

Appendix A

Equilibrium Temperature of a Simple Climate Model with Feedbacks

The planet is approximated as a black body, initially in equilibrium with the solar radiation field so, i.e.

$$s_o A_o = \sigma T_o^4$$

where T_o and A_o are the equilibrium temperature and albedo resp; σ is the Stefan-Boltzmann constant. Now for small temperature changes, the albedo can be approximated by a linear function of temperature to represent the effect of feedbacks, i.e. $A = x + y \delta T$. Let us now assume that the solar radiation field is subject to a small perturbation δs , which is equivalent to a net trapping of radiation by increased $[CO_2]$. The new equilibrium condition may then be written,

$$(s_o + \delta s)(A_o + \delta A) = \sigma(T_o + \delta T_{eq})^4$$

where δT_{eq} is the temperature rise to the new equilibrium configuration. Ignoring second order terms, this reduces to,

$$s_o \delta A + A_o \delta s = 4\sigma T_o^3 \delta T_{eq} \quad A1$$

In the absence of feedbacks, $\delta A = 0$ then

$$\delta T_{nf} = (A_o \delta s) / (4\sigma T_o^3)$$

and so (1) may be written,

$$\begin{aligned} \delta T_{eq} &= (s_o \delta A) / (4\sigma T_o^3) + \delta T_{nf} \\ &= g \delta T_{eq} + \delta T_{nf} \end{aligned}$$

where $g = (s_o \delta A) / (4\sigma T_o^3 \delta T_{eq})$ is the gain, which assuming the linear temperature dependence for the albedo is written,

$$g = (s_o y) / (4\sigma T_o^3)$$

independent of the temperature change. Using this notation, the new equilibrium temperature may be written

$$\delta T_{eq} = \delta T_{nf} / (1-g) = f \delta T_{nf}$$

where f is the "feedback factor"

The form of the gain g , implies that if a number of feedback processes occur in a given climate model, the gains simply add linearly to give the total net gain. However, since

$$f = (1-g)^{-1}$$

it is clear that the feedback factors do not combine in a simple manner. For example, if two feedback processes occur together, the net feedback factor representing the combination is

$$f = (f_1 f_2) / (f_1 + f_2 - f_1 f_2)$$

Therefore if $f_2 > f_1 / (f_1 - 1)$, the combined effect of the two feedbacks will have a greater effect on the resulting temperature than if they simply acted independently.

Appendix B

The Transient Response of the Atmosphere to CO₂ Forcing.

During the period when the climate is responding to the forcing, there will be a net imbalance in the radiation budget. The net flow of radiant energy into the earth will be (from A1 above),

$$F = S_o \delta A + A_o \delta S - 4\sigma T_o^3 \delta T$$

where δT is the transient temperature rise. Using the above notation, this can be written in the form,

$$F = 4\sigma T_o^3 (g \delta T + \delta T_{nf} - \delta T)$$

which simplifies to

$$F = F_o / \delta T_{eq} (\delta T_{eq} - \delta T)$$

where $F_o = 4\sigma T_o^3 \delta T_{nf}$, is the net flux into the planet at the beginning ($\delta T=0$).

Now the time rate of change of the planetary temperature is given by the solution of

$$\frac{dT}{dt} = \frac{d(c\delta T)}{dt} = F$$

where c is the effective specific heat capacity per unit area of the Earth, and so therefore,

$$\delta T = \delta T_{eq} (1 - e^{-\tau})$$

with $\tau = c \delta T_{eq} / F_o = (cf) / (4\sigma T_o^3) = f \tau_{nf}$, where τ_{nf} is the "no feedback" ($f=1$) response time.

Appendix C

Photosynthetic Processes in C₃, C₄ & CAM Plants.

It is common to divide the processes involved in photosynthesis into three major groups; diffusion, biochemical, and photochemical processes.

A). The diffusion processes.

These processes govern the transport of CO₂ from the external atmosphere to the fixation sites inside the chloroplasts. Part of the pathway is in the gaseous phase - atmosphere, boundary layer, stomata, and intercellular space - and part is in the liquid phase - cell wall, cytoplasm, and chloroplasts. The transport in the liquid phase is not entirely diffusive but that does not influence this description.

Diffusion is directly affected by external [CO₂] and indirectly by the light flux density. High atmospheric [CO₂] increases the concentration gradient between the atmosphere and the fixation sites inside the chloroplasts. On the other hand, high [CO₂] also decreases stomatal conductance. The rate of increase in leaf photosynthetic performance with increasing [CO₂] depends on the relative size of the effect on each of these two opposing processes. However, diffusion is only slightly affected by temperature (c. 30% between 20 - 30°C) through its effects on the diffusion coefficient of CO₂ in air and in the liquid phase. Temperature may affect the diffusion processes indirectly through its influence on stomata. Extreme temperatures may cause a complete closure of stomata but, in the normal range of 20 - 30°C, stomata do not change considerably unless in response to consequent changes in the leaf-airvapour pressure difference (VPD). Where VPD is kept small, stomata do not close over this range of temperature. Light affects the diffusion processes indirectly through its effects on stomatal conductance and on the internal [CO₂] along the CO₂ pathway in the leaf. These concentrations are determined by the interaction between all the diffusion, biochemical, and photochemical processes.

B). The biochemical processes.

The biochemical processes include that part of the CO₂ transport mechanism through the liquid phase pathway which does not seem to be purely diffusive. The major biochemical processes are the fixation of CO₂ by Ribulose Biphosphate Carboxylase Oxidase (Rubisco) and its further reduction which results in the formation of carbohydrate. The rates of these biochemical processes are strongly affected by temperature and [CO₂] but only slightly by light intensity. Temperature affects mainly the Michaelis constant and the maximum velocities of the numerous enzymic reactions which occur.

In photosynthesis, organic carbon is derived from atmospheric CO₂ by joining to an existing acceptor in such a way that a new carboxyl group is formed. For the process to continue the CO₂-acceptor must be regenerated and for plants to grow the amount of this

acceptor must be increased. Only one metabolic sequence meets these requirements (Fig C1. from Robinson & Walker, 1981). It is known as the Calvin cycle or, more often now, as the Photosynthetic Carbon Reduction Cycle (PCR cycle).

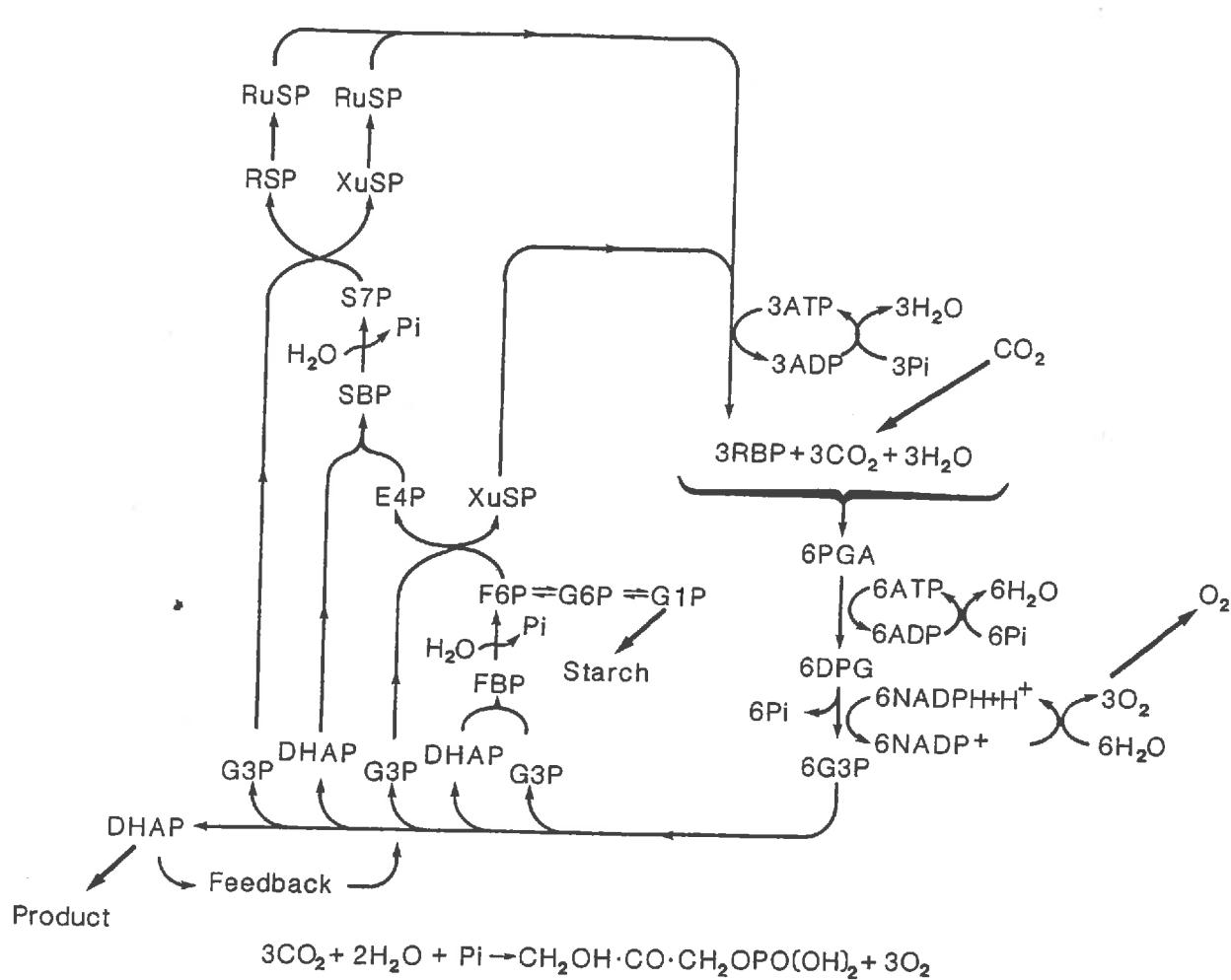


Figure C1. The photosynthetic carbon reduction cycle. On the right, three molecules of ribulose-1,5-P₂ (RBP) combine with three molecules of CO₂ and three molecules of water to give six molecules of phosphoglyceric acid (PGA). These are phosphorylated at the expense of ATP and the resulting ADP is reduced by NADPH to glyceraldehyde-3-P (G3P). The entire cycle can be divided into three phases. The initial carboxylation is followed by rearrangement to regenerate three C₃ molecules of CO₂ acceptor. It should be noted that the cycle consumes nine molecules of ATP and six molecules of NADPH in the formation of one triose phosphate product.

*Abbreviations: DHAP, dihydroxyacetone phosphate; DPG, 1,3-diphosphoglycerate; ATP, adenosine triphosphate; NADPH, nicotinamide adenine dinucleotide phosphate.

In fact there are now six distinct biochemical pathways known for photosynthetic assimilation of CO₂. The first involves simply the PCR cycle and is known as C₃ photosynthesis because

it involves the formation of three-carbon molecules (Phosphoglyceric acid, PGA). Of the other five pathways only two are sufficiently important to be mentioned here. They are C₄ photosynthesis and CAM (or Crassulacean Acid Metabolism) photosynthesis and each involves a more sophisticated system for fixing CO₂ but also each includes the PCR cycle. Figure C2. (from Black, 1986) gives an outline of the relation between the three major schemes.

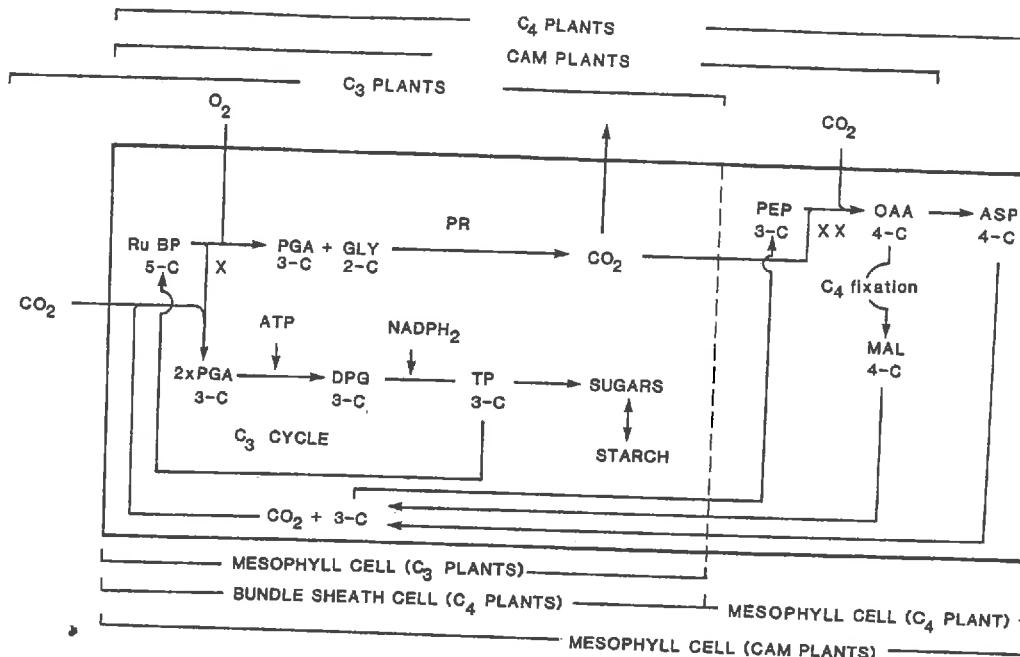


Figure C2. Principal carbon fixation reactions of C₃, C₄, and CAM plants. MAL, malate; ASP, aspartate; TP, triose phosphate; DPG, diphosphoglycerate; GLY, glycolate; PR, photorespiration; OAA, oxaloacetate; PEP, phosphoenolpyruvate; RuBP, ribulose biphosphate. x, action site of ribulose biphosphate; xx, action site of PEP;

C). The photochemical processes

These processes are responsible for the conversion of light energy into chemical energy to be used for the fixation and reduction of CO₂. The processes include light harvesting via pigment systems, electron transport through two photosystems, and photophosphorylation, which results in formation of NADPH and ATP. The rate of the photochemical process is mainly affected by light but also to a lesser extent by temperature. Electron transport in photosystem 1 increases with temperature up to 55°C, and in the whole chain it reaches a maximum at 45°C. The [CO₂] does not appear to affect the photochemical process within the range of ambient to c.1000 ppmv.

D). Important features characterising C₃, C₄ & CAM photosynthesis

D.1 C₃ photosynthesis

Diffusion processes limit photosynthesis at ambient [CO₂], 20-30°C, and saturating light. The process is, therefore, strongly dependent upon [CO₂]. Net photosynthesis is less than gross CO₂ fixation because of photorespiration.

Temperature has only a small effect on photosynthesis at ambient $[CO_2]$ and from 20-30°C. Above 30°C photorespiration increases sharply. At high $[CO_2]$, the influence of temperature is greater. The main effect of $[CO_2]$ is on fixation of CO_2 by Rubisco; higher $[CO_2]$ increases the competitive ability of CO_2 compared with O_2 .

D.2 C_4 photosynthesis

Anatomical and metabolic modifications result in an effective mechanism to raise the internal $[CO_2]$ at the carboxylation sites. The process is weakly dependent upon $[CO_2]$ above current ambient levels.

Photorespiration is severely restricted.

Most C_4 species perform best at higher temperatures of 30-40°C and at lower temperatures C_3 plants appear to have an advantage. Several mechanisms have been proposed e.g. Rubisco is a larger fraction of total soluble protein in C_3 plants (catalytic capacity in the PCR cycle) and there are differences in metabolite transport. Because of high mesophyll conductance (high carboxylation efficiency), C_4 plants can have lower stomatal conductance, so economizing on water use, and yet photosynthesize at rates equivalent to those of C_3 plants.

D.3 CAM photosynthesis

Carbon dioxide is fixed at night using an existing carbohydrate supply to form a CO_2 -acceptor, phosphoenolpyruvate (PEP). That fixed carbon is reduced by carboxylation in the PCR cycle during the subsequent light period.

Increased $[CO_2]$ increases CO_2 fixation only late in the daytime.

This adaptation confers the ability to fix CO_2 when evaporative demand is least and so gives the greatest water-use-efficiency.

Appendix D

Carbon dioxide and rate-limiting processes in photosynthesis.

Farquhar *et al.* (1980) presented a biochemical model of photosynthetic CO_2 assimilation in C_3 species and von Caemmerer & Farquhar (1981) showed that the CO_2 assimilation rate A ($\text{mol m}^{-2} \text{ s}^{-1}$), was given by

$$A = (1 - \Gamma_o/p_i)Vc - R_d \quad D1$$

where R_d is day respiration (not photorespiration), Vc is the rate of carboxylation, Γ_o is the CO_2 compensation point in the absence of day respiration, p_i is the intercellular partial pressure of CO_2 and Γ_o/p_i is the ratio of rates of photorespiration and carboxylation.

They suggested that RuP_2 would be saturating at low p_i and high light and that Vc was then given by the RuP_2 saturated rate of carboxylation, W_c .

$$W_c = p_i Vc_{\max} / (p_i + K_c(1 + o/K_o)) \quad D2$$

where o is the intercellular partial pressure of O_2 and K_c , K_o are Michaelis-Menten constants for CO_2 and O_2 .

Farquhar *et al.* (1980) derived an expression for the rate of electron transport required to satisfy the NADPH consumption by carboxylation and photorespiration such that the electron transport limited rate of carboxylation is given by

$$J/(4.5 + 10.5\Gamma_o/p_i) \quad D3$$

where J is the potential electron transport rate at a particular irradiance.

Von Caemmerer & Farquhar (1981) suggested that when RuP_2 is not saturating, the rate of regeneration is probably no slower than that allowed by electron transport/photo-phosphorylation so that

$$Vc = \min \{ W_c, J/(4.5 + 10.5\Gamma_o/p_i) \} \quad D4$$

Combining equations D1-D4, further expressions can be derived for the rate of CO_2 assimilation.

If $Vc = V_w$ then

$$A = (p_i - \Gamma_o) Vc_{\max} / (p_i + K_c(1 + o/K_o)) - R_d \quad D5$$

If

$$Vc = J/(4.5 + 10.5\Gamma_a/p_i)$$

then

$$A = (p_i - \Gamma_a) J/(4.5 + 10.5\Gamma_a/p_i) - R_d$$

D6

The slope, dA/dp_i , of the response of CO_2 assimilation to $[CO_2]$.

Farquhar *et al.* (1980) differentiated D5 (RuP_2 saturated fixation) to obtain

$$\frac{dA}{dp_i} = Vc_{max} (\Gamma_a + K_c(1 + o/K_o)) (p_i + K_c(1 + o/K_o))^2$$

D7

This should have only slight dependence on $[CO_2]$ because K_c is relatively large and dA/dp_i is linearly related to Vc_{max} as p_i approaches Γ_a .

At higher values of p_i the slope is derived from D6 as

$$\frac{dA}{dp_i} = (\Gamma_a J/4.5) / (10/3 (p_i + 7/3\Gamma_a)^2)$$

Here the dependence on p_i is no longer negligible, and dA/dp_i is linearly related to J

Transition from RuP_2 carboxylase limitation to RuP_2 regeneration limitation.

From D5 & D6, the transition between limits of CO_2 fixation is predicted to occur at

$$p_i = (K_c(1 + o/K_o) J/(4.5Vc_{max}) - 7/3\Gamma_a) / (1 - J/(4.5Vc_{max}))$$

The transition depends on the ratio J/Vc_{max} .

Appendix E

A particular leaf, at a particular instant of time has a certain rate of assimilation of CO_2 per unit area A , and a certain rate of transpiration, E . These are both, in part, determined by the aperture of the stomata. Since there is a relation between E and A , we may define evaporation as $E = E(A, s, t)$, the evaporation corresponding to a given assimilation rate from an element of leaf surface s , and at a time, t .

The average rates of assimilation $\langle A \rangle$ and transpiration $\langle E \rangle$ over the whole surface area, S of the foliage of a plant during a period of time T are

$$\bar{A} = (\int_0^T \int_0^S A \, ds \, dt) / TS$$

and

$$\bar{E} = (\int_0^T \int_0^S E(A, s, t) \, ds \, dt) / TS \quad E1$$

There exists a wide range of possible values of A (each associated with a value of stomatal conductance, g_s) and, if the function $E(A, s, t)$ were known, the magnitudes of $\langle A \rangle$ and $\langle E \rangle$ corresponding to each could be found.

Variation in E and A with s and t is optimal if $\langle A \rangle$ cannot be increased without increasing $\langle E \rangle$ and also, $\langle E \rangle$ cannot be decreased without decreasing $\langle A \rangle$. For that variation to be optimal

$$[E(A, s, t) - \lambda A] \, ds \, dt = \min$$

where λ is a constant (Cowan & Farquhar, 1977).

For the integral to be a maximum or minimum

$$\left. \frac{\partial E}{\partial A} \right|_{s,t} = \lambda \quad E2$$

and for the integral to be a minimum

$$\left. \frac{\partial^2 E}{\partial A^2} \right|_{s,t} > 0 \quad E3$$

the result is illustrated in Fig. III.1 where both relations are curved according to equation E3.

Cowan (1982) suggests that the parameter λ can be interpreted as a physiological parameter that depends on the amount of water available to the plant.

Simple functions (Cowan, 1977) or more rigorous ones (Cowan, 1982) may be used to describe E and A .

The simpler approach can be useful to indicate the upper limits to water use efficiency,

which can be expressed as

$$A/E = (p-p_s)/(e_s-e) \cdot g'/g$$

where p , e and p_s , e_s are the partial pressures of CO_2 and water vapour in the ambient air, and at the surface respectively, and g' , g are the conductances to CO_2 and water vapour in the ambient air and the boundary layer.

The properties of the atmosphere determine an upper limit to water use efficiency. The partial pressure of CO_2 at the surface cannot be less than zero, and the temperature of the surface cannot be less than that of a well-ventilated, shielded wet-bulb thermometer. Therefore,

$$A/E < p/(e'T_w - e) = p/(\Gamma(T-T_w))$$

where $e'T_w$ is the saturation vapour pressure at the wet bulb temperature T_w , T is the temperature of the air and Γ is again the psychrometric constant (67Pa/C).

The inequality represents only one set of constraints on physiological performance. Others relate to the transfer of CO_2 in the liquid phase and the biochemistry of CO_2 fixation. Nonetheless, this simple expression serves to show that at elevated ambient $[\text{CO}_2]$, i.e. at higher p , the maximum value of A/E is raised. Indeed if p is doubled, so too is A/E .

The question should be posed, and work should be undertaken to examine what strategies are available to the plant to approach this limitation - Removal or raising of the other constraints? An operating system for stomata, so that leaves assimilate rapidly when evaporative demand is low, or when water supply is adequate and assimilate slowly or not at all at other times?

Cowan (1982) used more rigorous expressions for E and A ,

$$E = g(e_i - e_a)/(1 - \langle e \rangle / P) \quad E4$$

$$A = 0.63g(p_i - p_a) - E\langle p \rangle / P \quad E5$$

where e, p are the partial pressures of water vapour and CO_2 , the subscripts i, a refer to intercellular and ambient air, and P is the atmospheric pressure. Allowance is made in Equation E4 for the influence of net mass transfer on vapour diffusion, and for the influence of vapour diffusion on CO_2 diffusion.

Equations E4 and E5 do not define the relation between E and A because the partial pressures, e_i and p_i , are partly dependent on the fluxes. In practice, the relation between E and A must be found numerically or experimentally. Consequently, it is not possible simply to calculate the effects of elevated $[\text{CO}_2]$ on water use efficiency, even if the changes in atmospheric humidity could be predicted. Instead, experimental studies should examine the plant characters that modify A/E at elevated $[\text{CO}_2]$ so as to identify plant strategies that would optimise water use efficiency.

Appendix F

Organisms causing diseases of Barley in Europe

<i>Viruses</i>		
<i>Name</i>	<i>Transmission</i>	<i>Ratings*</i>
Barley stripe mosaic virus (BSMV)	seed	1,?,+
Barley yellow mosaic virus (BarYMV)	soil fungus	3,+,+
Wheat soil-borne mosaic virus (SBWMV)	soil fungus	1,??
Cereal tillering disease virus (CTDV)	planthopper	1,+,?
Barley yellow striate mosaic virus	planthopper	1,+-
Barley yellow dwarf virus (BYDV)	aphid	2,+,+
Wheat streak mosaic virus (WSMV)	aphid	1,+,?
<i>Bacteria</i>		
<i>Pseudomonas syringae</i> pv. <i>atrofaciens</i>		1,+,?
<i>Xanthomonas campestris</i> pv. <i>translucens</i>		2,+,?
<i>Fungi</i>		
A) Oomycetes		
<i>Lagenaria radicicola</i> (Rootlet disease)		1,+,+
<i>Sclerophthora macrospora</i> (Downy mildew)		1,+-
B) Ascomycetes		
<i>Erysiphe graminis</i> f.sp. <i>hordei</i> (powdery mildew)		3,+,+
<i>Claviceps purpurea</i> (ergot)		2,?,+
<i>Hymenella cerealis</i> (cephalosporium stripe disease)		1,+,+
<i>Glomerella graminicola</i>		1,??
<i>Monographella nivalis</i> (snow mould)		2,-,+
<i>Leptosphaeria nodorum</i> (<i>Septoria</i>)		3,+,+
<i>Leptosphaeria avenae</i> (<i>Septoria</i>)		1,+,+
<i>Pyrenophora graminea</i> (<i>Drechslera</i>)		2,-,+
<i>Pyrenophora teres</i> (<i>Drechslera</i>)		3,?,+
<i>Cochliobolus sativus</i> (<i>Drechslera</i>)		2,+,+
<i>Septoria passerinii</i>		1,+,+
<i>Pseudoseptoria stomaticola</i> (halo spot)		2,+,+
<i>Pseudocercospora herpotrichoides</i> (eyespot)		2,?,+
<i>Rhynchosporium secalis</i> (leaf blotch)		3,?,+

C) Basidiomycetes

<i>Ustilago hordei</i> (covered smut of barley)	2,?,+
<i>Puccina graminis</i> f.sp <i>secalis</i> (stem rust)	1,+,+
<i>Puccina hordei</i> (brown rust)	3,+,+
<i>Puccinia striiformis</i> f.sp. <i>hordei</i> (yellow rust)	2,-,+
<i>Ceratobasidium cereale</i> (<i>Rhizoctonia</i>) (sharp eyespot)	2,+,+
<i>Typhula incarnata</i> (snow mould)	1,-,+

* Each organism has been given three ratings, eg (2,+, -). These are given in detail as follows:

1 not important: 2 sometimes important: 3 important disease.

+ more serious in 'warming' scenario: - less serious: ? no change or unclear.

+ occurs in UK: - does not occur: ? position unknown.

Appendix G

Organisms causing Diseases of Potato in Europe

Viruses and viroids

Name	Transmission	Rating*
Potato virus M (PVM) (paracrinkle)	aphid	2,+,+
Potato virus S (PVS)	aphid	2,+,+
Potato leafroll virus (PLRV)	aphid	3,+,+
Potato virus X (PVX)	contact	2,?,+
Potato virus A (PVA)	aphid	2,+,+
Potato virus Y (PVY) (includes PVYN)	aphid	3,+,+
Potato mop top virus (PMTV)	fungus	2,-,+ .
Potato tuber spindle viroid	mechanical, true seed	3,?- .
Tobacco rattle virus (TRV)	nematode	2,?,+

There are a number of other viruses found in potato but in general the above-mentioned are the most important.

Mycoplasmas and Bacteria

Potato stolbur MLO	transmission by insect	2,+,-?
<i>Pseudomonas solanacearum</i> (bacterial wilt)		3,+-
<i>Corynebacterium sepedonicum</i> (bacterial ring rot)		3,?-
<i>Erwinia carotovora</i> sub sp. <i>atroseptica</i> (blackleg & rots)		3,-,+ .
<i>Erwinia carotovora</i> sub sp. <i>carotovora</i> (soft rots)		3,-,+ .
<i>Erwinia chrysanthemi</i> (blackleg in warm climates)		3,+,-
<i>Streptomyces scabies</i> (common scab)		3,+,+ .

Fungi

A) Oomycetes

<i>Pythium ultimum</i> (watery wound rot)	1,-,+ .
<i>Phytophthora infestans</i> (late blight of tubers and foliage)	3,-,+ .
<i>Phytophthora erythroseptica</i> (pink rot)	2,-,+ .

B) Chytridiomycetes & Plasmodiophoromycetes

<i>Synchytrium endobioticum</i> (wart disease)	2,-,+ .
<i>Spongospora subterranea</i> f.sp. <i>subterranea</i> (powdery scab)	2,-,+ .

C) Ascomycetes

<i>Erysiphe cichoracearum</i> (powdery mildew)	1, +, +
<i>Leveillula taurica</i> (powdery mildew)	1, +, -
<i>Gibberella cyanogenia</i> (<i>Fusarium sulphureum</i>) (dry rot)	2, -, +
<i>Nectria hematococca</i> (<i>Fusarium solani</i> var. <i>coeruleum</i>) (dry rot)	3, +, +
<i>Fusarium oxysporum</i> f.sp. <i>tuberosi</i> (fusarial wilt)	2, +, -
<i>Verticillium albo-atrum</i> (verticillium wilt)	3, +, +
<i>Verticillium dahliae</i> (verticillium wilt)	3, +, +
<i>Colletotrichum coccodes</i> (black dot)	1, +, +
<i>Alternaria solani</i> (early blight)	2, +, +
<i>Phoma exigua</i> var. <i>foveata</i> (gangrene)	2, -, +
<i>Macrophomina phaseolina</i>	1, +, ?
<i>Helminthosporium solani</i> (silver scurf)	1, +, +

D) *Basidiomycetes*

Thanetophorus cucumeris (*Rhizoctonia solani*) (stem canker) 2,?,+
Corticium rolfsii (*Sclerotium rolfsii*) 1,+,+

* Each organism has been given three ratings, eg (2, +, -). These are given in detail as follows:

1 not important; 2 sometimes important; 3 important disease

+ more serious in 'warming' scenario: - less serious: 3 no change

+ occurs in UK: - does not occur: ? position unknown