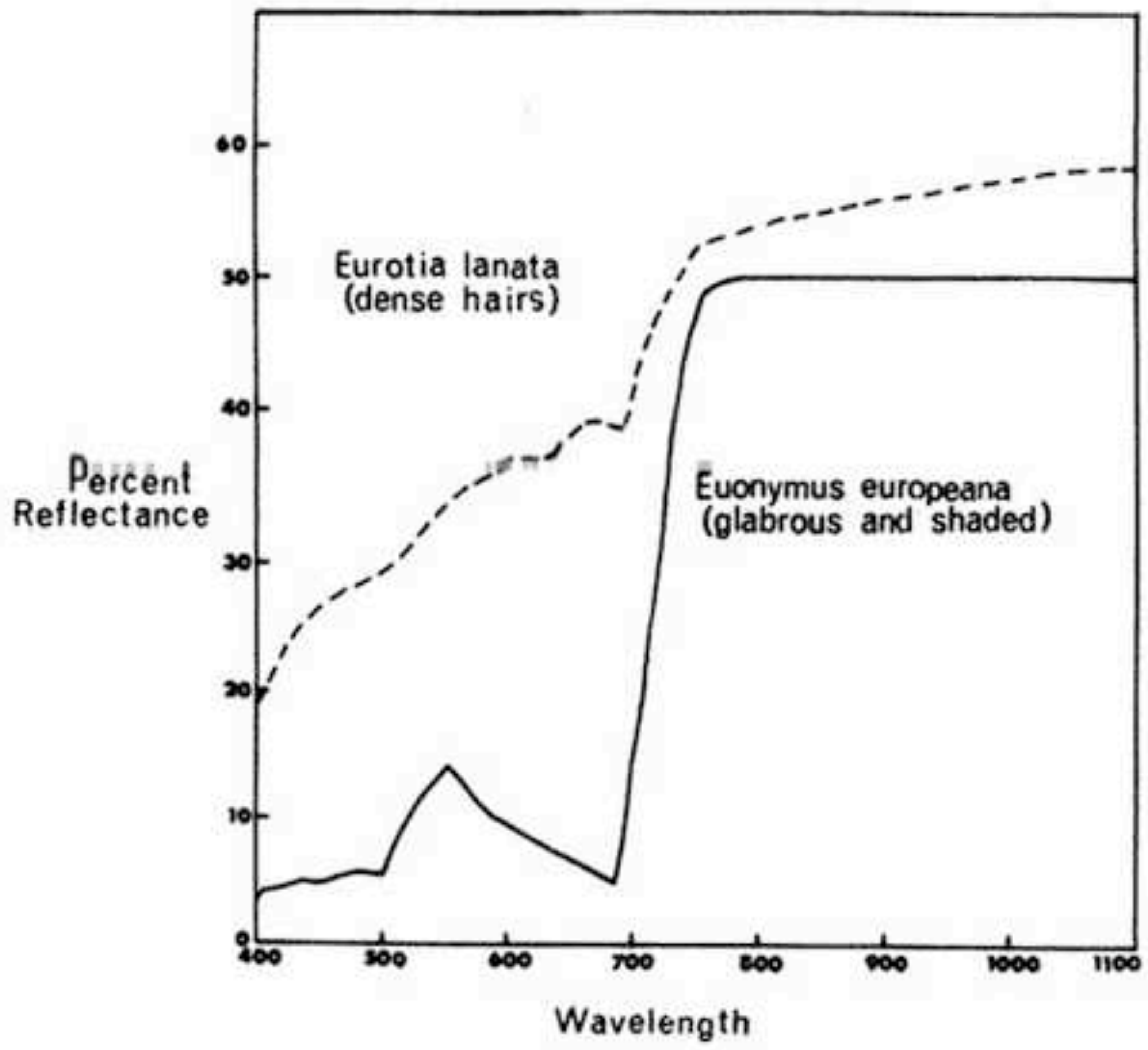


FIGURE 2. *Differences in leaf reflectance. After Billings and Morris (1951).*

Of that incoming radiation a considerable proportion of the solar, i.e. short wave radiation, may be reflected. This is the first avenue by which plants, can regulate their effective energy environment. There are considerable variations between species in their absorbance and reflectance both of visible and of short wave infra-red radiation. Forms with various mechanisms for reducing absorption by the leaf are common in environments characterised by high inflow of solar energy. But, high reflectance by an individual leaf does not always lead to high reflectance from the vegetation as a whole. Back reflectance from vegetation is determined by whether leaves are positioned to reflect back to the sky or down into the vegetation and soil surface, i.e. whether they lie horizontally or at an acute angle. For a considerable range of vegetation short wave reflectance is about 25%, but it may fall to under 20% or rise to over 30%.

A major proportion of the long and short wave radiation absorbed is disposed of by the long wave thermal radiation back to the sky and the atmosphere. The amount going out in this form is strongly dependent on surface temperature. At a surface temperature of 20°C. it is about 0.55 calories/sq.sm./min. A 5°C. change will give 7-8% variation in the amount radiated. It is important to remember that we are here concerned only with the net temperature of the surfaces of the upper leaves of a canopy which are directly exposed to the sky. These may be well below or well above temperatures of leaves lower down.

Apart from the small fractions being used in photosynthesis and heating of the soil, the remainder of the incoming energy is disposed of by evaporation of water and by the conduction and convection of heated air and water vapour away from the leaf. As that energy is carried in the air, as distinct from being radiated through it, these two processes are often termed the mass transfer of energy.

Factors regulating this transfer of sensible heat and water vapour have been intensively studied in recent years. The device of logic which has been found most useful is the analogy with resistances in an electrical circuit, or better still in a pipe flow-circuit.

For water vapour evaporating from inside the leaf the total resistance to flow out to the atmosphere can be subdivided into (i) resistances to movement across the surface of the mesophyll cell, (ii) resistance to movement in the intra-cellular spaces, and (iii) resistance

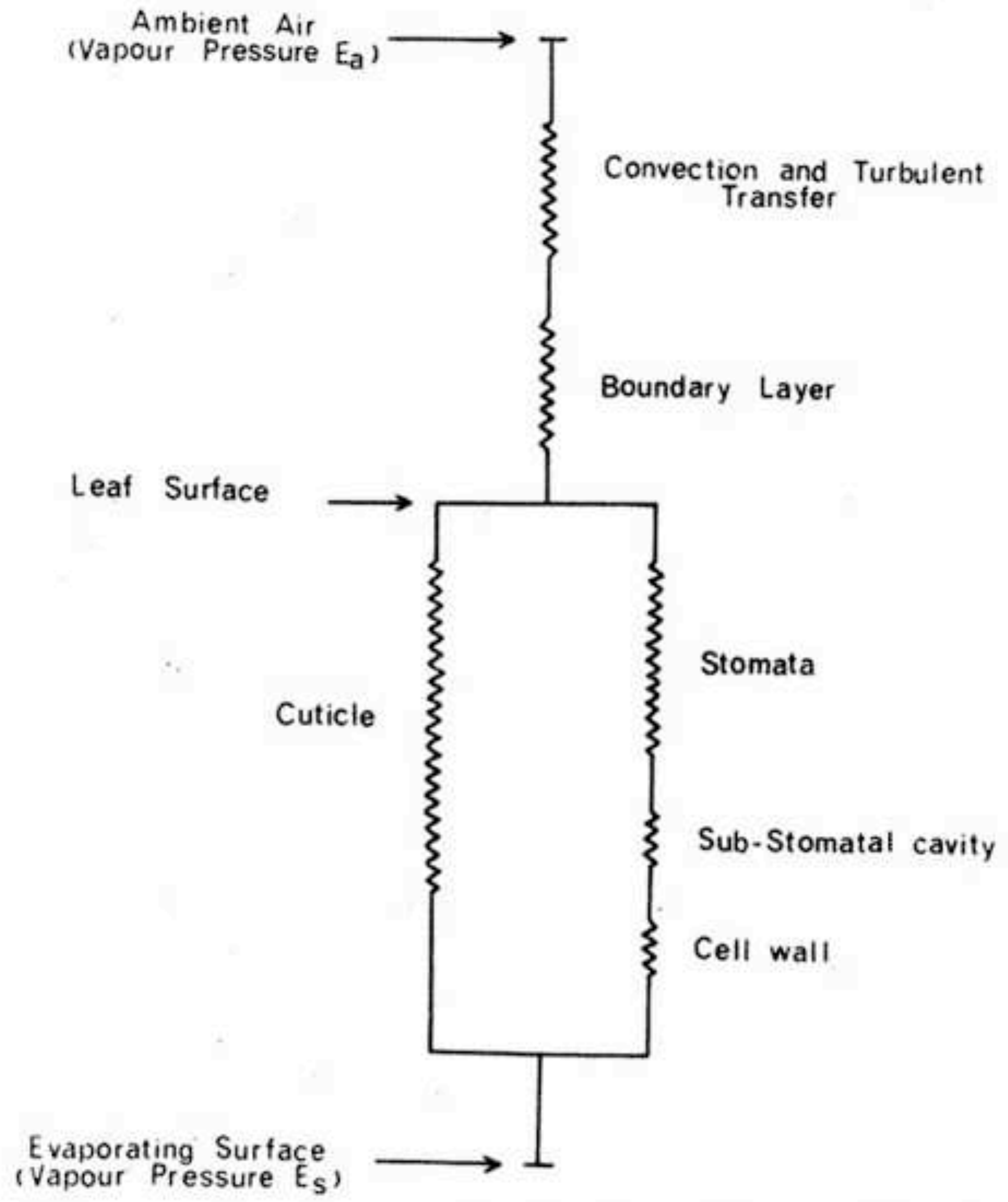


FIGURE 3. *Arrangement of resistances in the path of water vapour diffusing from the leaf. Approximate relative sizes of resistances are indicated.*

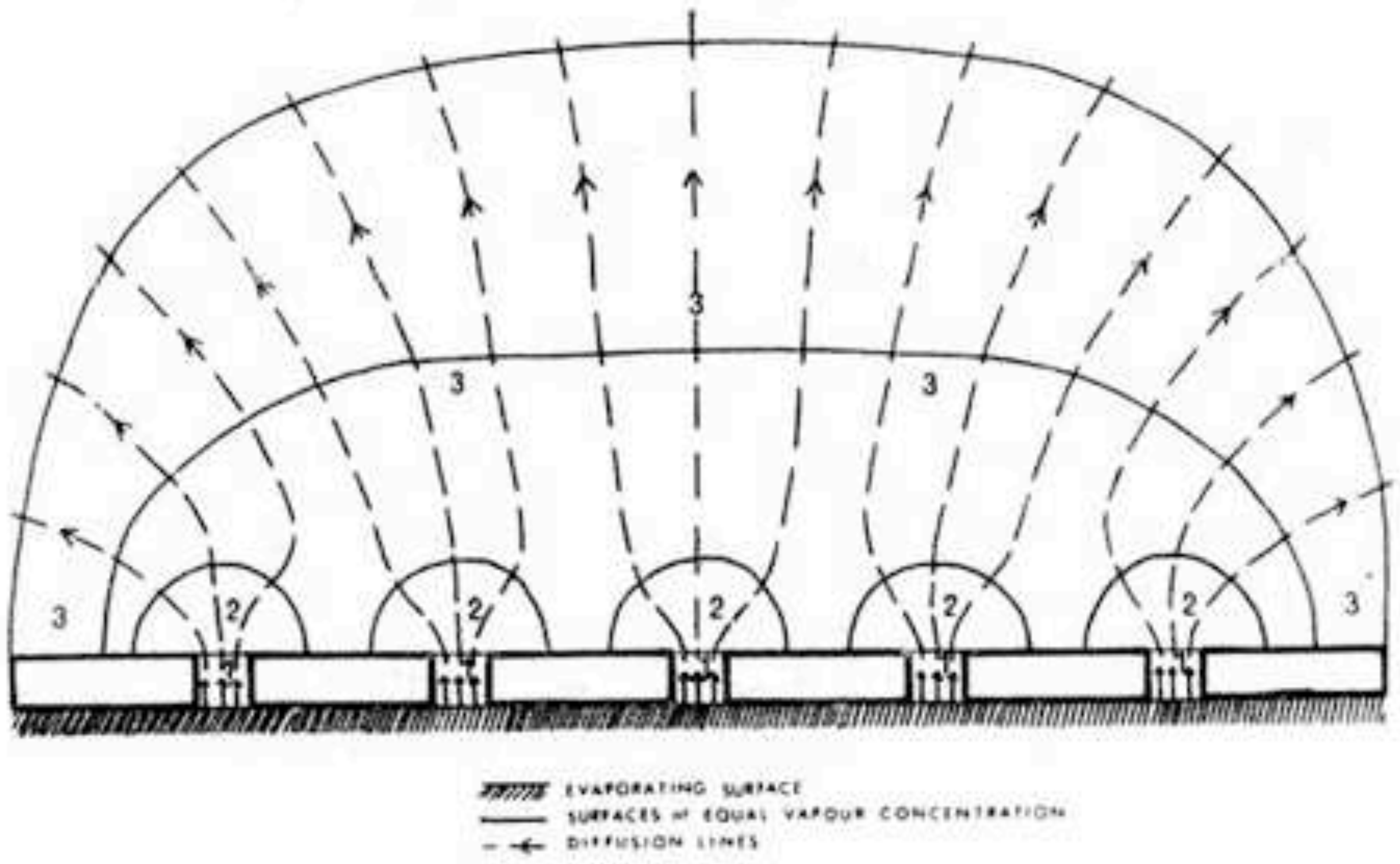


FIGURE 4. *Diffusion lines and surfaces of equal vapour pressure concentration over an evaporating surface over which a perforated septum has been placed. After Bange (1953).*

to flow through the stomata. In parallel with this is the resistance to flow across the cuticle. Outside the leaf, moisture vapour and sensible heat, i.e. heated air, face similar sets of resistances. There is the resistance of travel across the boundary layer of air, in which there is effectively no movement and passage is dominantly by vapour diffusion, and there is the resistance to the convectional and turbulent transfer of moistened and heated air out to the open atmosphere above. In this chain the dominating resistances are the transfer across the stomata and the transfer from the surface of the leaf out to atmosphere. When stomata are open the external resistance is often much the greatest of all.

For these transfers of water vapour and heated air out to the atmosphere the structure of the individual leaves may have a dominating effect on the apportionment of the energy dissipated. The inter-relationships have been well documented. (Milthorpe 1959, Gates 1965).

For a given level of radiation absorbed, the higher the resistance of the stomata due to their being closed or well sunken into a leaf the higher the leaf temperature will become before re-radiation and convection transfer of sensible heat rise sufficiently to establish an equilibrium. In general, the higher the temperature of a leaf in relation to its radiation and convection surroundings the lower will be the proportion of its absorbed energy disposed of as evaporation with a constant stomatal resistance. Conversely, the lower its temperature relative to its surroundings the higher will be the proportion of its absorbed energy disposed of as evaporation. These comments assume either free convection past the leaf or a constant rate of forced convection, i.e. constant wind speed.

For wind movement the situation becomes more complex. If the stomata remain open, i.e. internal leaf resistance remains constant, an increase in wind speed decreases the resistance to flow away from the leaf equally for both water vapour and heated air. This cools the leaf to a lower equilibrium temperature compared with that attained in still air. If heating from radiation in the still air has been large, this cooling will tend, at low wind flow, to decrease the proportion of energy disposed of in evaporation. But as the wind speed past the leaf increases the leaf temperature will continue to fall. Consequently temperature gradients between the leaf and adjacent air become correspondingly smaller; but the difference in vapour pressure between the evaporating surface in the leaf and the outside air remains more nearly constant. As a result the balance between evaporation and sensible heat transfer of energy reverses and evaporation transfer becomes the larger. With further increase in wind speed evaporation transfer of energy will become sufficiently high to cool

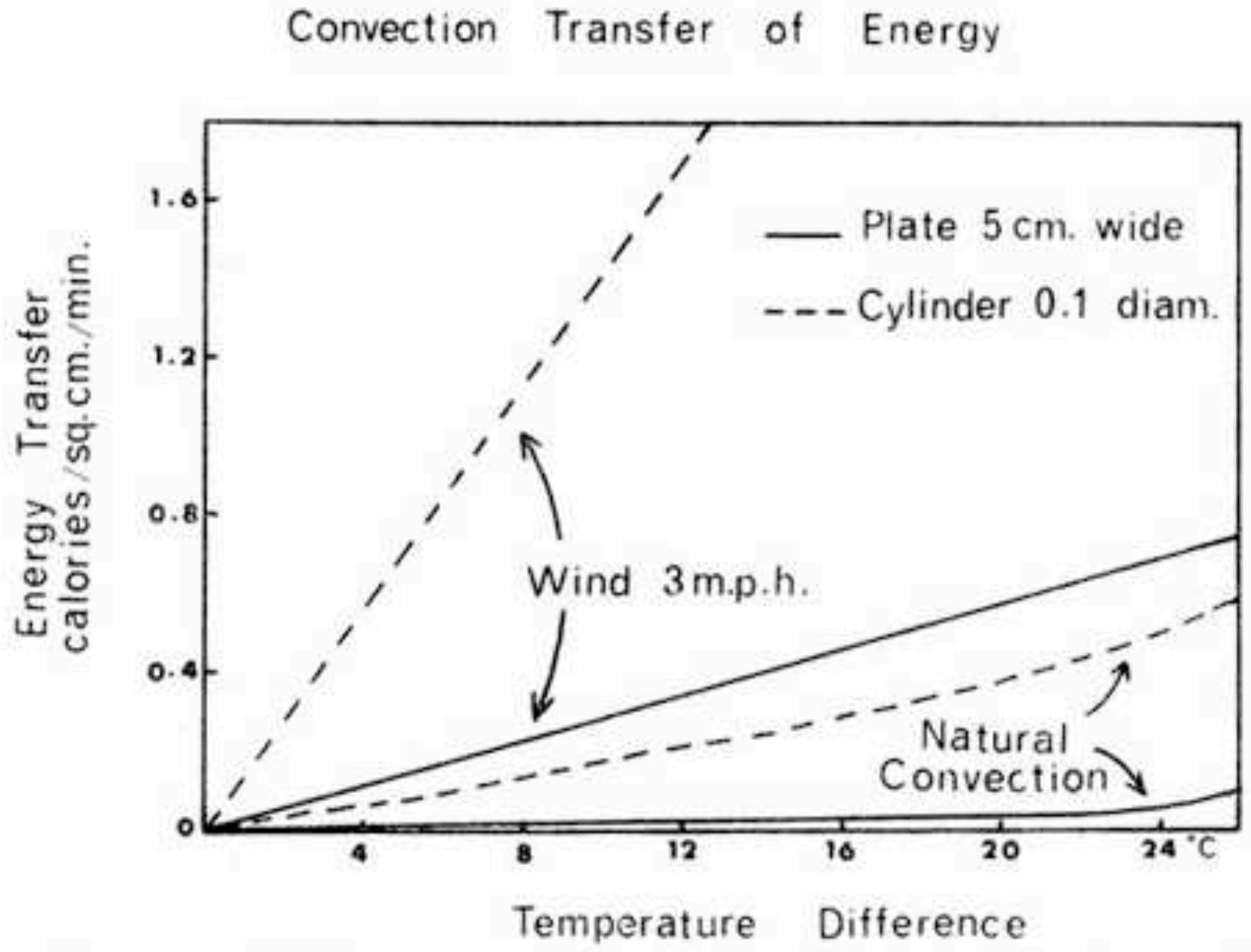


FIGURE 5. *Effects of leaf shape and wind speed on removal of energy from a leaf. After Gates (1963).*

TABLE 2. *Rise in temperature inside the vegetation on a sunny summer day compared with air temperatures at 4 ft.*

CROP	TEMPERATURE RISE
Long Ryegrass	17°F.
Short Ryegrass	12°F.
Long Clover	3°F.
Short Clover	9°F.
Tall Sweet Corn	2°F.

the leaf below the temperature of its surrounding air. The wind is then contributing sensible heat to the leaf which is then used to enhance the energy flow outwards by evaporation. A situation in which the total amount of energy being used in evaporation exceeds that available from the radiation balance alone, can often arise.

Fluctuating relationships between the amounts of evaporation and sensible heat transfer will also be found when considering the effects of various levels of radiation on leaves with a large surface area, or with various types of hair covering.

So far, discussion has been concerned with individual leaves fully exposed. It is this situation which has received most attention in the literature. However, for the greater part of the vegetation grown in this country, this is the exception. It is usual for one or several species to form a canopy in which large numbers of leaves are close together. For the leaves which are within the canopy, in particular, this gives a radical alteration in their energy exchange environment.

Firstly, where the hemisphere in direct line of sight around a leaf is largely that of other leaves at a similar temperature, the long wave radiation exchange becomes near neutral. There will be little heating or cooling from radiation exchange and the leaf will remain at a temperature close to that of the adjoining air.

Secondly, the intermingling of leaves in a canopy may create considerable additional resistance to the outward mass transfer of heat and water vapour. If this is occurring it will be shown by an appreciable increase of air temperature within a canopy under high solar radiation i.e., on calm sunny summer days. The greater the resistance, i.e., the higher the force needed to drive sufficient convectional and turbulent transfer of air to achieve thermal balance, the higher the rise in temperature for a given level of radiation.

If there is such an increase of temperature within a canopy the near thermal neutrality of the leaves inside the canopy will ensure little transfer of sensible heat will occur between these leaves and the air surrounding them. Both are at very much the same temperature. But the vapour pressure of the wet evaporating surface inside those leaves rises sharply and logarithmically with increase in temperature. In other words, just when the head of "pressure" available to drive transfer of sensible heat from the leaf to adjacent air is low the head of "pressure" available to drive the transfer of water vapour is sharply increased. In such circumstances the amount of moisture used increases considerably compared with that used by a canopy of equivalent leaf area which avoids a temperature rise within itself.

If the depth of vegetation interface becomes very shallow, heating from direct solar radiation is concentrated in a narrower layer and is liable to become more intense. When, also, a considerable amount of direct radiation passes through onto a compact soil surface, which then acts as a continuing heat store, the magnitude of the rise in temperature or the extended period at elevated temperature within that shallow layer of vegetation may produce as much, or greater, use of moisture than will occur from a leaf surface which is large but well ventilated and hence relatively cool.

TABLE 3. *Examples of differences in use of soil moisture by different types of vegetation and similarities in use irrespective of large differences in leaf area. Observations at Palmerston North. (Moisture use in inches per week.)*

November, 1962		January-February, 1963	
Crop Cover	Moisture Use	Crop Cover	Moisture Use
Long Ryegrass	0.81	Tall Sweet Corn	1.33
Short Ryegrass	0.56	Long Ryegrass	1.41
Long White Clover	0.17	Short Ryegrass	1.20
Short White Clover	0.27		

Three general points follow: Firstly, the higher the intensity of solar radiation, i.e., the higher the sun in the sky, the more marked will these heating effects on a canopy or soil surface become. Secondly, the higher the general level of air temperature the more markedly will any additional rise in temperature in a canopy stimulate use of moisture. Thirdly, with tall open vegetation, which has low resistance to mass transfer of air, temperatures in the lower layers will often be somewhat below temperature of the air above the vegetation when the air is still. Radiation heating of those leaves in these circumstances is negligible but there is still a considerable vapour pressure gradient. Hence there will be an upward flow of water vapour and a downward flow of sensible heat. Hence the coolness of air in our native forests.

The manner in which the form and arrangement of individual leaves and plants in a vegetation complex may interact with the radiation and wind environment to modify their absorption of light, their temperature, and their internal moisture status has obvious consequential effects on the ability of plants to grow in various climates. It is at this stage that consideration of the physiological characteristics of the individual plants becomes important. Which physiological characters are the more important varies with the climatic environment and type of productivity man seeks from the plants. Two which are of universal importance in economic crops are the temperature response curve for rate of growth and the photosynthetic efficiency at various levels of light intensity. In these, as with most other physiological features, there are wide variations between species.

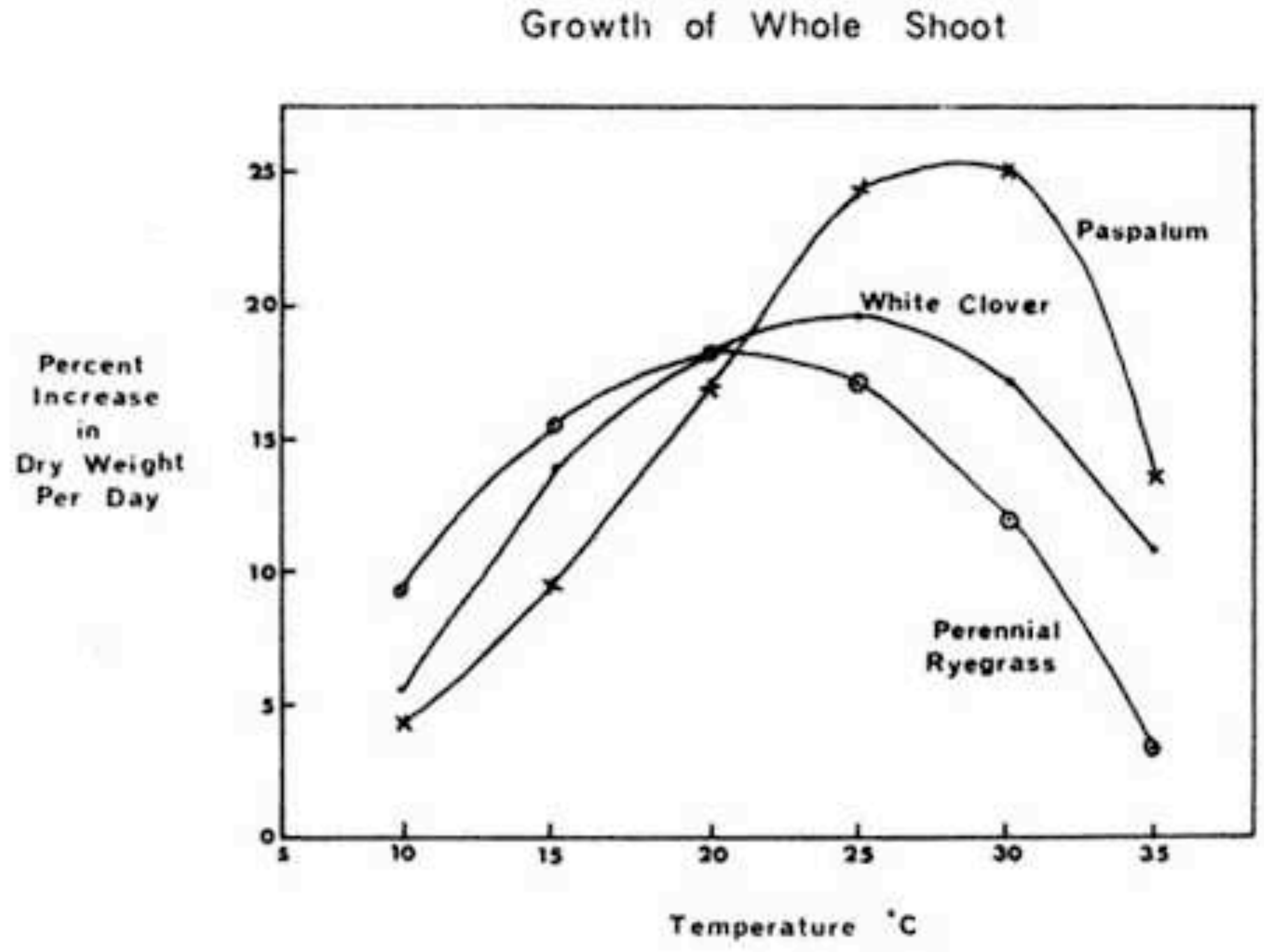


FIGURE 6. *Temperature response curves for growth of perennial ryegrass, white clover and* Paspalum dilatatum. *After Mitchell (1956).*

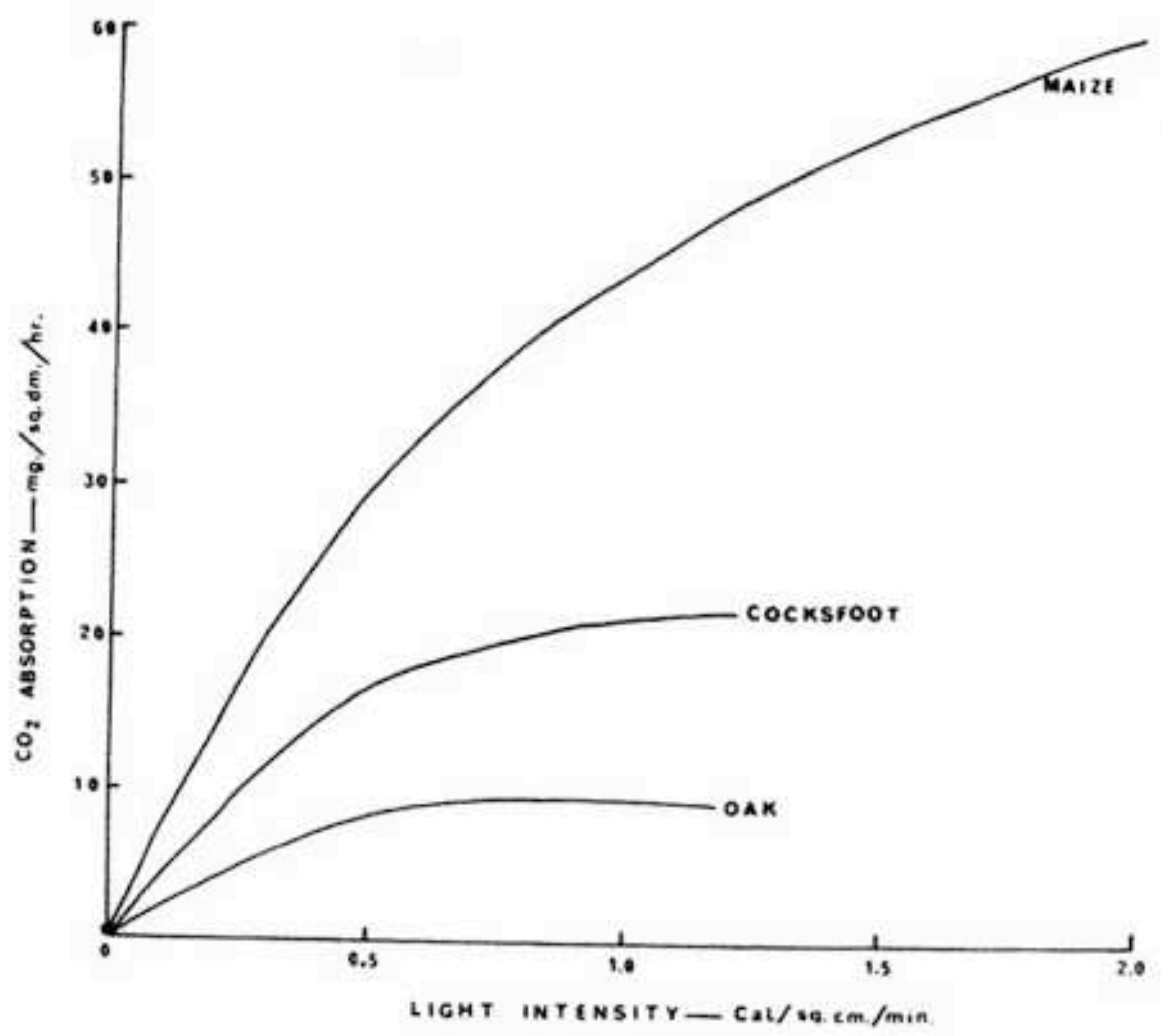


FIGURE 7. *Rates of CO$_2$ intake at various light intensities by maize, cocksfoot and oak. After Hesketh (1963).*

The essential point to be emphasised is that it is now practicable to measure quantitatively virtually every one of the factors commented on. This includes the environmental fluxes, the temperature, albedo, etc., of plants in the field; and their range of physiological responses which are relevant to effects of climate.

Provided all such measurements are always of specific physical and chemical entities, as distinct from the fallacious short-cut of integrating indices of environment or plant growth, a sound body of theoretical understanding of the processes involved may be built up.

If the effects of various radiation and wind conditions on leaf temperatures, and the effects of various leaf arrangements on distribution of light within the vegetation are known by measurement, and at the same time temperature and light response curves, etc., for growth are known, there may then be a synthesis that will give soundly-based understanding and prediction of field performance in various sets of climatic conditions. From such applications of these microclimatic and physiological techniques a number of potentialities for improved ecological understanding come to mind. For instance, there is ability to determine why certain species and vegetation forms of our indigenous vegetation preferentially occur in certain environments.

It also becomes practicable to construct models of what would be the most economically efficient forms of forage vegetation for sheep and cattle in various parts of the country. Preliminary work is already raising intensely interesting queries as to what extent present pasture forms will be found the most efficient for forthcoming farming technology and to what extent considerably different forms of forage crops will be called on. Integrated with this is the question of how far it is economically sound to use the doctrine of full utilisation of pasture to create a continuously hotter and drier soil surface in summer (which will often use more moisture and probably give an improved environment for pasture-eating insects) as against using management which aims at a vegetation cover which enhances coolness and moistness around the soil surface.

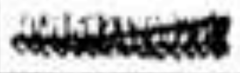
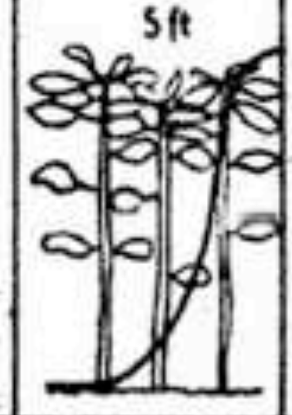
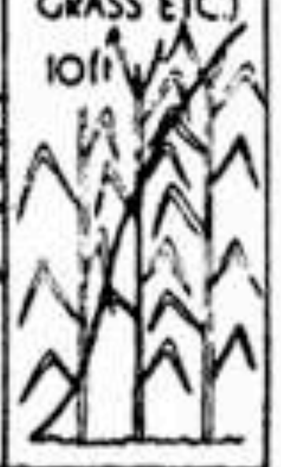
	SHORT GRAZED PASTURE	LONGISH SPELLS BETWEEN GRAZING	EXCESSIVE SPELLS BETWEEN GRAZING	CHOU MOLLIER	MAIZE EQUIVALENT (JOHNSTON GRASS ETC.)
GROWTH FORM AND LIGHT INTERCEPTION CURVE	HEIGHT 2-3 in 	HEIGHT 9-15 in 	HEIGHT 9-15 in 		
MAXIMUM LEAF AREA INDEX	4-5	10	12	6	16
PEAK SUMMER DAILY AIR REQUIREMENT	185 acre/ft	340 acre/ft	230 acre/ft.	440 acre/ft.	685 acre/ft
VENTILATION	EXCELLENT	FAIR - GOOD	POOR	GOOD	EXCELLENT
POTENTIAL ANNUAL PRODUCTION PALMERSTON NORTH (lbs/DM/acre)	12,000	22,000	15,000	26,000	42,000

FIGURE 8. *Inter-relationships between crop structure and potential production. Mitchell (1960).*

These differences in temperature and moisture content of the soil profile arising from different types of vegetation cover may have immediate effects on the availability of nutrients (Mitchell 1957) and, on a longer term, on the balance between various directions of soil type development.

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ASPECTS OF LIGHT UTILIZATION, LEAF DEVELOPMENT AND SENESCENCE AND GRAZING ON GRASS-LEGUME BALANCE AND PRODUCTIVITY OF PASTURES

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In this paper it is intended to describe some aspects of leaf development and leaf canopy structure of communities of two species of importance to New Zealand agriculture in relation to the light environment, then to illustrate some effects grazing has on the grass-legume balance and productivity of pastures.

Two species that have been studied in some detail at Grasslands Division are white clover (*Trifolium repens*) and the ryegrasses (*Lolium* spp.). The first is a stoloniferous type with individual leaves developing from the terminal buds of the stolons. When fully formed each leaf comprises a petiole supporting a lamina which is usually orientated horizontally. The *Lolium* spp. have a markedly different leaf development pattern with new leaves developing from the apex of the tiller unit and orientating themselves, when in a closed community, much more vertically. It is of importance to this discussion that these different leaf development patterns result in marked differences in the development and structure of the leaf canopy at certain times of the year and in turn significantly influence productivity.