Phenology and growth of European trees in relation to climate change

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Phenology and growth of European trees in relation to climate change

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Proefschrift

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This thesis contains results of a research project carried out at the Institute for Forestry and Nature Research in Wageningen, Bosrandweg 20 NL-6704 PH Wageningen, The Netherlands.

Stellingen

Fenotypische plasticiteit is een wezenlijk onderdeel van de adaptatie van planten aan hun omgeving, en verdient daarom meer aandacht in het onderzoek naar klimaatverandering.
Dit proefschrift

De gevolgen van klimaatverandering voor het natuurlijke verspreidingsareaal van boomsoorten worden bepaald door hun concurrentieverschillen.
Dit proefschrift

Er zal grote vooruitgang in fenologisch onderzoek geboekt worden als er een methode ontwikkeld wordt waarmee de diepte van de winterrust rechtstreeks gemeten kan worden.
Dit proefschrift

Bladuitloop en bladval van bomen in gematigde en boreale streken worden niet in gang gezet door een vaste daglengte.
Dit proefschrift

"*The perfect way to create better documents*" van een bekend tekstverwerkingspakket is niet perfect en geeft zelfs geen betere documenten.
Dit proefschrift

Het fileprobleem is op te lossen door een versnelde aanleg van de elektronische snelweg.

De grootste toename in plantengroei is te verwachten als de genetische informatie uit bacteriën om vrije stikstof om te zetten in nitraat in bladeren tot expressie wordt gebracht.

Wetenschap is ook dienstbaar aan de samenleving door produkten aan te dragen waar de samenleving helemaal niet om heeft gevraagd.

Inzicht in evolutie is voor biologie minstens even wezenlijk als inzicht in religie voor geschiedenis.

Een simulatiemodel is een instrument om waarnemingen te doen in de toekomst.

Stellingen behorende bij het proefschrift:

"Phenology and growth of European trees in relation to climate change"

Koen Kramer
Wageningen, 5 december 1995.

voor Han en Wil

Voorwoord

Dit proefschrift is het resultaat van het project: *"Phenological reactions of Dutch tree species to climate change described by a simulation model of the annual cycle"*, gedurende de periode maart 1991 tot en met maart 1995. Het project was onderdeel van het Nationale Onderzoekprogramma: Mondiale - Luchtverontreiniging en Klimaatverandering (850014 C). De afronding ervan is verricht in het kader van het LTEEF-project (EC Environment Research Programme, Climatology and Natural Hazards, contract: EV5V-CT94-0468).

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Account

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Selecting a model to predict the onset of growth of *Fagus sylvatica*. *Journal of Applied Ecology* **31**: 172-181.

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A modelling analysis on the effects of climatic warming on the probability of spring frost damage to tree species in The Netherlands and Germany. *Plant Cell and Environment* **17**: 367-377.

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Kramer K., Friend A.D. and Leinonen L., submitted

Modelling comparison to evaluate the importance of phenology for the effects of climate change on growth of mixed-species temperate-zone deciduous forests.

Contents

Chapter 1

General introduction

Climate change

Fossil fuel burning and large-scale deforestation result in a rise of the atmospheric carbon dioxide (CO_2) concentration at an unprecedented rate. CO_2 is transparent to short-wave incoming radiation from the sun, but is opaque to long-wave radiation which is emitted from the earth. Thus, the heat balance of the earth will be affected because CO_2 traps radiation in the lower atmosphere which would otherwise escape to space. It is possible that as a result of the altered atmospheric composition, the climate of the earth will change. General Circulation Models (GCMs), which simulate the weather patterns of the globe, indicate that the mean annual temperature may rise by 2 to 5°C, accompanied with an increase in precipitation. However, much uncertainty remains on the exact magnitude of the change in the climate. Furthermore, it is clear that there will be significant regional differences.

Focus of this study

This study was confined to the effects of climate change on phenology and growth of some important European tree species. The central methodology was to develop models describing the mechanism by which critical processes are driven by climatological variables. The effects of climate change scenarios on phenology and growth of trees can then be elucidated using the understanding provided by such models. The following general questions were addressed: (1) how can the triggering of phenological events be described using climatological variables? (2) what are the consequences of climate change on the probability of spring frost damage? (3) do trees possess plasticity in leaf unfolding and leaf fall? (4) what is the importance of phenology for growth of monospecies stands? and (5) what is the importance of phenology for growth of mixed-species stands? An overview of the species considered in the different analyses is presented in Table 1.1.

Table 1.1. Species ranked from early to late leaf or needle unfolding

species:	modelling phenology	spring frost damage	plasticity	growth	competition
Larix decidua	x	x	x		
Betula pubescens	x	x	x	x	x
Tilia platyphylla	x	x			
Fagus sylvatica	x	x	x	x	x
Tilia cordata	x	x	x		
Populus canescens	x		x		
Quercus rubra	x	x			
Quercus robur	x	x	x	x	x
Fraxinus excelsior	x	x			
Quercus petraea	x	x			
Picea abies	x	x	x		
Pinus sylvestris	x	x			

Phenology

Phenology is the study of annually recurring phenomena in the life cycle of an organism. Relevant events for this study are the moment of budburst in spring, and leaf or needle fall in autumn. The timing of these events is known to be triggered by temperature, but can also be influenced by photoperiod, precipitation, and nutritional status of the tree. To maximise reproductive success, a tree needs to synchronise the seasons favourable and unfavourable for growth, to the active and dormant period of its annual cycle. Since frost hardiness and growth are incompatible, a tree must minimise its risk of frost damage, but at the same time use maximally the available growing season. This mechanism leads to a close adaptation of a natural population of trees to their local climatological situation. Thus, a rapid climate change is likely to disturb this adaption: trees may either advance budburst which could make them more vulnerable to late spring frosts, or delay budburst thereby possibly not making full use of the available growing season. A differential response of species to climate change will alter the competitive abilities of these species when grown in mixture. Consequently, both the species composition of forests and the geographical distribution of species will change.

The relationship between phenology and climate is discussed in more detail in chapters 2 to 4. In chapter 2, a review is presented on the available models predicting the date of leaf unfolding, depending on temperature and/or photoperiod. The parameters of these models were estimated using 57 years of observations on the date of leaf unfolding of *Fagus sylvatica* in The Netherlands, and subsequently tested on 40 years of observations made in Germany. In chapter 3, the possible effects of climate change on the probability of spring frost damage are evaluated, using two phenological models and two climate change scenarios. Data on the date of leaf unfolding for eleven species observed in The Netherlands and nine species in Germany were used to evaluate this possibility using two models, and two different climatic scenarios. In chapter 4, the plasticity is discussed that tree species may possess with respect to leaf unfolding and leaf fall. If individual trees are able to respond phenotypically to a change in their environment, then the disruption of the synchronization brought about by climate change may be nullified. For this analysis, the response to different temperature regimes of clones of seven tree species relocated over a large latitudinal transect in Europe, was compared to the response of genetically differing trees which are assumed to be adapted to their local climate, along a part of the transect.

Growth

Growth is the increase in biomass of an organism. For plants, growth is determined by photosynthesis by which both carbon dioxide and water are converted into sugars and oxygen under influence of light. Gross photosynthesis is partly used to cover respiratory costs, which are the costs required for the process of growth, and the maintenance of a living plant. The sugars produced by photosynthesis are allocated to the different plant organs, and converted into structural biomass. This increase of structural biomass is reduced by losses of plants organs, such as leaves and branches. Models simulating growth of trees describe how the rates of photosynthesis, respiration, and allocation are affected by meteorological variables, such as radiation, temperature, precipitation, and wind speed. The forest growth model FORGRO, was applied and further developed in this study.

The relationship between growth and climate is discussed in chapters 5 and 6. The importance of differences in phenological characteristics between species on the effects of climate change on growth of deciduous trees was evaluated by modelling comparison. In chapter 5, extensions of FORGRO with different level of detail on photosynthesis and allocation were used to evaluate climate change impacts on growth of monospecies forests. In chapter 6, a modelling comparison is presented to evaluate the importance of phenology and the occurrence of spring frost damage on growth of mixed-species forests, integrating the effects of phenology on competition for light.

Methodology

Due to the size and longevity of trees, and the complexity of the processes involved, the question of how a future climate will influence growth and development of trees cannot directly be answered by experiments. Models provide an important means to bridge the spatial and temporal scales, and to integrate the relevant processes. Future projections of growth under climatic situations not encountered thus far, are only possible when the relationships between growth processes and the climate are modelled in a mechanistic manner. For this purpose, experiments on these processes provide essential information to design the models. Mechanistic modelling of forest growth, on a sound experimental base, in combination with climate change scenarios is thus the only means to obtain an impression of future forest growth. However, the climate change scenarios are still in development, and uncertainties remain in the descriptions of the processes and the parameter values of the forest growth models. To deal with the uncertainty of the future climate, the consequences of a range of scenarios was investigated. To deal with the uncertainties in the forest growth models, critical processes determining the response of growth to climate change scenarios were identified by comparing models with different levels of mechanistic detail. Nevertheless, any statement on consequences of climate change on phenology and growth made in this study should be regarded in the context of the validity of the forest growth models and the accuracy of the climate change scenarios, which are both simplifications of the real system.

Chapter 2

Selecting a model to predict the onset of growth of *Fagus sylvatica*

Introduction

The developmental processes in the bud that release dormancy and thus trigger the onset of growth of temperate zone trees are mainly regulated by temperature (Romberger 1963). This regulation is such that a period with chilling temperature (-5 to +10°C) followed by a period with forcing temperature (>0°C) induces budburst (Samish 1954; Vegis 1964; Wareing 1969; Nienstaedt 1974; Richardson, Seeley and Walker 1974; Lavender 1981).
Generally, the influence of photoperiod on trees requiring chilling is that a long photoperiod substitutes for a lack of chilling (Vegis 1964; Flint 1974; Nienstaedt 1974; Lavender 1981; Cannell and Smith 1983). However, for *Fagus sylvatica* the experimental evidence on the role of photoperiod in the timing of budburst is conflicting (Wareing 1953; Vegis 1964; Falusi and Calamassi 1990). Wareing (1953) found that budburst in *Fagus sylvatica* is induced when an absolute length of the dark period is achieved, even after a prolonged period of chilling. On the other hand, Falusi and Calamassi (1990) found that chilling completely eliminates dormancy, with very slight interaction between day length and chilling.
The aim of this study was to examine models presented in the literature and select the model that most accurately predicts the timing of the start of the growing period of *Fagus sylvatica*. Models that incorporate photoperiod as a substitute for chilling were compared with models that do not. In later studies this model could be coupled to a model describing primary production in order to evaluate the impact of climate change on growth and development.

Material and methods

Models

The definitions of the different phases during dormancy, which were introduced by Sarvas (1974), were adopted here. **Rest** is defined as the period in which buds remain dormant due to growth-arresting physiological conditions in the bud itself. The growth-arresting conditions are removed when buds are exposed to chilling temperature for a certain period. The subsequent stage of dormancy is called quiescence. **Quiescence** is defined as the period in which the buds remain dormant due to unfavourable environmental conditions. Budburst takes place when the buds are exposed to forcing temperatures for a prolonged period.

Taking a system-analytical approach, Hänninen (1990) formalised four models on dormancy release presented in the literature and introduced a **competence function** which is defined as the bud's potential to respond to forcing temperature. The values of the competence function range between zero and unity, so it indicates to what degree a bud responds to a forcing temperature relative to the potential response at that temperature.

The notation used is presented in Appendix 2.1, while the equations characterising the models are presented in Appendix 2.2.

The four models which Hänninen (1990) described have in common that: (1) the competence function depends on the state of chilling, (2) the rate of chilling during rest is assumed to have an optimum between minimum and maximum temperature thresholds (Equation 2.1, Figure 2.1), and (3) the rate of forcing during quiescence is assumed to be related to temperature according to a logistic function (Equation 2.2, Figure 2.2). Two models with other functions for the rate of chilling and forcing and with a competence function independent of the state of chilling, were characterised using Hänninen's terminology. In all models the state of chilling and the state of forcing are the summation of the rate of chilling and forcing, respectively, using a variable time step with a maximum of one day (Equations 2.3 and 2.4).

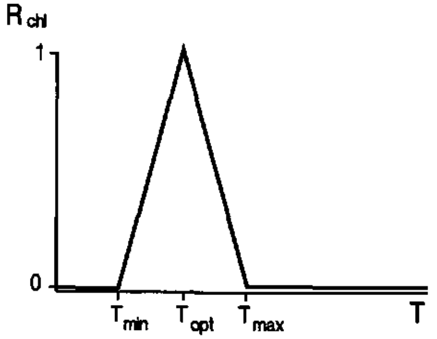

Figure 2.1. Rate of chilling for the parallel, sequential, deepening rest and four phase *model.*

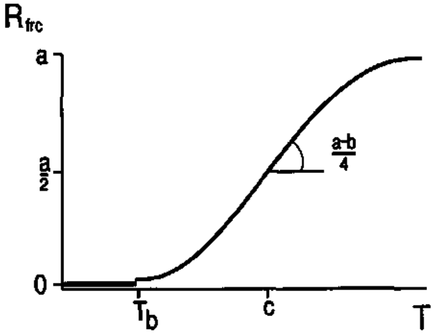

Figure 2.2. Rate of forcing for the parallel, sequential, deepening rest and four phase *model.*

Sequential model. Sarvas (1974) considered rest and quiescence as two strictly separate phases. On this basis, there will be no transition from rest to quiescence unless the critical state of chilling is attained (Equation 2.5). Similarly, there will be no transition from quiescence to the active phase unless the critical state of forcing is attained. This model was called the sequential model, because the state of chilling and the state of forcing increase sequentially in time (model I of Hänninen 1990).

Parallel model. Landsberg (1974) proposed a model for the development of apple fruit buds. He stated that for dormancy release it is essential that, even when the critical state of chilling has not yet been attained, response to forcing temperature must be possible. The bud's potential to respond to forcing temperature increases concomitantly with the time spent in chilling conditions (Equation 2.6, Figure 2.3). After attaining full chilling, the rate of development is logistically related to temperature (Equation 2.2, Figure 2.2). This model was called the parallel model, because the state of chilling and the state of forcing increase together in time (model II of Hänninen 1990).

Deepening rest model. Kobayashi, Fuchigami and English (1982) suggested a model for rest development in red-osier dogwood (*Cornus sericea*) based on the work of Fuchigami et al. (1982). During rest they discerned a phase of deepening rest and a phase of decreasing rest (Equation 2.7, Figure 2.4). After the end of rest a quiescence phase is defined (Kobayashi and Fuchigami 1983). During quiescence, developmental rates increase logistically with temperature (Equation 2.2, Figure 2.2). This model was called the deepening rest model, because the other models consider decreasing rest only (model III of Hänninen 1990).

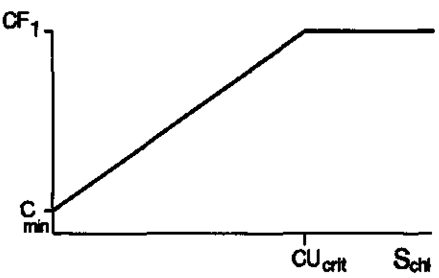

Figure 2.3. Competence function for the parallel model.

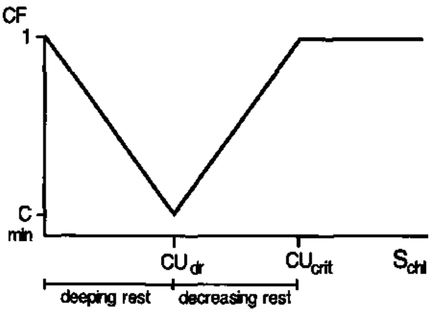

Figure 2.4. Competence function of the deepening rest model.

Four phase model. Vegis (1964) concluded that the range of external conditions in which development is possible narrows and widens during the annual cycle. Based on this idea, he defined three different phases during rest (rephrased in Hänninen's terminology: (1) pre-rest, development is still possible but only at a narrower range of external conditions than at the time of full growth activity, (2) true rest, development has stopped and cannot be resumed whatever the external conditions may be, and (3) post-rest, the range over which growth is possible widens again. Post-rest is followed by quiescence in which buds respond fully to forcing temperatures.

Hänninen formalised this mechanism by proposing an increasing temperature threshold during pre-rest and a decreasing threshold during post-rest (Equation

2.8, Figure 2.5). During true rest buds cannot respond to forcing temperatures. During pre-rest such a response is very unlikely because the temperature threshold increases while the temperature decreases. During post-rest, many more forcing units are accumulated per day because the temperature threshold decreases and the temperature possibly increases again. Transition from pre-rest to true rest, and from true rest to post-rest occurs when the *state of chilling attains critical* values (Equation 2.9, Figure 2.6). This model was called the four phase model, because the other models do not consider three phases during rest (model IV of Hänninen 1990).

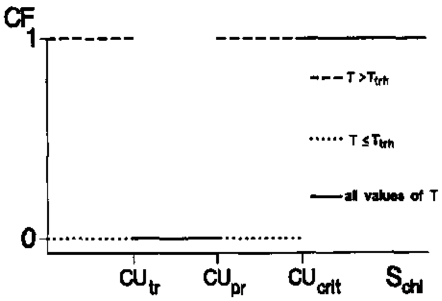

Figure 2.5. Competence function for the four phase model.

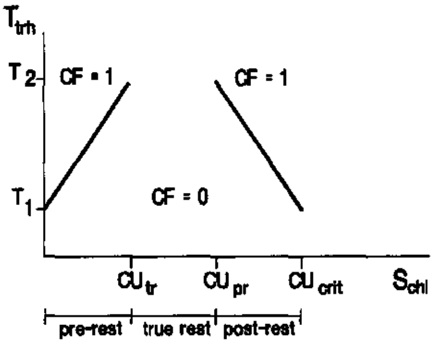

Figure 2.6. Temperature threshold for the four phase model.

Thermal time model. This model has been used frequently since Réaumur introduced it in 1735 (Robertson 1968). It was observed that the rate at which plants develop increases proportionally with temperature above a base temperature (Equation 2.10, Figure 2.7). Forcing units are accumulated since a given starting date, i.e. the onset of quiescence, so the duration of rest is assumed to be constant. This is equivalent to accumulating one chilling unit per day (Equation 2.11) from the onset of rest up to the onset of quiescence. The model is similar to the sequential model, with time equivalent to the rate of chilling, and the fixed onset of quiescence equivalent to the critical state of chilling. This model reflects the findings of Wareing (1953) that an absolute photoperiod is required to break rest. Since in natural situations this absolute photoperiod is reached every year at the same date, the onset of quiescence is fixed. This model was called the thermal time model by Cannell and Smith (1983).

Alternating model. Murray, Cannell and Smith (1989) used thermal time (Equations 2.10 to 2.12) as the state of forcing and the number of chilling days as the state of chilling to predict budburst among other species, of *Fagus sylvatica*. Days with an average temperature below the base temperature are regarded as chilling days (Equation 2.13). Cannell and Smith (1983) found that the critical thermal time required for budburst is not a constant, but declines exponentially with the state of chilling (Equation 2.14, Figure 2.8). This model differs from the other models in relating forcing to chilling. The rate of forcing is not increased when more chilling units are accumulated, but the critical state of forcing required for budburst is lowered when the state of chilling increases. It was called the alternating model because from the onset of quiescence on, either the state of chilling increases, when the temperature is below the base temperature, or the state of forcing is increased, when above.

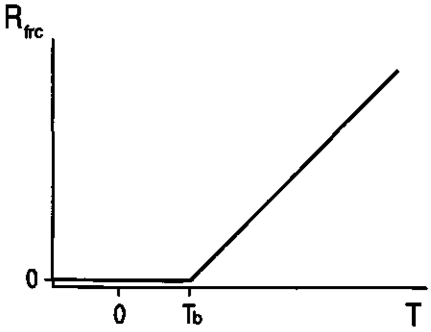

Figure 2.7. Rate of forcing for the thermal time model.

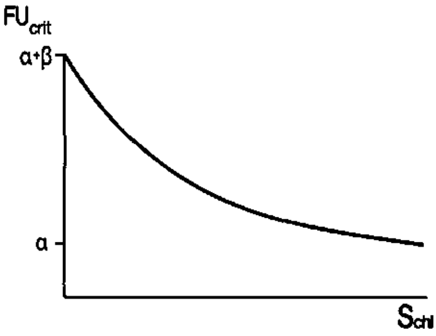

Figure 2.8. Critical state of forcing for the alternating model.

Photosensitivity

The most basic model relating the timing of budburst to photoperiod, proposes an absolute day length to induce budburst. This model was considered as the null model since it predicts budburst to occur each year at the same date.

Photoperiod was included additively to the rate of chilling in the models (Equation 2.15). With this formulation, photosensitivity guarantees that the chilling requirement is attained even when little chilling is accumulated due to high winter temperatures. As the thermal time model does not consider the rate of chilling, photoperiod was not included in this model.

Parameter estimation

The minimum sum of squares of the residuals (absolute differences between predicted and observed date of leaf unfolding) was used as criterion to identify the optimal set of parameter values for each of the models. Several searching methods were used to inspect the parameter space.

The parameter values of the models formalised by Hänninen (1990) were estimated with 'SENECA', a Simulation ENvironment for ECological Applications (Scholten, de Hoop and Herman 1990). Here, the parameters are constrained within user-defined limits. This guarantees that biologically realistic values are obtained. Using a 'controlled random search' (Price 1979) for all parameters simultaneously, the parameter range was reduced. Initial values for the parameter ranges were derived from the literature (Hänninen 1990) or set subjectively, but adjusted when the method found a boundary value to be optimal.

The critical state of forcing for the thermal time model was found by varying the starting day of accumulating thermal time from 1 November to 1 May using a step size of one day, and the base temperature from -5 to 10°C with a step size of 0.1 °C. The parameters of Equation 2.14 of the alternating model were fitted with GENSTAT using the directive FITNONLINEAR, because the same method was applied by Murray et al. (1989). This was done repeatedly, by varying the onset of quiescence between 1 December and 1 February with a step size of 14 days, and the base temperature from 0 to 10°C with a step size of 1 °C.

Data

The models were fitted using phenological observations gathered in the time span 1901-1968 from many locations throughout The Netherlands. Data for 1931-1939, 1945 and 1954 are lacking. The models were tested using data gathered at three phenological stations in Germany in the period 1951-1990. The average of the daily minimum and maximum temperature was used. The temperature series from De Bilt (52.06°N, 5.20°E), which is located in the centre of The Netherlands, was available for the Dutch observations. For the German observations the temperature series of Celle (52.36°N, 10.02°E) was used.

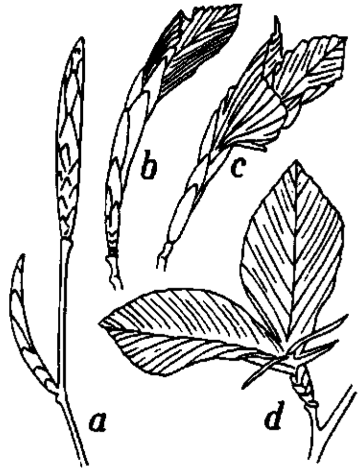

Figure 2.9. Budburst of *Fagus sylvatica*. a: buds still closed, b and c: leaves protruding, but not yet unfolded, d: first leaves have emerged to leaf base, and have unfolded: leaf unfolding (DWD 1962).

The phenological stage considered is called 'leaf unfolding'. Leaf unfolding is defined by the Hoffman-Ihne instruction for observers (Bos 1893) as follows: at two or three places in the tree a normal, unwrinkled, leaf surface should be visible, but full leaf size has not yet been attained (Figure 2.9d). The observations should be done on free-standing individuals, not standing in especially favoured or unfavoured sites (south side of wall, very wet or dry soils, etc.). Particularly early or late individuals should be excluded. The average date of leaf unfolding should preferably be taken from several individuals standing near each other. In the Dutch observations before 1930, the observer was allowed to make observations on different groups of *Fagus sylvatica* in subsequent years (Bos 1893). Since 1940 it has been mandatory to observe the same group every year (Anonymous 1950). The observers are urged to inspect their trees daily because in a warm spring the stages depicted in Figure 2.9 can occur within a week.

The advantage of the Dutch data set is that it covers a relatively long period. It contains 1964 individual observations covering 57 years. Its disadvantages are that the provenance of the observed trees is unknown and that the sites of observation as well as the number of observations vary between years. Yearly averages were taken because only one temperature series covering the full time span of phenological observations was available. From the south to the north of The Netherlands the date of leaf unfolding is delayed by 2.8 days per degree latitude, which coincides with a difference in average yearly temperature of about 1 °C (1950-1987). From east to west the delay in the day of leaf unfolding is 0.6 days per degree longitude.

The four German phenological stations are all located within 0.5°N and 0.5°E of the meteorological station at Celle. For these stations were 160 individual observations available, covering 40 years. For testing the models, yearly averages were taken. For the German observations yearly averages were taken of the results from the four phenological stations.

Results

Table 2.1 presents the parameter sets of each model yielding lowest sum of squares of the residuals, SS_{res}, found. For the four phase model without day length no results are presented because, for this model, the parameter set with the best result predicted the date of leaf unfolding in only 10 of the 57 years. In the other years the state of forcing did not reach the critical state required for leaf unfolding. The SS_{res} of the thermal time model and the alternating model varied very little when the onset of quiescence was varied between 1 December and 1 February, and the base temperature was adjusted accordingly. Therefore, for both models the onset of quiescence was fixed at 1 January.

It was found that the SS_{res} for the fit of the models exceeded the SS_{res} for the fit of the null model, i.e. the mean (Table 2.2). Including day length as a substitute for chilling decreased the SS_{res} of each of the models. With the parameter values presented in Table 2.1, the date of leaf unfolding of the German data was predicted. Again it was found that the SS_{res} of the predictions exceeded the SS_{res} of the null model, and that including day length decreased the SS_{res} of a model (Table 2.2).

Improving the fit of the model

Since all models performed worse than the null model, an attempt was made to develop a model with a higher accuracy of prediction than the current models. The sequential model without day length appears the most promising model to improve. Therefore, this model was adapted in two ways. Firstly, the constraint on the parameter range was released, so the parameters were allowed to take biologically unrealistic values. Secondly, the temperature asymptote of the logistic function of forcing, *a*, was set at unity, reducing the number of parameters to estimate. This model was called the sequential-I

Table 2.1. Parameter values yielding the lowest SS_{res}. See Appendix 1 for an explanation of the parameter names. Abbreviation of the models are: s, sequential; p, parallel; dr, deepening rest; 4p, four phase; tt, thermal time; a, alternating, s-l, improved sequential. + L indicates a model including day length

	s	s + *L*	p	p + *L*	dr	dr + *L*	4p + *L*	tt	a	a + *L*	s-l
$t_1^{a)}$	1 Nov	1 Nov	1 Nov	1 Nov	1 Nov	1 Nov	1 Nov		1 Nov	1 Nov	1 Nov
$t_2^{a)}$								1 Jan	1 Jan	1 Jan	
C_{crit}	57.40	59.11	117.18	105.96	95.71	74.91	170.90				117.83
F_{crit}	262.53	264.44	224.30	191.50	166.51	164.96	302.76	206.40			9.66
T_{min}	-3.80	-4.58	-3.87	-4.01	-0.96	-2.65	-3.23				-17.02
T_{opt}	0.41	2.38	1.47	4.95	2.57	1.67	2.58				-1.34
T_{max}	12.43	12.02	10.33	13.68	8.73	10.86	8.87				92.15
T_b	0.00$^{b)}$	0.00$^{b)}$	0.00$^{b)}$	0.00$^{b)}$	0.00$^{b)}$	0.00$^{b)}$	0.00$^{b)}$	4.50$^{a)}$	5.00$^{a)}$	5.00$^{a)}$	0.00$^{b)}$
a	26.49	27.75	31.33	29.95	29.10	31.38	20.41				1.00$^{b)}$
b	-0.19	-0.23	-0.15	-0.17	-0.17	-0.20	-0.30				-0.12
c	-17.07	-18.52	-23.34	-24.99	-19.50	-23.18	-14.08				-20.54
δ		94.21		95.59		93.22	2.12			58.51	
K_{min}			0.26	0.11	0.11	0.24					
C_{dr}					31.69	31.29					
C_{tr}							56.97				
C_{dr}							113.93				
T_1							10.82				
T_2							17.47				
α									66.00	72.83	
β									511.00	546.58	
γ									0.017	0.016	

$^{a)}$ fixed after initial testing, $^{b)}$ fixed.

Table 2.2. Statistics for the fit and predictions of the models. SS_{res}, sum of squares of the residuals; MAX_{res}, maximum residual; LU_{avg} , average date of leaf unfolding. + L indicates a model including day length. N_{par}, number of parameters in the model

	Fit (The Netherlands, $n=57$)			Prediction (Germany, $n=40$)			
Model	SS_{res}	MAX_{res}	LU_{avg}	SS_{res}	MAX_{res}	LU_{avg}	N_{par}
null	1622	11	1 May	2494	21	1 May	0
sequential	1624	11	1 May	3108	15	7 May	10
parallel	2623	19	3 May	6256	25	10 May	11
deepening rest	3352	17	27 April	9461	32	12 May	12
sequential + *L*	3882	25	1 May	4837	26	9 May	11
parallel + *L*	4117	24	29 April	5516	27	9 May	12
deepening rest + *L*	13351	40	16 April	3923	24	7 May	13
four phase + *L*	5209	27	25 April	4817	24	9 May	15
thermal time	4602	24	2 May	5810	41	24 May	3
alternating	2034	18	28 April	6797	32	19 April	6
alternating + *L*	5190	14	29 April	9879	47	11 April	7
sequential-I	488	9	2 May	885	12	6 May	9
Data:			1 May			1 May	

model. Mathematically the sequential-I model is equivalent to the sequential model. However, the biological interpretation of the rate of forcing changes. The rate of forcing is now expressed relative to the maximal rate of forcing at the optimal forcing temperature. The sequential-I model was fitted using Newtons method of a directed search in the parameter space (Gill and Murray 1978). This was done with the subroutine E04FCF of the NAG FORTRAN library (Anonymous 1990). The parameter values of the sequential-I model are presented in Table 2.1. The criterion for this method of a global minimum of SS_{res} was, however, not attained. The SS_{res} of the fit and predictions are presented in Table 2.2. It was found that the SS_{res} for both the fit of the Dutch data and the prediction of the German data were reduced considerably, compared both to the other models and to the null model. However, the sequential-I model overestimated the date of leaf unfolding systematically, especially for the German data.

Discussion

Models

The underlying physiological mechanisms leading to dormancy release are largely unknown, but cannot be related simply to an increase of a growth-promoting substance or to a decrease of a growth-inhibiting substance (e.g. Powell 1969; Wareing 1969). It is known that temperate-zone tree species require a certain period with chilling temperature, followed by a period with a higher temperature, forcing a bud to burst. Based on this very simple empirical model the average date of the onset of growth of *Fagus sylvatica* can be predicted with considerable accuracy.

In the model with the lowest SS_{res}, the sequential-I model, chilling was allowed to occur at a very wide range of temperatures (Table 2.1). This means that the rate of chilling is virtually independent of temperature, because the curve in Figure 2.1 then shows a very broad plateau close to unity in the range of actual winter temperatures (about -10 to +10°C). Consequently, the onset of quiescence varies little between years (11 March ± 5.4 days). So the sequential-I model nearly reduces to the thermal time model with a logistic rate of forcing instead of a linear one. However, the SS_{res} of the sequential-I model was found to increase when the model was simplified by using a linear rate of forcing instead of the logistic function.

Photosensitivity

The experimental evidence that photoperiod can substitute for a lack of chilling (Vegis 1964; Flint 1974; Nienstaedt 1974; Lavender 1981; Cannell and Smith 1983) suggests an additive model. Photosensitivity then guarantees that the chilling requirement is attained when, in a warm winter, little chilling is accumulated. A similar formulation was used by Primault (in Robertson 1973), and by Hänninen et al. (1990) for the joint factor model on growth cessation of trees.

Multiplicative models and polynomials of the rate of chilling and photoperiod are also frequently used (Nuttonson 1948; Robertson 1968; Caprio 1974; Campbell and Sugano 1975). However, when photoperiod is multiplicatively coupled to the rate of chilling, photoperiod has no effect when the rate of chilling equals zero, i.e. due to high temperature. So this model does not represent photoperiod as a substitute for chilling.

Fitting an additive model of the state of chilling and an absolute photoperiod was not possible. For such a model, finding both the best photoperiod and the best critical state of chilling entails increasing the critical state of chilling by an amount equal to that added to the state of chilling. Thus, there is an infinite number parameter sets for this model yielding the same result. So the effects of photoperiod cannot be evaluated using this type of model. A similar reasoning holds true for a multiplicative model of the state of chilling and an absolute photoperiod. Therefore, it was concluded that the additive model of the rate of chilling and photoperiod is a simple and realistic way to incorporate photoperiod. Nevertheless, the result of this way of introducing photoperiod was that the SS_{res} of the model increases, thus making the model more complex as well as a worse predictor for the date of leaf unfolding.

Parameter estimation

The models have in common that state variables must attain one or more thresholds for which no data are available. Finding optimal parameter values for such a model is particularly difficult because the same result can be obtained by either lowering the threshold, or by tuning the rate parameters so that the threshold is attained earlier. There is little hope that, even when constrained parameter ranges are used, a fitting procedure will find biologically realistic parameter values as long as no direct measurements of the parameters are available. The reason that the deepening rest and the four phase model perform poorly may be the introduction of additional thresholds during rest. Due to the correlation between these thresholds, many different thresholds yield the same prediction. Consequently, a poor fit not necessarily indicates that the structure of the models is inappropriate.

Conclusion

The modified version of the sequential model performs better than the other models considered, including the null model. The aim of this study was to select the model that most accurately predicts the onset of growth of *Fagus sylvatica.* It appears that the sequential-I model could be used for further study of impacts of climatic warming on primary production of *Fagus sylvatica.*

Appendix 2.1. Notation

Symbol		Units
Arbitrary units		
CU	Chilling units	
FU	Forcing units	
Variables		
R_{chl}	Rate of chilling	CU day^{-1}
R_{frc}	Rate of forcing	FU day^{-1}
S_{chl}	State of chilling, integral of rate of chilling	CU
S_{frc}	State of forcing, integral of rate of forcing	FU
K	Competence function: bud's potential to respond to forcing temperature [0-1]	-
T	Mean daily temperature	°C
L	Day length	h day^{-1}
t	Time	day
Parameters		
C_{crit}	Critical value of state of chilling for the transition form rest to quiescence	CU
F_{crit}	Critical values of state of forcing for the transition from quiescence to the active period, i.e. budburst	FU
K_{min}	Minimum potential of unchilled bud to respond to forcing temperature	-
C_{dr}	Critical state of chilling for transition from deepening rest to decreasing rest	CU
C_{tr}	Critical value of state of chilling for transition from pre-rest to true rest.	CU
C_{pr}	Critical value of state of chilling for transition from true rest to post-rest.	CU
T_{min}	Minimum temperature for rate of chilling	°C
T_{opt}	Optimal temperature for rate of chilling	°C
T_{max}	Maximum temperature for rate of chilling	°C
T_b	Base temperature	°C
T_1	Lower value of temperature range for which development is possible	°C
T_2	Upper value of temperature range for which development is possible	°C
T_{trh}	Temperature threshold above which development is possible and below which development is impossible	°C
t_1	Date of onset of rest.	day
t_2	Date of onset of quiescence	day
$a, b, c, \alpha, \beta, \gamma, \delta$	Constants	

Appendix 2.2. Equations

Rate of chilling for the parallel, sequential, deepening rest and four phase model

$$R_{chl} = \begin{cases} 0 & T \leq T_{min} \\ \dfrac{T - T_{min}}{T_{opt} - T_{min}} & T_{min} < T \leq T_{opt} \\ \dfrac{T - T_{max}}{T_{opt} - T_{max}} & T_{opt} < T < T_{max} \\ 0 & T \geq T_{max} \end{cases} \qquad 2.1$$

Rate of forcing for the parallel, sequential, deepening rest and four phase model

$$R_{frc} = \begin{cases} 0 & T \leq T_b \\ K \dfrac{a}{1 + e^{b(T + c)}} & T > T_b \end{cases} \qquad 2.2$$

State of chilling (all models)

$$S_{chl} = \sum_{t_1}^{t} R_{chl} \qquad 2.3$$

State of forcing (all models)

$$S_{frc} = \sum_{t_2}^{t} R_{frc} \qquad 2.4$$

Sequential model

$$K = \begin{cases} 0 & S_{chl} < C_{crit} \\ 1 & S_{chl} \geq C_{crit} \end{cases} \qquad 2.5$$

Parallel model

$$K = \begin{cases} K_{min} + \dfrac{1 - K_{min}}{C_{crit}} S_{chl} & S_{chl} < C_{crit} \\ 1 & S_{chl} \geq C_{crit} \end{cases} \qquad 2.6$$

Deepening rest model

$$K = \left\{ \begin{array}{ll} 1 - \dfrac{1 - K_{min}}{C_{dr}} S_{chl} & S_{chl} < C_{dr} \\ K_{min} + \dfrac{(1 - K_{min})(S_{chl} - C_{dr})}{C_{crit} - C_{dr}} & C_{dr} \leq S_{chl} < C_{crit} \\ 1 & S_{chl} > C_{crit} \end{array} \right\} \qquad 2.7$$

Four phase model

$$K = \left\{ \begin{array}{ll} 1 & S_{chl} < C_{tr}, T > T_{trh} \\ 0 & S_{chl} < C_{tr}, T \leq T_{trh} \\ 0 & C_{tr} \leq S_{chl} < C_{pr} \\ 0 & C_{pr} \leq S_{chl} < C_{crit}, T \leq T_{trh} \\ 1 & C_{pr} \leq S_{chl} < C_{crit}, T > T_{trh} \\ 1 & S_{chl} \geq C_{crit} \end{array} \right\} \qquad 2.8$$

$$T_{trh} = \left\{ \begin{array}{ll} T_1 + \dfrac{T_2 - T_1}{C_{tr}} S_{chl} & S_{chl} < C_{tr} \\ T_1 + \dfrac{(T_1 - T_2)(S_{chl} - C_{crit})}{C_{crit} - C_{pr}} & C_{pr} \leq S_{chl} < C_{crit} \end{array} \right\} \qquad 2.9$$

Thermal time model

$$R_{trc} = \left\{ \begin{array}{ll} 0 & T \leq T_b \\ K\,(T - T_b) & T > T_b \end{array} \right\} \qquad 2.10$$

$$R_{chl} = 1 \qquad 2.11$$

$$K = \left\{ \begin{array}{ll} 0 & t < t_2 \\ 1 & t \geq t_2 \end{array} \right\} \qquad 2.12$$

Alternating model

$$R_{chl} = \begin{Bmatrix} 1 & T \leq T_b \\ 0 & T > T_b \end{Bmatrix} \qquad 2.13$$

$$F_{crit} = \alpha + \beta e^{-\gamma S_{chl}} \qquad 2.14$$

Photosensitivity

$$R_{chl} = R_{chl} + \delta L \qquad 2.15$$

Chapter 3

A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in The Netherlands and Germany

Introduction

The timing of leaf unfolding of trees is mainly regulated by temperature (Romberger 1963). Chilling and forcing temperatures are both required to induce leaf unfolding of temperate tree species (Vegis 1964), and climatic warming is likely to influence the timing of this process. However, it is not clear whether warmer winters will advance or delay the date of leaf unfolding: the chilling requirement may be attained later while the critical temperature sum for leaf unfolding is likely to be attained earlier. Such shifts may have consequences on the occurrence of frost damage. Different tree species may respond differently to climatic warming, and thus, alter their competitive ability.

In this study, the effects of changing winter temperature on the date of leaf unfolding were evaluated using models presented in the literature. Kramer (1994a, Chapter 2) showed that the onset of the growing season of *Fagus sylvatica* in The Netherlands is described accurately by the model developed by Sarvas (1974) and refined by Hänninen (1990), and also by the model developed by Cannell and Smith (1983).

Hänninen (1991) applied the Sarvas (1974) approach in a theoretical study to evaluate the effects of a doubled CO_2 temperature scenario (Bach 1987) on the probability of frost damage in northern trees, using parameter values which represent a generalised central Finnish tree species. He used a non-uniform climatic warming scenario, in which the mean temperature is expected to increase most in January and least in July. He found an increased probability of frost damage for central Finland due to a much earlier budburst.

Murray et al. (1989) used a thermal time approach (cumulative temperature above 5°C, Cannell and Smith 1983) to predict how much the date of budburst of fifteen tree species in Britain would be shifted after uniform climatic warming by one to three degrees. They concluded that the probability of frost damage would not increase in the British lowland sites, but might increase in cool upland sites for species with small chilling requirement.

The difference in results found by Hänninen (1991) and Murray et al. (1989) may be caused by (1) different species characteristics, the species truly responding differently to a change in temperature because they are adapted to different climates, (2) because different models were used, each with its own shortcomings, or (3) because different climatic warming scenarios were used, since these were the methodological differences between both studies. To clarify this, in this study both models were fitted to data on the date of leaf unfolding of eleven tree species collected as part of a phenological network in The Netherlands and Germany. The shift in the date of leaf unfolding attributable to uniformly and non-uniformly changing winter temperature was subsequently quantified. The impact of this shift on the occurrence of spring frost damage was evaluated using the shift in the relative number of years in which freezing temperatures occurred in the critical period around the date of leaf unfolding.

Material and methods

Models selected to predict the date of leaf unfolding of trees (Kramer 1994a, Chapter 2) were fitted to available observations on the date of leaf unfolding of *Larix decidua*, *Betula pubescens*, *Tilia platyphylla*, *Fagus sylvatica*, *Tilia cordata*, *Quercus rubra*, *Quercus robur*, *Fraxinus excelsior*, *Quercus petraea*, *Picea abies*, *Pinus sylvestris*, collected in Germany and The Netherlands.

These models were applied to predict the shift of the date of leaf unfolding using two temperature change scenarios: (1) the uniform temperature change scenario, used by Murray et *al.* (1989), comprised of a shift of -2 to 8°C of the historical temperature series, in steps of 1°C, (2) the non-uniform temperature change scenario, used by Hänninen (1991), developed for Finland in a 2 x CO_2 climate, in which winter temperature is expected to rise more than summer temperature. Mean daily temperature in the months January to December was assumed to rise by 6.2, 5.7, 5.1, 4.4, 3.3, 2.1, 1.6, 2.1, 3.2, 4.3, 5.2, 5.9°C respectively (Bach 1987).

The effect of the shift of the date of leaf unfolding on the occurrence of frost damage was evaluated for the period from five days before to five days after the predicted date of leaf unfolding. This period was arbitrarily chosen as the frost-susceptible period. When the lowest value of the minimum daily temperatures on one of the days in this period (T^*) dropped below 0°C, then frost damage was possible. The probability of frost damage was defined as the fraction of years with freezing temperature in the period around the date of leaf unfolding: $P(T^*<0)$. The probability of frost damage around the date of leaf unfolding based on the unaltered temperature series (zero-change scenario) was compared with the probability of frost damage around the date of leaf unfolding of the other scenarios. Temperatures below zero do not necessarily imply frost damage. However, few data were available on the temperature threshold below which frost damage is certain. Therefore, an empirical approach was adopted, using the temperature thresholds below which 10% ($T^*_{0.10}$) and 25% ($T^*_{0.25}$) of the observations of T^* occur. These thresholds were defined as: $P(T^*<T^*_{0.10})=0.10$ and $P(T^*<T^*_{0.25})=0.25$. Thus, when using $T^*_{0.10}$ as temperature threshold for frost damage for a given species, then by definition the probability of frost damage is 10% for this species. On the other hand, when using 0°C as a frost damage threshold for all species, the probability of frost damage has to be determined for each species. The observed values of P_0, $T^*_{0.25}$ and $T^*_{0.10}$ are presented in Table 3.1. Figure 3.1

shows the distribution of T^*, as well as the 10% and 25% percentiles for the data of *Fagus sylvatica* in The Netherlands ($n = 57$ years). Although $T^*_{0.10}$ may be a better threshold to indicate frost damage experienced by trees, the number of observations in the 10% percentile was rather small, i.e. 5 of the 57 years of observations for *Fagus sylvatica* in The Netherlands (Figure 3.1). It was investigated whether the probability of frost damage using 0°C as threshold is a good indicator of the probability of frost damage with $T^*_{0.10}$ as threshold temperature.

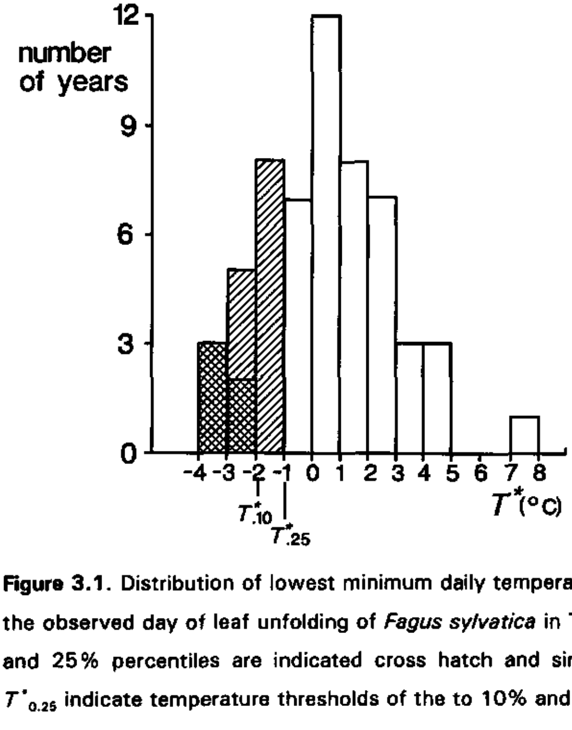

Figure 3.1. Distribution of lowest minimum daily temperature (T^*) in an 11-day period around the observed day of leaf unfolding of *Fagus sylvatica* in The Netherlands (n = 57 years); 10% and 25% percentiles are indicated cross hatch and single hatch, respectively. $T^*_{0.10}$ and $T^*_{0.25}$ indicate temperature thresholds of the to 10% and 25% percentiles, respectively.

To test the importance of adaptation to local climate, hypothetical provenance transfers were analysed. Using the parameter values estimated by Murray et al. (1989) for each of the 15 northern British tree species for the alternating model, and by Hänninen (1990) for the generalised central Finnish tree species for the sequential model (see section 'Models'). The response of species from Britain and Finland to both the uniform and non-uniform temperature change scenario was evaluated using the Dutch temperature series. Thus, it was possible to distinguish between differences caused by the models, by the temperature change scenarios used, and by the species responses to their local climate.

Data

The data on leaf unfolding had been collected in The Netherlands and in the adjacent part of Germany. Leaf unfolding is defined as the day on which a normal unwrinkled leaf is visible at several places in the tree, but has not fully expanded (Bos 1893). The same definition was used for the German observations on deciduous species (DWD 1991). Needle flush of the German observations on coniferous species is defined as the day on which the first buds burst and the needles have not yet spread out (DWD 1991). For convenience, the term 'leaf unfolding' will be used for both deciduous and coniferous tree species in this paper. The Dutch data were obtained from the Royal Dutch Meteorological Institute (KNMI), and the German data from the German Weather Service (DWD). Table 3.1 presents species characteristics and the periods of observation. The advantage of these observations is that they cover a large time span, and therefore, are valuable for studies of climate change. The disadvantages are that the provenance of the trees is unknown, and the sites of observations and the number of observations vary between years. The temperature series observed at De Bilt (5.20°E, 52.06°N) was used for the analysis of the Dutch data on leaf unfolding. Mean annual values of the date of leaf unfolding of all Dutch data per species were used, since only one temperature series was available. For the analysis of the German data the observations from 11 phenological stations were divided into three groups situated near a meteorological station, and averaged per group. Table 3.2 shows the composition of these groups and the location of the meteorological stations.

Table 3.1. Statistics on the dates of leaf unfolding in The Netherlands (Nl) and Germany (D): periods with data on leaf unfolding; average date of leaf unfolding (*U*) with standard deviation; number of individual observations (n); probability of sub-zero temperature around the date of leaf unfolding (P_0); and freezing temperature threshold belonging to 10% ($T^*_{0.10}$) and 25% ($T^*_{0.25}$) percentiles of frequency distribution of minimal temperature in the 11-day period around the date of leaf unfolding

species	period	missing years	U ± s.d.	n	P_0	$T^*_{0.25}$	$T^*_{0.10}$
Larix decidua (D)	1951-1990		20 Apr ± 10.3	429	0.50	-1.9	-3.1
Betula pubescens (Nl)	1901-1946	'31-'39,'45	22 Apr ± 7.7	718	0.58	-2.2	-3.7
Betula pubescens (D)	1951-1990		23 Apr ± 9.4	489	0.43	-1.7	-3.0
Tilia platyphylla (D)	1951-1990		29 Apr ± 10.3	452	0.35	-1.3	-2.6
Fagus sylvatica (Nl)	1901-1968	'31-'39,'45,'54	1 May ± 5.4	1966	0.37	-1.0	-2.3
Fagus sylvatica (D)	1951-1990		1 May ± 8.0	473	0.37	-0.7	-2.6
Tilia cordata (D)	1951-1990		3 May ± 9.5	392	0.28	-0.6	-2.5
Quercus rubra (Nl)	1940-1959	'45,'54	3 May ± 7.4	509	0.17	0.1	-2.1
Quercus robur (D)	1951-1990		4 May ± 7.3	482	0.27	-0.4	-2.1
Quercus robur (Nl)	1901-1968	'31-'39,'45,'54	6 May ± 6.7	1462	0.18	0.2	-1.1
Fraxinus excelsior (D)	1951-1990		7 May ± 8.7	435	0.18	0.6	-1.1
Quercus petraea (Nl)	1940-1968	'45, '54,'60,'61	8 May ± 6.2	287	0.12	0.1	-1.1
Picea abies (D)	1951-1990		10 May ± 8.1	451	0.14	0.8	-0.8
Pinus sylvestris (D)	1951-1990		13 May ± 7.0	369	0.15	1.1	-0.5

Models

In an earlier study of various models (Kramer 1994a) tested for *Fagus sylvatica*, two models incorporating chilling and heat requirement were found to predict the onset of the growing season well. They were the sequential and the alternating models. Sarvas (1974) proposed a two-stage model to describe the development of the plant during dormancy: (1) a rest phase which is defined as the period in which buds remain dormant due to growth-arresting

Table 3.2. German phenological and meteorological data. Mean annual values of phenological observations per species are taken from the three groups of stations as indicated

phenological station	lat. (°N)	long. (°E)	meteorological station (representing group)	lat. (°N)	long. (°E)
Oldenburg	53.09	8.12	Oldenburg	53.06	8.15
Bremen-Oberneuland	53.05	8.56	(for group 1)		
Mellinghausen	52.45	8.50			
Eielstaedt	52.19	8.22			
Walsrode	52.52	9.36	Celle	52.36	10.02
Celle	52.38	10.05	(for group 2)		
Grasdorf	52.18	9.48			
Kolenfeld	52.24	9.27			
Heldenbergen	50.14	8.52	Karlsruhe	49.02	8.22
Gross-Umstadt	49.52	8.56	(for group 3)		
Moersch	48.58	8.18			

physiological conditions in the bud itself.These conditions are removed when the buds are exposed to chilling temperature ($-5<T<10$°C) for a certain period, and (2) a quiescence phase which is defined as the period in which the buds fail to grow owing to un-favourable environmental conditions. Budburst takes place when the buds are exposed to forcing temperature ($T>0$°C) for a prolonged period. The rates at which 'chilling units' (CU) are accumulated during rest and 'forcing units' (FU) are accumulated during quiescence, and the threshold values for rest completion and budburst are species-specific. Hänninen's (1990) formalization of the Sarvas approach is presented in Equation

$$S_c = \sum_{t_1}^{t} R_c \qquad S_f = \sum_{t_2}^{t} R_f \qquad 3.1$$

3.1. Table 3.3 presents the variable and parameter names used and their dimensions.The date of the onset of rest (t_1) was arbitrarily set at 1 November for all species. Rest ends (t_2) when the state of chilling exceeds its critical value. Similarly, quiescence ends (t_3) when the state of forcing exceeds its critical value. The duration of the rest and quiescence phases is defined as the number of days between t_1 and t_2, and t_2 and t_3, respectively.

Table 3.3. *Variables, parameters in the sequential and alternating models and their dimensions,* as well as other statistics and abbreviations used in this study

Variables		Units			
S_c	State of chilling	CU	T_i	Minimum temperature for chilling	°C
S_f	State of forcing	FU	T_o	Optimal temperature for chilling	°C
R_c	Rate of chilling	CU day^{-1}	T_a	Maximum temperature for chilling	°C
R_f	Rate of forcing	FU day^{-1}	T_b	Base temperature	°C
			b, c, α, $ß$, r		Constants
Parameters		**Units**	**Other statistics**		**Units**
C^*	Critical value of state of chilling for the transition from the rest phase to the quiescence phase	CU	T	Mean daily temperature	°C
F^*	Critical value of state of forcing for the transition from quiescence to the active phase	FU	T^*	Lowest temperature in the frost-susceptible period	°C
K	The bud's ability to respond to forcing temperatures	-	$T^*_{0.10}$	10% percentile of observations of T^*	°C
t_1	Date of onset of rest	d	$T^*_{0.25}$	25% percentile of observations of T^*	°C
t_2	Date of onset of quiescence	d	P_0	Probability of sub-zero temperature in frost-susceptible period	-
t_3	Date of leaf unfolding	d	U	Date of leaf unfolding	-
			R	Duration of rest period	-
			Q	Duration of quiescence period	-

The rate of chilling is a triangular function of temperature, defined as:

$$R_c = \begin{cases} 0 & T \leq T_i \\ \dfrac{T - T_i}{T_o - T_i} & T_i < T \leq T_o \\ \dfrac{T - T_a}{T_o - T_a} & T_o < T < T_a \\ 0 & T \geq T_a \end{cases} \qquad 3.2$$

The rate of forcing is a truncated logistic function of temperature, defined as:

$$R_f = \begin{cases} 0 & T \leq T_b \\ K \dfrac{1}{1 + e^{-b(T-c)}} & T > T_b \end{cases} \qquad 3.3$$

$$K = \begin{cases} 0 & S_c < C^* \\ 1 & S_c \geq C^* \end{cases} \qquad 3.4$$

K *is a competence function* (Hänninen 1990) *determining* whether a bud can respond to forcing temperatures. The base temperature was set at 0°C for all species to reduce the number of parameters to be estimated. In Figure 3.2 both the rate of chilling and the rate of forcing are presented, using the parameter values of Hänninen (1990), scaled between zero and unity. This model was called the sequential model because the state of chilling and forcing increase sequentially in time.

Cannell and Smith (1983) described the effect of chilling in a different way. They found that the state of forcing needed at budburst declines exponentially with the current state of chilling. Using the same notation as presented above (Table 3.3), this model can be presented as follows:

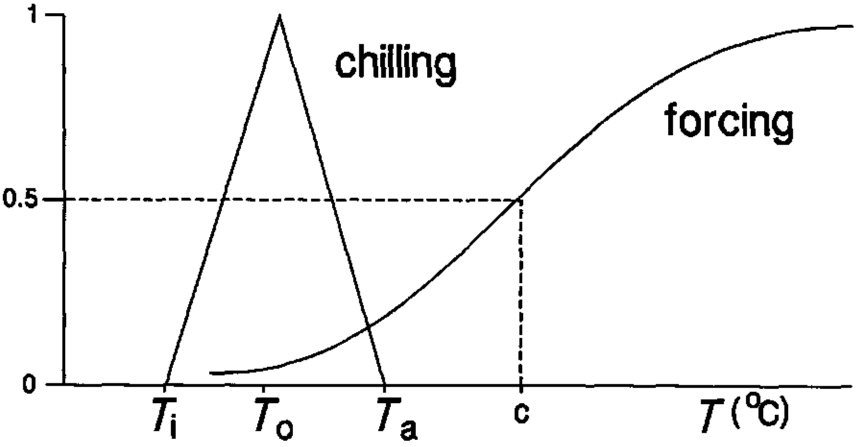

Figure 3.2. Rate of chilling (triangular) and rate of forcing (truncated logistic) scaled between zero and unity. Parameter values according to Hänninen (1990).

$$R_c = \begin{Bmatrix} 1 & T \leq T_b \\ 0 & T > T_b \end{Bmatrix} \qquad 3.5$$

$$R_f = \begin{Bmatrix} 0 & T < T_b \\ K\ (T - T_b) & T \geq T_b \end{Bmatrix} \qquad 3.6$$

$$K = \begin{Bmatrix} 0 & t < t_2 \\ 1 & t \geq t_2 \end{Bmatrix} \qquad 3.7$$

$$F^* = \alpha + \beta r^{S_c} \qquad 3.8$$

Leaf unfolding is predicted as the day on which the state of forcing exceeds its critical value. The critical value of state of forcing is not a constant but decreases monotonically with time. Following Murray et al. (1989) the state of chilling was accumulated from 1 November ($t_1 = 1$), the state of forcing was accumulated from 1 January ($t_2 = 61$), and the base temperature was set at 5°C, because these values were found to be applicable to the Dutch situation (Kramer 1994a, Chapter 2). Thus, implicitly a rest period of two months is assumed, since the state of forcing is not allowed to increase between 1 November and 1 January. From Equation 3.8 it can be seen that the critical state of forcing required for budburst equals $\alpha+\beta$ if the state of chilling equals zero, and approaches α if the state of chilling becomes very large. Thus r determines how sensitive is the critical state of forcing required for budburst to the state of chilling. If r equals unity, then F^* is independent of the state of chilling, whereas this sensitivity is inversely related to r.

The parameter values of both models were estimated by minimizing the residual sum of squares. The GENSTAT directive FITNONLINEAR was used for the alternating model, and the E04FCF subroutine of the NAG Fortran library was used for the sequential model. The explained variance presented was calculated based on the mean square of the residuals and the total mean square (adjusted R^2).

Results and discussion

Parameter values

The estimated parameter values and the variance explained by the sequential model are presented in Table 3.4. It appears that the parameter values of the rate of chilling (T_i, T_o, T_a) span a much wider range than the range [-5,10] that would normally be considered as chilling temperature. Although a temperature around T_o results in the fastest rate of chilling, with these parameter values even low or high temperature will contribute to chilling. The parameter values of the sequential model cannot easily be compared between species. The critical values for the state of chilling and forcing, C^* and F^*, are mutually dependent and correlate with other parameters (correlation matrix not presented); therefore, locally optimal parameter values were found by the estimating routine. However, using simpler versions of the sequential model increased the residual sum of squares and did not yield globally optimal parameter values.

Table 3.4. Parameter values and percentage variance explained (R^2) by the sequential model for The Netherlands (Nl) and Germany (D), and parameter values determined by Hänninen (1990) in central Finland (see Table 3.3 for the explanation of the parameter names)

species	T_i	T_o	T_a	C^*	b	c	F^*	R^2
Larix decidua (D)	-13.2	-2.2	101.4	91.4	0.13	34.3	1.3	0.73
Betula pubescens (Nl)	-12.0	-0.9	37.8	99.4	0.19	18.3	5.4	0.86
Betula pubescens (D)	-10.3	-10.0	58.3	84.3	0.13	38.4	1.0	0.76
Tilia platyphylla (D)	-11.2	-2.8	98.6	91.5	0.15	33.9	1.2	0.78
Fagus sylvatica (Nl)	-19.4	-0.2	77.0	117.6	0.10	33.1	3.6	0.68
Fagus sylvatica (D)	-21.4	-1.8	69.7	115.6	0.08	47.4	2.0	0.49
Tilia cordata (D)	-51.5	3.2	49.9	106.7	0.11	39.1	2.0	0.58
Quercus rubra (Nl)	-11.5	-1.1	22.7	94.1	0.16	22.4	5.5	0.87
Quercus robur (D)	-11.4	-3.8	39.3	101.7	0.11	37.8	1.9	0.55
Quercus robur (Nl)	-20.6	-0.8	58.9	112.2	0.17	16.2	11.7	0.82
Fraxinus excelsior (D)	-20.4	-3.5	165.8	140.4	0.09	53.1	0.7	0.28
Quercus petraea (Nl)	-24.0	-0.2	113.8	129.0	0.17	15.3	12.7	0.70
Picea abies (D)	-11.4	0.1	16.3	82.5	0.14	35.9	1.6	0.41
Pinus sylvestris (D)	-13.8	-1.2	16.5	85.3	0.11	37.6	2.4	0.33
(Finland)	-3.4	3.5	10.4	30.00	0.185	18.431	5.29	

The estimated parameter values and the variance explained by the alternating model are presented in Table 3.5. For *Fraxinus excelsior* and *Tilia platyphylla* negative values are found for the asymptote α. This means that when the state of chilling is large, F^* is negative, which is impossible. However, because of the high value of r, these species are relatively insensitive to changes

Table 3.5. Parameter values and percentage variance explained (R^2) by the alternating model for The Netherlands (Nl) and Germany (D), and parameter values of the 5 groups defined by Murray et al. (1989) in northern Britain (UK) (see Table 3.3 for the explanation of the parameter names)

species	*r*	ß	α	R^2
Larix decidua (D)	0.98	644	72	0.45
Betula pubescens (Nl)	0.97	860	129	0.57
Betula pubescens (D)	0.98	591	89	0.51
Tilia platyphylla (D)	0.99	619	-58	0.51
Fagus sylvatica (Nl)	0.98	731	121	0.52
Fagus sylvatica (D)	0.99	763	12	0.58
Tilia cordata (D)	0.99	659	99	0.44
Quercus rubra (Nl)	0.88	1355373	264	0.49
Quercus robur (D)	0.99	785	92	0.58
Quercus robur (Nl)	0.98	704	191	0.48
Fraxinus excelsior (D)	1.00	1208	-582	0.50
Quercus petraea (Nl)	0.90	161083	278	0.45
Picea abies (D)	0.98	978	162	0.43
Pinus sylvestris (D)	0.98	1218	164	0.47
Group 1 (UK)	0.99	1084	-147	
Group 2 (UK)	0.99	602	-56	
Group 3 (UK)	0.98	514	36	
Group 4 (UK)	0.97	468	39	
Group 5 (UK)	0.95	961	46	

Group 1: *Fagus sylvatica*; group 2: *Robinia pseudoacacia, Tsuga heterophylla, Picea sitchensis*; group 3: *Rubus idaeus, Sorbus aucuparia, Betula pendula, Corylus avelana*; group 4: *Sambucus nigra, Rosa rugosa, Salix viminalis, Larix decidua, Prunus avium*; group 5: *Populus trichocarpa, Crataegus monogyna.*

in the state of chilling, and because $\alpha+\beta>0$ a negative state of forcing will not be required. On the other hand, high values of β were found for *Quercus petraea* and *Q. rubra.* This means that a large value of the state of forcing will be required when the state of chilling attains low values. Due to the low values of r, these species are relatively sensitive to the state of chilling. Thus, a low value for the state of chilling will considerably reduce the critical state of forcing required for budburst. The deviant behaviour of both oak species may be attributable to the fact that the parameters were estimated from a relatively short series of observations (Table 3.1) and therefore the values found are not necessarily correct. Data were available from both The Netherlands and Germany for *Betula pubescens, Fagus sylvatica* and *Quercus robur,* and parameter values for each species were very similar in both countries. These three species differ mainly with respect to the value of α (the state of forcing required for budburst given sufficient chilling). The parameter values estimated by Murray et al. (1989) are also presented in Table 3.5. Group 1 consists of *Fagus sylvatica,* and group 4 contains *Larix decidua.* In the absence of chilling, the state of forcing required for leaf unfolding ($\alpha+\beta$) of the British provenance of *Fagus sylvatica* is of a similar magnitude to that of The Netherlands. The British provenance of *Larix decidua* appears to require a lower value of the state of forcing in the absence of chilling compared to the German provenance, which is mostly due to the differences of the value of β.

Uniform temperature increase scenario

Figures 3.3a and 3.3b present the results of the sequential and the alternating models, respectively, for the uniform climatic warming by -2 to +8°C on *Fagus sylvatica* in The Netherlands. The error bars cover 95% of the predicted values attributable to variation between the years ($n=57$ years). The sequential model predicts that the mean date of leaf unfolding will be advanced by 3.6 days per degree temperature change [Figure 3.3a(i)]. This results in the probability of potential frost damage decreasing by 0.08 per °C [Figure 3.3a(v) upper line]. The change in the date of leaf unfolding is the result of a shorter quiescence phase [Figure 3.3a(iv)] rather than a longer rest phase [Figure 3.3a(iii)], since these phases change with temperature at rates of -3.8 and 0.2 day per °C, respectively. Figure 3.3a(v) also presents the shift in the probability of potential frost damage when instead of 0°C, $T^*_{0.25}$ and $T^*_{0.10}$ are used as frost damage thresholds (Table 3.1). Based on Figure 3.3a(v) and similar figures prepared for all other species it was concluded that 0°C can be used as the threshold to evaluate the shift in frost damage with changing winter temperature for the sequential model.

The alternating model predicts a greater advancement of the mean date of leaf unfolding than the sequential model, namely 7.7 days per °C [Figure 3.3b(i)]. Even then, the probability of potential frost damage is found to decrease by 0.03 per °C [Figure 3.3b(v) upper line]. The state of chilling decreases by 16.9 d °C^{-1} with increasing temperature [Figure 3.3b(iii)]. Thus, an increasingly greater amount of state of forcing is required for leaf unfolding, namely 48.9 FU °C^{-1} more [Figure 3.3b(iv)]. This state of forcing is attained in fewer days, resulting in an earlier date of leaf unfolding. As the critical state of forcing required for leaf unfolding directly depends on the state of chilling, it cannot be decided whether the earlier date of leaf unfolding is caused by a slower accumulation of the chilling or by a faster accumulation of the forcing. The increase in the probability of potential frost damage for the higher temperature scenarios [Figure 3.3b(v)] is due to an increased variability of the minimal temperature around the date of leaf unfolding [Figure 3.3b(ii)]. Based on Figure 3b(v) and similar figures for all other species, it was concluded that, for the alternating model, 0°C can also be used as the threshold value to evaluate the effects of changing winter temperature on the probability of frost damage.

When similar figures were prepared for the other species in Germany and The Netherlands, in virtually all cases linear relations were found between the mean of the variables mentioned above and the temperature scenarios in the range T-2 to T+4. Therefore, linear regression was applied. The derivatives are presented in Tables 3.6 and 3.7 for the sequential and the alternating models, respectively, indicating the rate of change of the variable considered per degree temperature change. In Table 3.6, it can be seen that according to the sequential model, species differ in their response to uniform climatic warming. The shift in leaf unfolding ranges from about 1 to 6 days; however, for all species the probability of frost damage around the date of leaf unfolding is found to decrease. For most species, the duration of the rest period varied little with increasing temperature: however, exceptions are *Picea abies* and *Pinus sylvestris*, which have a relatively low R^2. This is the consequence of the broad range at which chilling is allowed to occur. Thus, given the parameter values obtained, the advancement in leaf unfolding found for all species is due to a shorter quiescence phase and a rather constant rest phase.

Figure 3.3 →. Results of temperature change of the Dutch temperature series by -2 to +8°C according to (a) the sequential model fitted to Dutch data on *Fagus sylvatica*, (b) the alternating model on the same data, and (c) the sequential model using parameter values derived for a generalised central Finnish tree species. U, date of leaf unfolding; T^*, minimum temperature around leaf unfolding; R, duration of rest period; Q, duration of quiescense period; S_c, state of chilling at leaf unfolding; S_f state of forcing at leaf unfolding; P, probability of frost damage around leaf unfolding, represented by: $P(T^*<0)$ (upper line), $P(T^* < T^*_{0.25})$ (middle line), and $P(T^*<T^*_{0.10})$ (lower line).

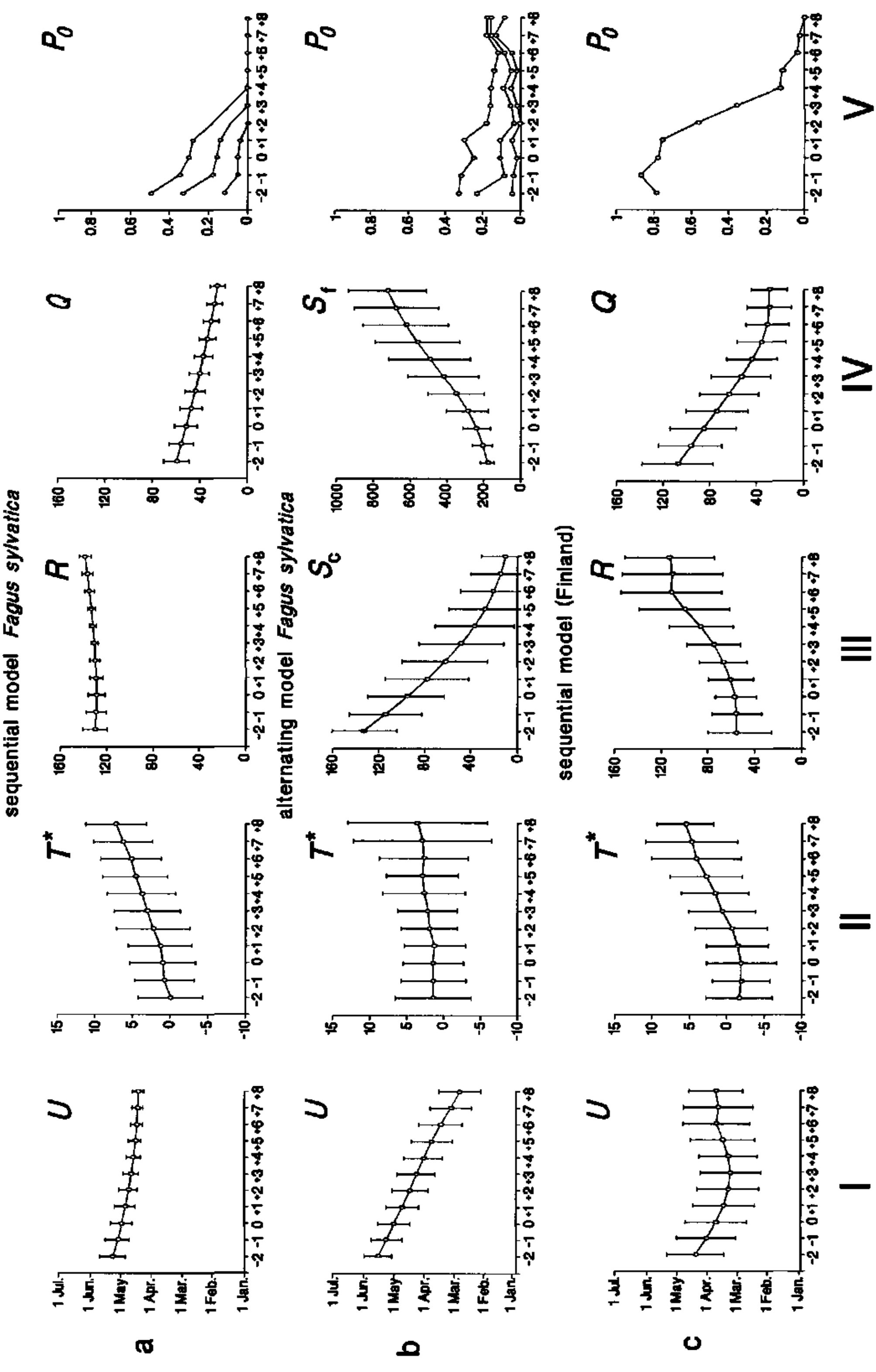
sequential model Fagus sylvatica
alternating model Fagus sylvatica
sequential model (Finland)
a
b
c
U
T*
R
Q
P0
Sc
Sf
I
II
III
IV
V
1 Jul.
1 Jun.
1 May
1 Apr.
1 Mar.
1 Feb.
1 Jan.
-2 -1 0 +1 +2 +3 +4 +5 +6 +7 +8

Table 3.6. Mean values of the date of leaf unfolding (U), probability of sub-zero temperature around the date of leaf unfolding (P_0), duration of rest period (R) and duration of quiescence period (Q) of the sequential model with the zero-change scenario, and their mean derivatives to temperature in the range T-2 to $T+4$. Plus the results of the hypothetical provenance transfer from central Finland to The Netherlands

species	U	$\delta U/\delta T$	P_0	$\delta P_0/\delta T$	R	$\delta R/\delta T$	Q	$\delta Q/\delta T$
Larix decidua (D)	16 Apr	-5.3	0.54	-0.10	101	0.4	65	-4.9
Betula pubescens (Nl)	22 Apr	-5.0	0.53	-0.08	119	1.2	54	-6.2
Betula pubescens (D)	20 Apr	-4.8	0.51	-0.09	105	1.2	64	-6.0
Tilia platyphylla (D)	25 Apr	-6.0	0.34	-0.06	103	0.5	73	-5.2
Fagus sylvatica (Nl)	1 May	-3.6	0.30	-0.08	129	0.2	52	-3.8
Fagus sylvatica (D)	28 Apr	-2.9	0.35	-0.08	128	0.5	50	-3.4
Tilia cordata (D)	1 May	-4.6	0.29	-0.05	116	0.2	66	-4.9
Quercus rubra (Nl)	3 May	-3.4	0.17	-0.09	127	3.5	57	-7.0
Quercus robur (D)	2 May	-3.4	0.27	-0.06	126	1.6	56	-4.9
Quercus robur (Nl)	6 May	-4.6	0.12	-0.06	125	0.8	61	-5.4
Fraxinus excelsior (D)	7 May	-2.6	0.17	-0.05	149	0.0	39	-2.6
Quercus petraea (Nl)	8 May	-4.3	0.08	-0.05	139	0.0	50	-4.1
Picea abies (D)	8 May	-1.9	0.20	-0.04	117	6.2	72	-8.1
Pinus sylvestris (D)	10 May	-1.1	0.15	-0.04	122	7.0	68	-8.1
(Finland)	22 Mar	-5.8	0.78	-0.11	57	4.9	86	-10.6

Comparing Tables 3.6 and 3.7 it can be seen that for all species the advancement in leaf unfolding is larger according to the alternating model than to the sequential model, namely about 4 to more than 8 days per degree. This shift in date of leaf unfolding is such that for all the species the probability of frost damage around the date of leaf unfolding remains virtually constant. Furthermore, it can be seen that the state of chilling and their rate of change with changing temperature is nearly constant in each country. Given the zero-change scenario, the number of days to leaf unfolding is 96-98 days and the

Table 3.7. Mean values of date of leaf unfolding (U), probability of sub-zero temperature around the date of leaf unfolding (P_0), state of chilling (S_c) and state of forcing at leaf unfolding (S_f) of the alternating model with the zero-change scenario, and their mean derivatives to temperature in the range T-2 to T+4. Plus the results of the hypothetical provenance transfer of the different species groups discerned by Murray et al. (1989) from northern Britain to The Netherlands

species	U	$\delta U/\delta T$	P_0	$\delta P_0/\delta T$	S_c	$\delta S_c/\delta T$	S_f	$\delta S_f/\delta T$
Larix decidua (D)	18 Apr	-7.8	0.48	-0.05	104	-15.1	179	35.1
Betula pubescens (NI)	22 Apr	-8.5	0.42	-0.01	96	-17.4	197	46.8
Betula pubescens (D)	21 Apr	-8.2	0.47	-0.04	104	-15.2	194	33.1
Tilia platyphylla (D)	27 Apr	-7.6	0.27	-0.03	105	-15.1	223	34.8
Fagus sylvatica (NI)	1 May	-7.7	0.25	-0.03	96	-16.9	241	48.9
Fagus sylvatica (D)	29 Apr	-5.8	0.25	-0.04	105	-15.1	233	45.8
Tilia cordata (D)	2 May	-7.0	0.19	-0.01	105	-15.1	253	38.7
Quercus rubra (NI)	6 May	-7.0	0.17	-0.02	97	-16.4	290	50.3
Quercus robur (D)	3 May	-5.9	0.18	-0.02	105	-15.1	260	45.4
Quercus robur (NI)	6 May	-8.7	0.14	-0.00	96	-16.9	241	48.9
Fraxinus excelsior (D)	8 May	-6.4	0.13	-0.02	105	-15.2	290	42.4
Quercus petraea (NI)	10 May	-7.1	0.04	-0.01	98	-16.1	302	52.3
Picea abies (D)	10 May	-6.4	0.10	-0.02	105	-15.2	290	42.4
Pinus sylvestris (D)	12 May	-4.2	0.10	-0.02	105	-15.2	321	61.5
Group 1 (UK)	12 May	-4.1	0.10	-0.04	96	-16.1	311	76.9
Group 2 (UK)	20 Apr	-9.6	0.48	-0.04	96	-16.2	200	43.3
Group 3 (UK)	27 Mar	-10.2	0.76	-0.06	91	-16.6	129	42.1
Group 4 (UK)	3 Mar	-10.3	0.84	-0.05	79	-16.3	102	39.1
Group 5 (UK)	14 Feb	-6.7	0.93	-0.06	68	-14.5	89	44.5

Group 1: *Fagus sylvatica*; group 2: *Robinia pseudoacacia, Tsuga heterophylla, Picea sitchensis*; group 3: *Rubus idaeus, Sorbus aucuparia, Betula pendula, Corylus avelana*; group 4: *Sambucus nigra, Rosa rugosa, Salix viminalis, Larix decidua, Prunus avium*; group 5: *Populus trichocarpa, Crataegus monogyna.*

rate of change 16 d °C^{-1} in The Netherlands, whereas the corresponding numbers are 104-105 days and 15 d °C^{-1} in Germany. This means that differences in the shift in date of leaf unfolding found between species are due to differences in the critical state of forcing that must be attained for leaf unfolding to occur.

Hypothetical provenance transfer

Hänninen (1990) estimated values for the parameters of the rate of chilling and the rate of forcing based on microscopic observations performed by Sarvas (1972, 1974) (Table 3.4). However, the chilling rate parameters were observed on a different species than the forcing rate parameters and should be considered as provenance characteristics of a generalised tree species. Following Hänninen (1991), F^* was varied between 50, 100, 150 and 200 FU, while C^* varied between 30 and 50 CU, with 28.361 forcing units per day as asymptote for the rate of forcing. Figure 3c show the results of the combination $C^*=30$ and $F^*=5.29$ (150/28.365) since these values were used in the analysis by Hänninen (1991) when scaling the rate of forcing between zero and unity. The results obtained are presented in the lower part of Table 3.6. The curves of the other seven combinations differ only in level and not so much in rate of change with changing temperature. For all combinations, the results showed an advancing date of leaf unfolding, an increasing minimal temperature around budburst for the $T+1$ to $T+4$ scenarios, thus a decreasing probability of frost damage, and a delay in budburst for $T+4$ to $T+8$ scenarios which was accompanied by decreasing probability of frost damage at budburst. Given these settings of C^* and F^*, the date of budburst is greatly advanced compared to the Dutch provenances, namely 22 March [Figure 3.3c(i)]. However, other settings of these thresholds alter this result. The decline in the probability of frost damage changes with other settings of C^* and F^*, but the overall pattern of a rapid decline does not. Due to the narrower temperature range for chilling, the length of the rest period increases more strongly [4.9 d °C^{-1}, Figure 3.3c(iii)] compared to the Dutch provenances. The Finnish values for the forcing rate parameters cause the duration of the quiescence phase to be more sensitive to changing temperature [-10.6 d °C^{-1}, Figure 3.3c(iv)] than the Dutch settings. Nevertheless, the rate at which the probability of frost damage around budburst decreases is of a similar magnitude [0.11 °C^{-1}, Figure 3.3c(v)] to that found for the Dutch provenances.

Murray et al. (1989) discerned 5 groups of species on the basis of similar temperature dependence of the rate of development during dormancy, and derived group parameter values for the alternating model. In Table 3.7, it can be seen that these groups do indeed respond differently when using these parameter values in combination with the Dutch temperature series. The groups 2-5 are likely to experience frost damage when transferred to The Netherlands. On the other hand, group 1, the British provenance of *Fagus sylvatica*, showed that when transferred to The Netherlands the date of budburst will be later than the date of leaf unfolding of the Dutch provenance of *Fagus sylvatica* (12 May versus 1 May). Furthermore, the advancement of the date of budburst of the British provenance of *Fagus sylvatica* is less than the advancement of the date of leaf unfolding of the Dutch provenance (4.1 versus 7.7 d °C^{-1}). Both of these effects are caused by the larger amount of state of forcing required for budburst of the British provenance for leaf unfolding than of the Dutch provenance, 76.9 and 48.9 FU, respectively. The state of chilling at budburst and the rate this changes with increasing temperature are the same for both provenances. A slow decrease in the probability of frost damage around budburst is found for all species groups. So according to the alternating model, given the Dutch temperature regime, the British provenances respond similarly to the Dutch provenances to a uniform change in temperature.

Both Murray et al. (1989) and Hänninen (1991) used the minimum daily temperature on the date of budburst to evaluate the probability of frost damage. When this one-day assessment was used for the Dutch and German temperature series considered here, the same qualitative results were obtained as when the minimum temperature in the 11-day period around the date of leaf unfolding was used, i.e. a reduced probability of frost damage with increasing temperature. Quantitatively, the shift in the probability of frost damage with uniformly changing temperature using the one-day method was more variable than the 11-day period method. In order to estimate the change in the probability in frost damage with changing temperature, the method using the 11-day period was found to be much more stable than the one-day method.

Non-uniform temperature increase scenario

In Table 3.8, the impacts are presented of the non-uniform temperature scenario of both the sequential and the alternating models on the day of leaf unfolding and the probability of frost damage. To compare these results with the uniform temperature increase scenario, the equivalent uniform temperature increase has been calculated as the weighted temperature increase in the period from 1 November to the predicted day of leaf unfolding according to the non-uniform temperature increase scenario. This equivalent uniform temperature increase is usually between 5.5 and 6.0°C, which is beyond the range where the uniform temperature change has a linear effect on both the date of leaf unfolding and the probability of frost damage: $[T\text{-}2, T+4]$.

Table 3.8 shows that the predicted date of leaf unfolding according to both models is a few days earlier with the uniform temperature increase compared to the non-uniform warming scenario. However, the probability of frost damage predicted by both models with the uniform warming scenario is somewhat less compared to the non-uniform warming scenario. This is because the temperature increase around the date of leaf unfolding is higher for the uniform warming scenario, i.e. 5.5 to 6.0°C, compared to the non-uniform warming scenario, i.e. 5.1°C in March and 4.4°C in April.

As was found with the uniform temperature increase scenarios (Tables 3.6 and 3.7), the alternating model predicts a larger advancement of the date of leaf unfolding than the sequential model. Consequently, the probability of frost damage is greater according to the alternating model than the sequential model. According to the sequential model the probability of frost damage will be sharply reduced in the Finnish 2 x CO_2 scenario compared to the zero scenario (Table 3.6). To a lesser extent the same is true for the alternating model (Tables 3.7 and 3.8).

No results are presented for *Picea abies* and *Pinus sylvestris* with the sequential model, because the chilling or the forcing requirements of these species were frequently not met, and consequently the date of leaf unfolding could not be predicted. Using a 5.5°C increase in mean winter temperature and the linear relationship between temperature and the date of leaf unfolding as found with the uniform temperature increase scenarios, *Picea abies* and *Pinus sylvestris* are expected to flush their needles on 28 April and 4 May, respectively, with a zero probability of frost damage for both species.

Table 3.8 also presents the results of the non-uniform warming scenario and equivalent uniform temperature increase scenario on the British and Finnish provenances using the Dutch temperature series. No results have been presented for group 5 because they are very variable. The same pattern was found as described earlier, i.e. an earlier date of leaf unfolding, but nevertheless, a reduced probability of frost damage.

Conclusions

For uniform and non-uniform climatic warming scenarios, the sequential and the alternating models both predict an increasing or constant minimum temperature around the date of leaf unfolding for German and Dutch provenances of *Larix decidua, Betula pubescens, Tilia platyphylla, Fagus sylvatica, Tilia cordata, Quercus rubra, Quercus robur, Fraxinus excelsior, Quercus petraea,*

Table 3.8. Mean values of leaf unfolding (U) and the probability of sub-zero temperature around the date of leaf unfolding (P_0) according to the non-uniform climatic warming scenario of Hänninen (1991), and to the uniform warming equivalent scenario of both the sequential and the alternating models

	Sequential model				Alternating model			
	Non-uniform		Uniform		Non-uniform		Uniform	
Species	U	P_0	U	P_0	U	P_0	U	P_0
Larix decidua (D)	24 Mar	0.09	22 Mar	0.06	6 Mar	0.40	5 Mar	0.36
Betula pubescens (Nl)	9 Apr	0.03	7 Apr	0.00	23 Mar	0.22	21 Mar	0.08
Betula pubescens (D)	2 Apr	0.03	31 Mar	0.03	4 Mar	0.36	3 Mar	0.36
Tilia platyphylla (D)	30 Mar	0.03	29 Mar	0.03	28 Feb	0.29	27 Feb	0.30
Fagus sylvatica (Nl)	19 Apr	0.00	16 Apr	0.00	20 Mar	0.19	19 Mar	0.11
Fagus sylvatica (D)	20 Apr	0.03	18 Apr	0.03	23 Mar	0.18	21 Mar	0.13
Tilia cordata (D)	15 Apr	0.05	12 Apr	0.02	21 Mar	0.17	19 Mar	0.13
Quercus rubra (Nl)	17 May	0.00	12 May	0.00	17 May	0.00	7 Jul	0.00
Quercus robur (D)	26 Apr	0.03	23 Apr	0.02	31 Mar	0.07	29 Mar	0.07
Quercus robur (Nl)	21 Apr	0.02	18 Apr	0.00	24 Mar	0.18	22 Mar	0.09
Fraxinus excelsior (D)	29 Apr	0.04	27 Apr	0.02	17 Mar	0.14	16 Mar	0.13
Quercus petraea (Nl)	24 Apr	0.00	22 Apr	0.00	27 Apr	0.00	11 Jun	0.00
Picea abies (D)					17 Apr	0.02	14 Apr	0.01
Pinus sylvestris (D)					2 May	0.03	27 Apr	0.02
Group 1 (UK)					9 Apr	0.00	8 Apr	0.00
Group 2 (UK)					13 Feb	0.30	12 Feb	0.30
Group 3 (UK)					3 Feb	0.42	2 Feb	0.45
Group 4 (UK)					23 Jan	0.45	27 Jan	0.46
Group 5 (UK)								
(Finland)	21 Mar	0.06	17 Mar	0.12				

Picea abies, and *Pinus sylvestris*. As a result, the probability of spring frost damage may decrease. The hypothetical provenance analysis showed that provenances of northern tree species respond to the Dutch temperature regime in a similar way to Dutch provenances. Thus, it can be concluded that the decreasing probability of frost damage with climatic warming holds over a wide range of parameter values for the sequential and the alternating models. Furthermore, both models agree that differences between species, in the advancement of the date of leaf unfolding with changing winter temperature, are attributable to differences in response to forcing temperature rather than to chilling temperature.

From the analysis done in the present study, it can be seen that the results obtained by of Murray et al. (1989), i.e. a declining probability of frost damage given climatic warming, and those of Hänninen (1991), i.e. an increasing probability of frost damage, are mutually consistent. If the sequential model were applied to the British species it could be expected that it would predict a smaller advancement of the date of budburst than the alternating model, consequently confirming the reduced probability of frost damage as found by Murray et al. (1989). Conversely, if the alternating model were applied to the Finnish species it could be expected that the alternating model would predict a greater advancement of the date of budburst compared to the sequential model, consequently confirming the increased probability of frost damage as found by Hänninen (1991). Moreover, the difference in results between the uniform and non-uniform warming scenarios is small for both models. Thus, the disparity between the results found by Murray et al. (1989) and Hänninen (1991) can be attributed to differences in response of tree species to the local climatic conditions.

This study further reveals that species differ in the frequency of freezing temperature around the date of leaf unfolding (Table 3.1), and in their response to a changing winter temperature (Tables 3.6 and 3.7). Species which unfold their leaves during the end of April appear to respond more strongly to temperature change than the species which unfold their leaves during the first weeks of May (Table 3.6). It can be expected that this affects competitive relationships between those species when grown in mixtures, because existing differences between species are enhanced by such a differential response.

Chapter 4

Phenotypic plasticity of the phenology of seven European tree species, in relation to climatic warming

Introduction

Trees species have adapted closely to their local climate by evolving certain phenological characteristics (Chabot and Hicks 1982; Reich, Walters and Ellsworth 1992; Kikuzawa 1989). The dormant period can be thought of as a strategy to avoid unfavourable circumstances (Woolhouse 1969; Levins 1969). *It is generally assumed that species of temperate and boreal zone* trees have optimally adapted to their local environment by minimising the occurrence of frost damage, while maximising the duration of the growing season (Lockhart 1983; Lechowicz 1984). These conflicting demands and the fact that frost hardiness is minimum during the onset and cessation of growth (Parker 1963; Levitt 1969; Fuchigami et al. 1982) make trees particularly susceptible to spring and autumn frosts. Temperature has been found to be the most efficient environmental signal for the tree to use for the optimal timing of the onset of growth (Häkkinen and Hari 1988). For the cessation of growth of northern trees, night length has been found to be the most efficient environmental signal to avoid autumn frost damage (Hänninen et al. 1990). However, Koski and Sievänen (1985) argued the importance of adaptation to variation between years, i.e. regulation by temperature, and to the long term average, i.e. regulation by photoperiod, with respect to the cessation of growth. The large body of literature supports the theoretical results of a temperature regulation for the onset of growth, and a combined regulation of temperature and photoperiod for the cessation of growth (Doorenbos 1953;

Samish 1954; Wareing 1956, 1969; Nitsch 1957a,b; Vaartaja 1959; Romberger 1963; Vegis 1964; Perry 1971).

Given the importance of temperature on the phenology of trees, climatic warming is likely to affect the timing of the onset and cessation of growth, causing tree species to be less closely adapted to their local environment. One effect of climatic warming may be an increased probability of frost damage (Cannell 1984; Cannell and Smith 1983; Murray, Cannell and Smith 1989; Cannell, Grace and Booth 1989; Hänninen 1991). These studies found that a much advanced date of leaf unfolding could lead to an increased occurrence of spring frost damage. Another effect of climatic warming may be an altered competitive balance between tree species, if species differ in their temperature response with respect to the onset and cessation of growth, and consequently in the duration of the growing season. These effects may influence the survival and eventually the distribution of trees, because of a lack of adaptation to an altered environment. Little adjustment can be expected from a change in the genetic composition of tree species by natural selection, if the climate changes within the life span of individual trees (Houghton, Jenkins and Ephraums 1990).

In addition to the adaptive significance of phenology as mentioned above, individual trees may posses the ability to respond phenotypically when its environment changes. Recently there is renewed interest in the adaptive and ecological significance of this phenotypic plasticity (Grime, Crick and Rincon 1986, Sultan 1992, Scheiner 1993, Via 1993) based on the review of Bradshaw (1965) who provided ample evidence that the plasticity of a character is an independent property and is under its own specific genetic control. If trees are plastic in their phenology with respect to temperature, they may accommodate temperature rise brought about by climate change.

To elucidate the phenotypic plasticity of tree species, research was done to answer the following questions: (1) can clones of tree species accommodate a change in their local environment? (2) what is the magnitude of the change of the duration of the growing season of clones of different tree species? (3) can the onset and cessation of the growing season be explained by the variables temperature and photoperiod? and (4) are there differences among clones of different tree species in the minimum temperature which occurs during the onset and cessation of the growing season?

Material and methods

Data

Two phenological data sets were analysed to find answers for the questions posed above. Firstly, the data set of the International Phenological Gardens (IPG). It contains observations of clones of many woody plant species that have been transferred over a large latitudinal and longitudinal distance (Figure 4.1). These data were used to represent the potential response of individual tree species to a change in their local climate. The second data set, from Germany, was from 14 phenological stations. It contains observations on local trees of some of the species in the IPG data set (Figure 4.1). Phenological differences found between these stations were used to represent the adaptive response of tree species to different climates. This made it possible to compare the magnitude of the phenotypic response to that of the adaptive response.

In 1958, Schnelle and Volkert (1957, 1974) set up a network of phenological gardens in Europe (Figure 4.1), for the study of the relationship between climate and the phenology of woody plants. Clones were used, to ensure that any differences found between the stations could not be attributed to specific responses of different genotypes. The selection of the stations, and the arrangement of the trees at a station were stipulated. To minimise observer error, detailed descriptions and pictures were supplied per species of the exact stage to be observed, and of preceding and succeeding stages. The observations started after the trees had attained a certain size and had sufficiently acclimatised to the site (Schnelle and Volkert 1967). The observations have been presented yearly since 1958 in *Arboreta Phaenologica*, together with full details on selecting and arranging stations, and the instructions for the phenological observations. More details on instructions for the phenological observations can be found in Schnelle (1966). The provenance of these clones was presented in Volkert and Schnelle (1968). In the present study, only the data on the date of leaf unfolding and the date of leaf fall were used. For convenience, the terms leaf unfolding and leaf fall were used for both deciduous and coniferous tree species. Each garden has three individuals of the same clone. Only yearly averaged values for each clone were available, therefore no intra-clone variation per year and per station could be estimated. The time span of the observations differs greatly between the species and between the stations, moreover, not all stations contain all species and all clones of the same species. Daily meteorological observations from 1955 to 1987 were available for 26 meteorological stations adjacent to 34 phenological stations (Figure 4.1) and at approximately the same altitude.

The time span with observations of the 14 German stations ranges from 1951 to 1990 for most species and stations, with few data lacking. Leaf unfolding was observed using the same description as for the clones; however, the date of leaf colouring was observed, instead of leaf fall. The IPG data set showed that there is a constant number of days between leaf colouring and leaf fall. The average duration of this period varies between 16.4 and 17.5 days, depending on the clone. Therefore, the leaf colouring data were converted to leaf fall by adding 17 days.

Factors influencing leaf unfolding and leaf fall

To evaluate the combined effect of temperature and photoperiod on leaf unfolding and leaf fall, models using temperature and day length as explanatory

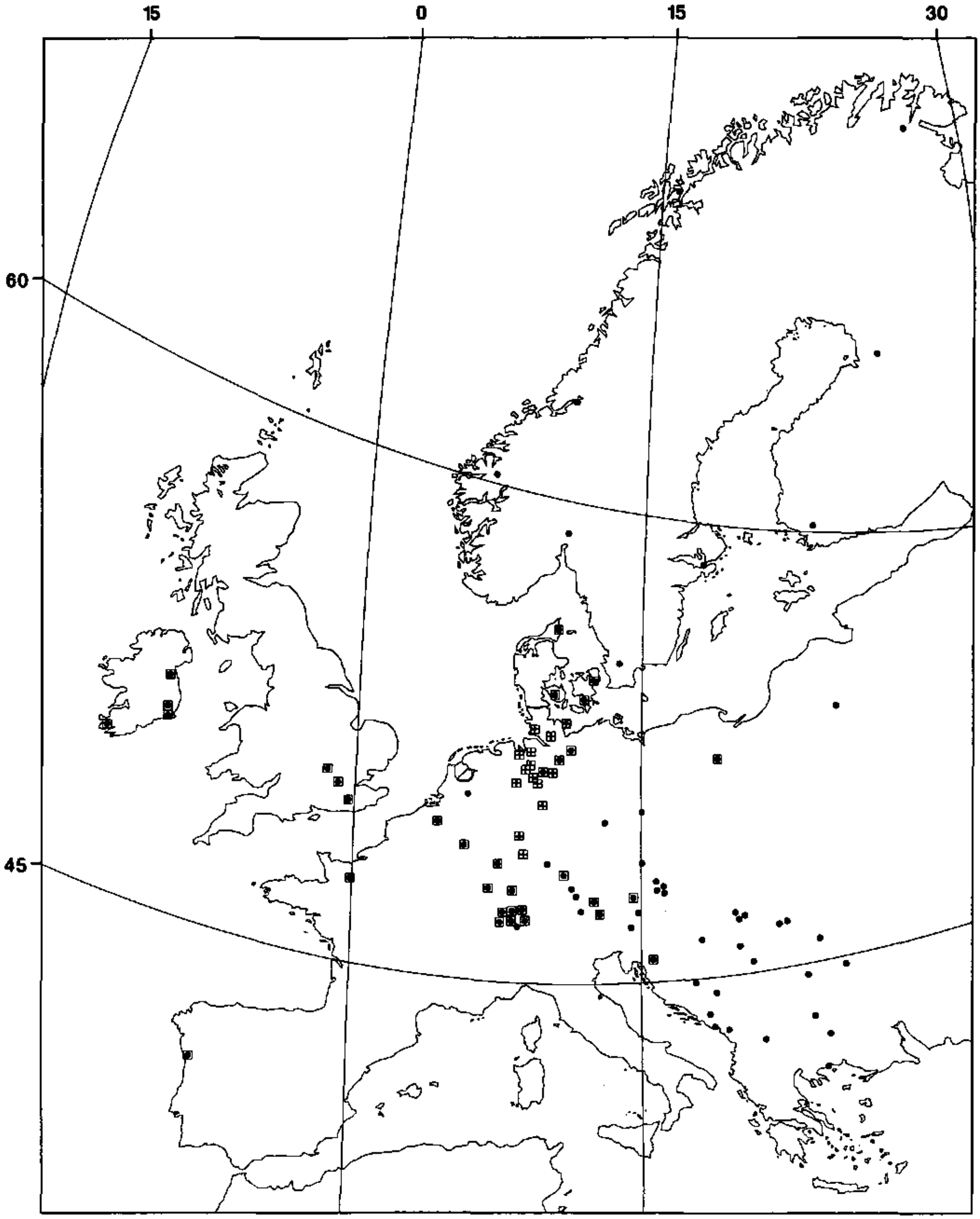

Figure 4.1. Location of the stations of the International Phenological Gardens (●) and the German stations (+) in Europe. A square around a symbol indicates that meteorological observations were available.

variables were tested. Both additive and multiplicative models of temperature and day length were used, with the aim of finding a model in which the integral over time attains a constant value at the date of leaf unfolding and leaf fall. The form of the temperature and photoperiod models is explained below.

To compare the response to temperature between tree species, the shift in leaf unfolding per degree mean winter temperature, and the shift in leaf fall per degree summer temperature were calculated. The mean winter temperature was calculated from the mean daily temperature from 1 November until the date of leaf unfolding, while the mean summer temperature was calculated from the mean daily temperature from 1 May until the date of leaf fall, thus splitting the year in half.

Once the effects of temperature on leaf unfolding and leaf fall are known, the effect of temperature on the duration of the growing season can be calculated. The duration of the growing season was defined as the cumulative day length between the date of leaf unfolding and leaf fall, and thus reflects the number of hours of exposure to light. The mean temperature during the growing season was calculated from the mean daily temperature from the date of leaf unfolding until the date of leaf fall. The day length at a given latitude and date was calculated according to Jones (1992).

Photoperiod

Other researchers have reported experimental results that indicate that an absolute photoperiod may trigger the date of leaf unfolding and of leaf fall for some species (Wareing 1956; Nitsch 1957a,b; Vaartaja 1959). If this is the case, then the response of clones of this species to the latitudinal transfer cannot be used to represent the response of an individual tree to a change in its local environment brought about by climate change. Therefore, the effect of photoperiod was evaluated by plotting the day length on the date of leaf unfolding versus the date of leaf unfolding, day length on the date of leaf fall, versus the date of leaf fall. If absolute day length triggers leaf unfolding or leaf fall, this day length will be the same at all stations.

For the evaluation of photoperiod on leaf unfolding the day length was accumulated from 1 November until the date of leaf unfolding. For leaf fall, the day length was accumulated from 1 May until the date of leaf fall.

Temperature

To analyse the effect of temperature on the timing of leaf unfolding and leaf fall, several dynamic models describing the rate of development during dormancy and the growing season were tested. For the timing of leaf unfolding, Sarvas (1974) considered two developmental phases during the dormant period of a bud.

Firstly, **rest**, during which the bud is susceptible to chilling temperatures (-5 to 15°C), and secondly, **quiescence**, during which the bud is susceptible to forcing temperatures (>0°C). Hänninen (1990) refined this concept and used a triangular function with temperature for the rate at which 'chilling units' are accumulated, and a logistic function with temperature for the rate at which 'forcing units' are accumulated (Figure 4.2). Forcing units are only accumulated after a critical number of chilling units have been accumulated during rest, thus triggering the onset of quiescence. Leaf unfolding is induced when a critical number of forcing units have accumulated. This model was called the sequential model because the accumulation of chilling and forcing units occurs sequentially in time (Kramer 1994a,b, Chapters 2 and 3).

The total response of the date of leaf unfolding to temperature can thus be broken down into a response induced by a change in the duration of the rest phase and the duration of the quiescence phase. The duration of the rest phase was defined as the number of days required to attain the critical number of chilling units, counted since 1 November, while the duration of quiescence was defined as the number of days from the onset of quiescence until

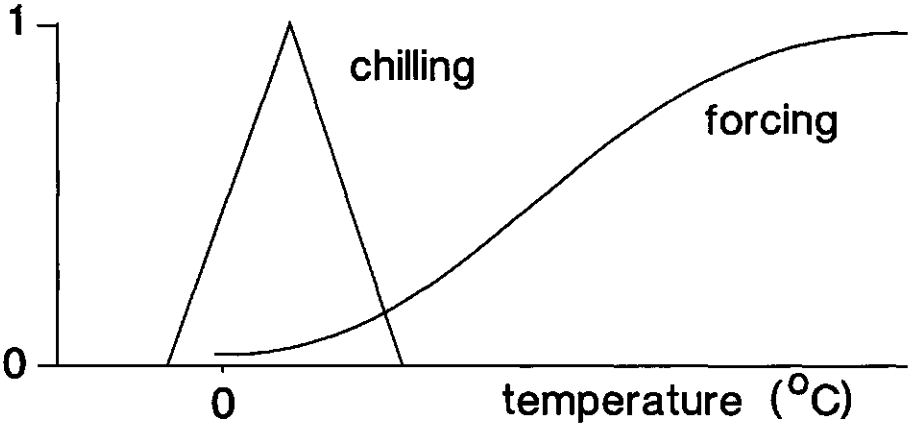

Figure 4.2. Rate of accumulating chilling units during rest (triangular), and forcing units during quiescence (truncated logistic), as a function of temperature.

the date of leaf unfolding. Simpler models to relate leaf unfolding to temperature were tested in addition to the accumulated temperature as formulated by the sequential model. These were the accumulated chilling temperature ($T<0°C$), the accumulated forcing temperature ($T \geq 0°C$), and linear combinations thereof, and also temperature sum models with different base temperatures and starting dates.

In contrast to the massive literature on dormancy and leaf unfolding, relatively little is known on leaf senescence and leaf fall. In general, the experimental findings indicate that there is a strong relationship between the timing of leaf fall and photoperiod, and that the timing of leaf fall may be mediated by temperature. In an attempt to relate temperature to the developmental processes leading to leaf fall, both the temperature sum and a logistic function were tested. The starting date for both temperature functions was set at 1 May.

Frost thresholds

The occurrence of frosts was evaluated using the lowest minimum daily temperature in a frost-susceptible period around leaf unfolding and leaf fall

(T^*). The frost-susceptible period around leaf unfolding was arbitrarily chosen as the period ranging from five days before to five days after leaf unfolding. Similarly, the period from five days before leaf fall until leaf fall was chosen for the frost susceptible period for leaf fall. When T^* is less than 0°C, frost damage may occur. The probability of frost (P_0) was defined as the fraction of years with freezing temperatures in the frost-susceptible period: $P_0 = P(T^* < 0°C)$.

The values of T^* around leaf unfolding and leaf fall of the clones may indicate the lowest temperature at which the clone can survive. This was analysed by calculating the values of P_0 around both leaf unfolding and leaf fall and comparing them between the clones and with the corresponding values for the genetically different trees of the same species. When the value of P_0 of the clone exceeds the value of the genetically different tree, then obviously the value of T^* does not represent a threshold below which the clone cannot survive. Conversely, when the value of P_0 of the clone is less than or equals the value of the genetically different tree of the same species, this suggests that T^* indicates a critical threshold.

Parameter estimation and statistical analysis

The parameter values required for the models were estimated using the Simplex method and Newton's method alternately, because it was found that this improves the fit. The algorithms for the Simplex method were obtained from Press et al. (1986), and those for Newton's method from the NAG FORTRAN Library (Anonymous 1990).

All statistical analyses were performed with the GENSTAT statistical package (Payne 1989). To evaluate the different models, the explained variance based on the mean sum of the square of the residuals and the total mean sum of squares (R^2-adjusted) was used. Variance components were estimated using the REML directive (restricted maximum likelihood). The statistics presented are significant at least at the 0.05 probability level. The variance components presented are the variance over the stations (s^2_s) and the variance over the years, within the stations, (s^2_y). In a balance design, the total variance would be $s^2_s + n\ s^2_y$. Here adjustments were made to use the correct value of n.

For both the estimation of the parameters for the models and the statistical analyses of a clone, only stations with at least five years with observations were used.

Results

General characteristics

Table 4.1 presents statistics of leaf unfolding, leaf fall and the duration of the growing season of the clones, ranked from an early to a late date of leaf unfolding. An indication of the total magnitude of the response to a change in the environment can be obtained by comparing the lowest and highest station means between the clones. An analysis of variance showed that there are statistically significant differences between the stations ($P \leq 0.001$) for all clones in terms of date of leaf unfolding, leaf fall, and the duration of the growing season. For all clones most of the variation in leaf unfolding is attributable to differences between the stations, while in nearly all clones most of the variation in leaf fall can be attributed to differences between years, within stations (Table 4.2). For the duration of the growing season the ratio of variance between stations to variance between years differs considerably between clones.

The effect of photoperiod on both leaf unfolding and leaf fall of the clones was evaluated graphically, by plotting the day length on the date of leaf unfolding versus the date of leaf unfolding, and the day length on the date of leaf fall versus the date of leaf fall, of all observations for each clone. Figures

Table 4.1. Overall mean (mn), lowest station mean (min) and highest station mean (max) of leaf unfolding, leaf fall (in daynumber: d) and the duration of the growing season (in hours: h) of the clones. Furthermore, the number of observations (n) and the number of stations with observations are given in brackets

	leaf unfolding				leaf fall				duration growing season			
	mn (d)	min (d)	max (d)	n	mn (d)	min (d)	max (d)	n	mn (h)	min (h)	max (h)	n
Larix decidua	109	89	130	546 (40)	315	284	329	450 (32)	2871	2555	3149	400 (21)
Betula pubescens	113	76	154	1109 (62)	303	287	342	963 (58)	2678	1972	3090	885 (43)
Tilia cordata	116	84	151	735 (51)	297	272	318	596 (48)	2534	1854	2804	513 (34)
Populus canescens	121	88	163	1156 (65)	297	265	343	609 (53)	2526	1968	3067	505 (30)
Quercus robur (early)	121	91	150	373 (39)	311	293	338	243 (30)	2668	2331	3177	171 (11)
Quercus robur (late)	121	92	144	397 (39)	311	267	337	267 (30)	2664	2324	3154	190 (13)
Fagus sylvatica (early)	123	104	144	663 (50)	300	253	324	407 (43)	2521	1950	2736	317 (21)
Fagus sylvatica (middle)	125	98	141	571 (45)	306	253	324	340 (36)	2536	2296	2705	249 (15)
Fagus sylvatica (late)	127	98	141	494 (42)	302	253	325	274 (33)	2461	2211	2633	195 (13)
Picea abies (early)	127	98	161	1207 (67)								
Picea abies (late)	133	104	178	1175 (67)								
Picea abies (northern)	136	103	177	1126 (65)								

4.3 and 4.4 present the results for *Betula pubescens*, one of the most variable clones, and the early clone of *Fagus sylvatica*, the least variable clone. Cleary, neither leaf unfolding nor leaf fall occur at a constant day length at any station. Similar figures were obtained for the other clones. Therefore it was concluded that there is no single photoperiod threshold that triggers either leaf unfolding or leaf fall in any of the clones.

Response of leaf unfolding, leaf fall and duration of the growing season to temperature

The relationships between the mean winter temperature versus the date of leaf unfolding, and between the mean summer temperature versus the date of leaf fall are shown in Figure 4.5 for the clone of *Betula pubescens* and in

Table 4.2. Variance components between stations (s^2_s) and between years (s^2_y) of leaf unfolding, leaf fall and the duration of the growing season of the clones

	leaf unfolding		leaf fall		duration growing season	
	s^2_s (d²)	s^2_y (d²)	s^2_s (d²)	s^2_y (d²)	s^2_s (h²)	s^2_y (h²)
Larix decidua	115.0	104.0	82.4	110.8	19517	24383
Betula pubescens	199.3	94.4	55.0	118.9	35771	26849
Tilia cordata	151.9	76.7	95.0	129.9	36028	28967
Populus canescens	226.2	93.2	140.0	138.5	49893	34303
Quercus robur (early)	141.1	70.8	73.2	151.2	45508	26653
Quercus robur (late)	117.7	76.6	90.0	137.0	41423	20941
Fagus sylvatica (early)	72.4	51.7	94.3	137.6	29725	20807
Fagus sylvatica (middle)	71.1	40.1	73.9	169.3	10787	15789
Fagus sylvatica (late)	68.1	40.3	126.3	145.6	17844	17250
Picea abies (early)	194.4	79.1				
Picea abies (late)	205.2	65.8				
Picea abies (northern)	202.2	76.4				

Figure 4.6 for the early clone of *Fagus sylvatica*. Table 4.3 presents the statistics of linear regressions through these data for all clones. It appears that for most species an increase in temperature advances the dates of both leaf unfolding and of leaf fall.

This phenomenon has an opposite effect on the duration of the growing season: an advanced leaf unfolding increases the duration of the growing season, whereas an advanced leaf fall decreases it. Whether the duration of the growing season changes, depends on the magnitude of the change of leaf unfolding and leaf fall with temperature, and on the day length. As shown in Figures 4.3 and 4.4, more hours of light are gained when leaf unfolding occurs one day earlier, than are lost when leaf fall occurs one day earlier. Table 4.3 shows that for *Larix decidua* and both clones of *Quercus robur* the response

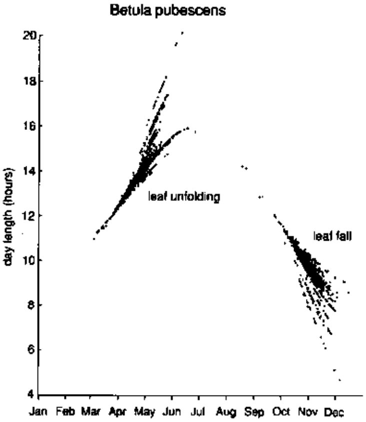

Figure 4.3. Day length on the date of leaf unfolding versus the date of leaf unfolding, and day length on the date of leaf fall versus the date of leaf fall of *Betula pubescens*.

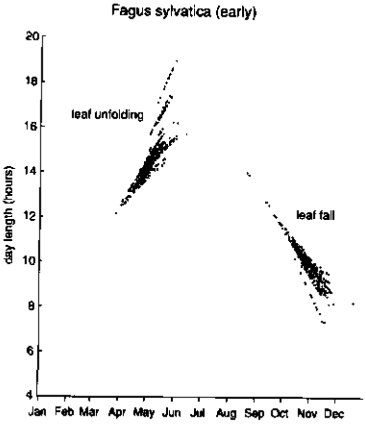

Figure 4.4. Day length on the date of leaf unfolding versus the date of leaf unfolding, and day length on the date of leaf fall versus the date of leaf fall of the early clone of *Fagus sylvatica*.

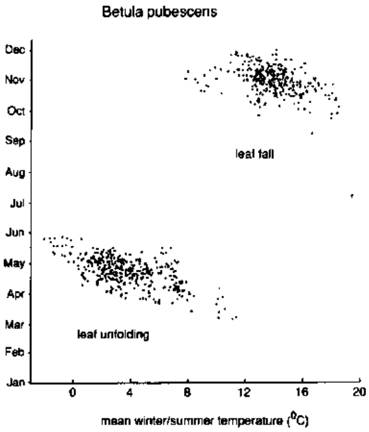

Figure 4.5. Date of leaf unfolding versus mean winter temperature, and date of leaf fall versus mean summer temperature of *Betula pubescens* (x-axis has two meanings).

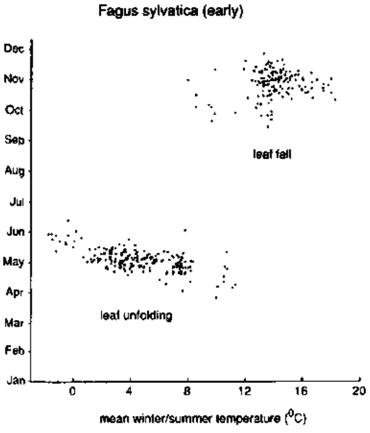

Figure 4.6. Date of leaf unfolding versus mean winter temperature, and date of leaf fall versus mean summer temperature of the early clone of *Fagus sylvatica* (x-axis has two meanings).

Table 4.3. Slopes of the linear regression of leaf unfolding on mean winter temperature ($\delta U/\delta T_w$), leaf fall on mean summer temperature ($\delta F/\delta T_s$) and the duration of growing season on mean temperature during the growing season ($\delta G/\delta T_g$) of the clones. R² indicates the variance explained by the linear model, se the standard error of the slope, and n the number of observations

	leaf unfolding				leaf fall				duration growing season			
	$\delta U/\delta T_w$ (d °C^{-1})	R² (%)	se (d)	n	$\delta F/\delta T_s$ (d °C^{-1})	R² (%)	se (d)	n	$\delta G/\delta T_g$ (h °C^{-1})	R² (%)	se (h)	n
Larix decidua	-2.8	10	0.60	181	-8.5	40	0.85	151	-85	18	-15.5	149
Betula pubescens	-3.7	37	0.24	401	-3.0	17	0.35	344	-27	4	-7.0	339
Tilia cordata	-2.8	24	0.29	306	-1.4	3	0.52	232	19	2	9.3	225
Populus canescens	-3.0	23	0.27	418	-3.8	13	0.61	262	-76	19	-10.1	258
Quercus robur (early)	-2.1	9	0.55	134	-7.2	36	1.00	91	-121	35	-19.8	90
Quercus robur (late)	-1.7	5	0.67	99	-5.6	19	1.28	79	-66	19	-17.4	76
Fagus sylvatica (early)	-2.5	39	0.21	215		(ns)		149	42	12	9.9	148
Fagus sylvatica (middle)	-2.4	34	0.23	208	-2.6	6	0.79	149	-33	11	-8.3	147
Fagus sylvatica (late)	-2.3	31	0.26	179		(ns)		123		(ns)		121
Picea abies (early)	-3.5	30	0.26	413				0				0
Picea abies (late)	-4.0	35	0.27	419				0				0
Picea abies (northern)	-3.3	29	0.26	408				0				0

of leaf fall to temperature is greater than the response of leaf unfolding, resulting in a shorter growing season. For *Betula pubescens* and *Populus canescens* the advancement of leaf unfolding is of a similar magnitude, while for *Tilia cordata* and *Fagus sylvatica* the date of leaf fall appears unaltered, whereas the date of leaf unfolding advances with increasing temperature (Table 4.3).

Table 4.4 shows that the genetically different trees of *Betula*, *Tilia*, *Quercus* and *Fagus* advance leaf unfolding less than the clones do (Table 4.3). For *Larix* the opposite is true, while the response of *Picea* differs greatly between

Table 4.4. Slopes of the linear regression of leaf unfolding on mean winter temperature ($\delta U/\delta T_w$), leaf fall on mean summer temperature ($\delta F/\delta T_s$) and the duration of growing season on mean temperature during the growing season ($\delta G/\delta T_g$) of the genetically different trees. R², variance explained by the linear model; se, standard error of the slope; n, number of observations

	leaf unfolding				leaf fall				duration growing season			
	$\delta U/\delta T_w$ (d °C^{-1})	R² (%)	se (d)	*n*	$\delta F/\delta T_s$ (d °C^{-1})	R² (%)	se (d)	n	$\delta G/\delta T_g$ (h °C^{-1})	R² (%)	se (h)	n
Larix decidua	-3.3	11	0.45	435				0				0
Betula pubescens	-2.6	7	0.43	471	-4.0	7	0.66	459	-58	21	5.4	447
Tilia cordata	-1.3	2	0.44	384				0				0
Quercus robur	-1.4	2	0.41	466	-4.8	13	0.57	461	-49	19	4.8	448
Fagus sylvatica	-2.0	7	0.34	458	-3.7	9	0.56	446	-31	9	4.5	440
Picea abies	2.6	5	0.72	222				0				0

the clones and the genetically different trees. The genetically different trees also show a larger advancement of leaf fall with mean summer temperature than leaf unfolding with mean winter temperature, as was found for the clones. The low values of the explained variances indicate that the magnitude of the response may not have been reliably estimated possibly because the data on the genetically different trees cover a smaller latitudinal range, and thus a smaller temperature gradient, than the data on the clones (Figure 4.1). In general it can be concluded that the response of the clones to temperature is the same magnitude or greater than, the response of the genetically different trees of the same species.

Models

To analyse the temperature response of the date of leaf unfolding, one set of parameter values required for the sequential model was found for each clone. However, the criterion for a globally optimal parameter set was not met. Table 4.5 presents the explained variance of leaf unfolding with sequential model. All simpler temperature models tested (see section Material and methods) had lower explained variances. Linearly additive and multiplicative combinations of the sequential model and photoperiod did not increase the explained variance. To evaluate the impacts of climatic warming on the phenology of trees, the model should represent the temperature dependence accurately. To evaluate this, the model output was regressed against mean winter temperature. The sequential model systematically overestimates the shift in leaf unfolding with mean winter temperature (Tables 4.3 and 4.5), by 0.5 to 1.9 days $°C^{-1}$.

This temperature response of leaf unfolding is the result of a change in the duration of both the rest and quiescence phases. Figures 4.7 and 4.8 show that these phases do not necessarily respond linearly to temperature. For the late clone of *Fagus sylvatica* an increase in mean winter temperature in the range 0°C to 4°C increases the rate at which chilling units are accumulated. Consequently, the critical amount of chilling to induce quiescence is attained earlier and the duration of the rest phase is shortened. The rate at which forcing units are accumulated does not keep pace. Thus the critical number of forcing units is attained later, resulting in a longer duration of the rest phase.

In the range from 4°C to 12°C of the mean winter temperature, the rate of accumulating chilling units decreases, thus lengthening the duration of the rest phase, whereas the rate of accumulating forcing units increases more sharply, thus shortening the duration of the quiescence phase. Other patterns of the duration of the rest and quiescence phase were also found. For example, with increasing mean winter temperature the late clone of *Picea abies*

Table 4.5. Slope of the linear regression of leaf unfolding predicted by the sequential model on mean winter temperature ($\delta U/\delta T_w$). R^2, variance explained by the linear model; se, standard error of the slope

	leaf unfolding		
	$\delta U/\delta T_w$ (d °C^{-1})	R^2 (%)	se (d)
Larix decidua	-4.4	66	0.53
Betula pubescens	-4.5	56	0.20
Tilia cordata	-3.3	67	0.25
Populus canescens	-3.5	70	0.22
Quercus robur (early)	-4.0	45	0.54
Quercus robur (late)	-2.6	41	0.49
Fagus sylvatica (early)	-2.6	58	0.15
Fagus sylvatica (middle)	-2.7	56	0.12
Fagus sylvatica (late)	-3.0	27	0.23
Picea abies (early)	-4.1	63	0.17
Picea abies (late)	-4.8	66	0.17
Picea abies (northern)	-3.5	59	0.20

shows a virtually constant duration of the rest phase and a shorter quiescence phase. For some other clones a monotonous decrease was found in the duration of both the rest and quiescence phases. The sequential model thus explains a linear shift of the date of leaf unfolding with temperature in terms of different underlying patterns. Experiments should be done to test whether these patterns truly reflect the characteristics of the clones.

For the cessation of growth, both a linear and a logistic function of the rate of development with temperature were tested. The linear model was the thermal time model. The optimal base temperature out of a range -2 to +8°C was 0°C for all species. This model explained 0 to 5% of the variation observed, depending on the species. The logistic model, also with 0°C as base tempera-

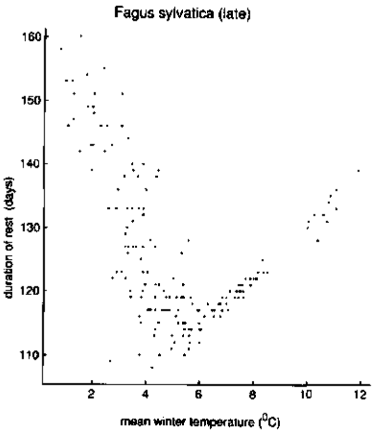

Figure 4.7. Duration of the rest period versus mean winter temperature of the late clone of *Fagus sylvatica*.

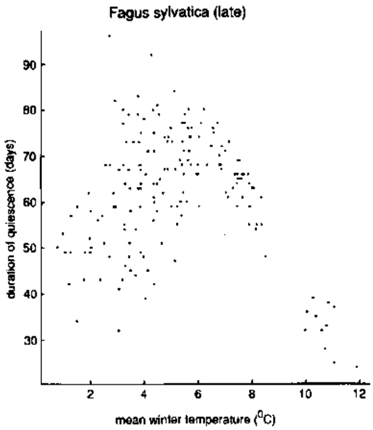

Figure 4.8. Duration of the quiescence period versus mean winter temperature of the late clone of *Fagus sylvatica*.

ture, performed little better, and for some clones worse. Linearly additive and multiplicative combination of both temperature model and photoperiod could not improve the results. For most clones the optimal parameter set found yielded approximately the average date of leaf unfolding, with very little variation around this date. Therefore, it was concluded that the null model, i.e. the mean date of leaf fall, is the best and simplest model to describe the date of leaf fall. Since in this case the residual mean square equals the total mean square, the variance explained by the null model equals zero. Furthermore, the null model cannot explain the shift in leaf fall that accompanies increasing summer temperature.

Frost thresholds

Table 4.6 shows that the clones differ in the lowest temperature observed in the frost-susceptible period around leaf unfolding and before leaf fall. The variance components indicate that for both leaf unfolding and leaf fall most of the variation of this temperature can be attributed to differences between the years, rather than to differences between stations (Table 4.6).

Table 4.6. Lowest daily minimum temperature in the frost susceptible period (T^*) around leaf unfolding and before leaf fall. Mean (mn), standard deviation (sd), and variance components between stations (s^2_s) and between years (s^2_y). *r* indicates the rank order of leaf fall from early to late (see Table 4.1)

	leaf unfolding				leaf fall				
	mn (°C)	sd (°C)	s^2_s (°C²)	s^2_y (°C²)	mn (°C)	sd (°C)	s^2_s (°C²)	s^2_y (°C²)	*r*
Larix decidua	-0.2	2.41	0.7	5.3	-1.9	3.67	3.4	11.0	7
Betula pubescens	0.5	2.59	2.6	4.6	-0.1	3.76	7.9	8.3	4
Tilia cordata	1.8	2.66	1.8	5.4	1.1	4.17	7.4	9.2	1
Populus canescens	2.1	2.56	1.4	5.3	1.2	3.97	5.6	10.4	1
Quercus robur (early)	1.8	2.57	(ns)	6.8	-2.3	3.59	1.4	11.6	6
Quercus robur (late)	1.7	2.50	0.6	5.7	-1.5	2.86	0.6	7.6	6
Fagus sylvatica (early)	1.5	2.55	1.7	5.0	0.8	4.05	6.2	9.8	2
Fagus sylvatica (middle)	2.5	2.65	1.2	5.8	-0.1	4.22	6.7	11.1	5
Fagus sylvatica (late)	2.5	2.47	1.0	5.2	0.0	4.02	6.1	9.5	3
Picea abies (early)	2.1	2.63	1.9	5.2					
Picea abies (late)	3.1	2.78	2.6	5.4					
Picea abies (northern)	3.4	2.81	2.2	5.9					

Table 4.7 shows that the probability of frost around leaf unfolding for the clones is less (*Betula*), or similar to that of the genetically different trees. For the probability of frost before leaf fall there seems to be no clear pattern in the difference between the clones and the genetically different trees (Table 4.7). Similar results were obtained when the definition of the frost-susceptible period around leaf unfolding and before leaf fall was altered. For example when

U-5 to *U*+25 is chosen as the frost-susceptible period around leaf unfolding (*U*), the numbers in Table 4.7 alter somewhat but the results are qualitatively the same. The results presented in Table 4.6 remain virtually the same. The same is true when the duration of the frost-susceptible period before leaf fall is increased.

Table 4.7. Probability of freezing temperature during frost susceptible period around leaf unfolding and before leaf fall of the clones (*c*) and the genetically different trees (*g*)

	leaf unfolding		leaf fall	
	c	*g*	*c*	*g*
Larix decidua	0.47	0.54	0.50	
Betula pubescens	0.37	0.51	0.33	0.14
Tilia cordata	0.27	0.29	0.23	
Populus canescens	0.21		0.27	
Quercus robur (early)	0.27	0.27	0.48	0.32
Quercus robur (late)	0.23		0.44	
Fagus sylvatica (early)	0.31	0.30	0.20	0.33
Fagus sylvatica (middle)	0.17		0.32	
Fagus sylvatica (late)	0.17	0.27		
Picea abies (early)	0.19	0.20		
Picea abies (late)	0.14			
Picea abies (northern)	0.13			

Discussion

Due to the longevity of trees and the projected rapid change of the climate (Houghton et al. 1990) it can be hypothesised that currently growing trees will not be adapted to their future environment (Botkin and Nisbet 1992). However, it is now being recognised that the plasticity of a character is under genetic control and is subject to natural selection in it self (Sultan 1992;

Scheiner 1993). Furthermore, plasticity plays an important ecological role in both the control of reproductive effort and the capture of resources from the environment (Grime et al. 1986). Thus both the adaptive and the ecological significance of phenotypic plasticity are a central aspect of the integration of a phenotype in its natural environment and need to be considered if its local environment changes due to a human induced climate change. The results of this study indicate that the phenotypic response of both leaf unfolding and leaf fall to temperature of the clones is of a similar magnitude as the adaptive responses of genetically different trees (Tables 4.5 and 4.6). It may be expected that when the temperature experienced by an individual tree increases, the tree has a certain amount of plasticity to accommodate such a change. This opposes the findings of Billington and Pelham (1991) who concluded that for *Betula pubescens* and *B. pendula* there is insufficient genetic and phenotypic variation to meet the selection potential as projected by Cannell and Smith (1986) for Scotland. Their projected advancement of budburst, 40 days given a 2°C increase in winter temperature is, however, large compared to the data presented in this study.

In the present study it was found that for clones of *Larix decidua* and *Quercus robur* the magnitude of the advancement of leaf fall with increasing summer temperature may be larger than that of leaf unfolding with increasing winter temperature (Table 4.3). The overall result of a rising temperature is then a shorter growing season. For clones of *Tilia cordata* and *Fagus sylvatica*, the date of leaf unfolding advances, while the date of leaf fall stays essentially the same, thereby increasing the duration of the growing season. Consequently, growth is expected to be differently affected by a rise in temperature, and this will affect the competitive abilities of these species when grown in mixture. However, to be conclusive on the differential impacts of climate change on growth, the possible differences between tree species in the direct effect of CO_2 on photosynthesis has to be taken into account as well.

The descriptive dynamic models showed that the main part of the variance of date of leaf unfolding can be accounted for by the sequential model, using only temperature. However, it was very difficult to account for the variance in the date of leaf fall with models containing temperature and photoperiod as explanatory variables. This may be because most of the variability in leaf fall can be attributed to variations in the local environment (Table 4.2). Thus, environmental factors other than temperature and photoperiod are likely to influence the date of leaf fall as well.

The data analysed in this study support the hypothesis that the survival of the clones was curtailed by frost occurring around the date of leaf unfolding. This is based on the findings that: (1) the probability of frosts around leaf unfolding of the clones does not exceed that of the genetically different trees of the same species (Table 4.7), (2) this probability of frost is relatively constant over a wide range of temperature regimes (Table 4.6), whereas (3) the date of leaf unfolding is not (Table 4.3). These results indicate that for leaf unfolding the survival of these clones could be determined by freezing temperatures below T^* during the frost susceptible period. However, this could not be derived from the data because no systematic reports on survival were available. For leaf fall the relationship with the occurrence of frost is not clear, and could also be due to other factors such as respiratory costs outweighing photosynthetic gains.

Thus, by evaluating the relationship between temperature and leaf unfolding and leaf fall, both the direct effects of the climatic warming (frost damage), and indirect effects (competitive ability), are accounted for. This makes leaf unfolding and leaf fall, and the frost hardiness attained at these points in time, particularly sensitive characteristics for evaluating climatic warming. In other studies, (e.g. Sakai and Weiser 1973; George et al. 1974) the geographical distribution of trees was found to be closely correlated to the lowest winter temperature. However, more detailed information is required for the evaluation of the impact of climatic warming on the areas of species, for two reasons.

Firstly, because species in the same physiognomic class are generally resistant to the same lowest winter temperature (Sakai and Larcher 1987; Woodward 1987). Secondly, when the lowest winter temperature rises, a shift in area will be due to a shift in competitive abilities, and cannot be due to differences in frost hardiness during dormancy. Thus, the correlation between the area of a species and the lowest winter temperature may be less appropriate for evaluating the impacts of climatic warming on species areas because it does not represent an altered competitive balance between species.

Chapter 5

Modelling comparison to evaluate the importance of phenology for the effects of climate change on growth of temperate-zone deciduous forests

Introduction

As a result of natural selection, the annual biological cycle of the growth and dormancy of trees is synchronised to the annual climatic cycle of light, temperature and precipitation, thus determining growth. If the climate changes within the life span of a tree, this synchronization may be partly lost. Consequently, either a part of the growing period of a tree may occur when the climate is not favourable for growth, or the growing period may not fully exploit the period when the climate is favourable for growth. On the other hand, the species may be able to adjust by phenotypic plasticity. Earlier studies have predicted, that based on climate change scenarios, the probability of spring frost damage is likely to decrease in temperate zone Europe (Kramer 1994b, Chapter 3; Murray et al. 1989). It has also been found that trees do possess a considerable plasticity to accommodate a change in their local environment phenotypically (Kramer 1995a, Chapter 4). The aim of the study reported in this chapter was to evaluate the importance of differences in phenological response to temperature for the effects of climate change on the growth of deciduous, temperate-zone tree species. Two models of photosynthesis and two models of allocation were compared, to elucidate the consequences of describing these processes with different levels of mechanistic detail.

In an earlier study, three phenological patterns induced by a structural rise in temperature were found: (1) a similar advance of both leaf unfolding and leaf fall, (2) an advance of leaf unfolding, but no change in leaf fall, and (3) a larger advance of leaf fall than leaf unfolding (Kramer 1995a, Chapter 4). These three phenological types correspond to *Betula*, *Fagus*, and *Quercus*, respectively.

Models incorporating detailed descriptions of light interception, photosynthesis, respiration and allocation are required to evaluate the effects of climate change on growth of deciduous trees. The models compared in this study were: (1) FORGRO (Mohren 1987, 1994) using the descriptions of photosynthesis of Goudriaan et al. (1985) and fixed keys for allocation, (2) FORGRO coupled to PGEN (Friend 1993), substituting the biochemical photosynthesis model of Farquhar and Von Caemmerer (1982) for the photosynthesis model, and (3) FORGRO coupled to the ITE-Edinburgh model (Thornley 1991), in which the allocation keys of FORGRO are replaced by the transport-resistance approach of partitioning.

Two aspects of climate change and growth of deciduous trees were studied through model comparison: (1) the consequences of the phenological types on the effects of climate change scenarios on gross photosynthesis, and (2) the sensitivity of the scenario-induced response of gross photosynthesis to a change in parameter values of the models.

Material and methods

Phenology

To avoid inaccuracies in the date of both leaf unfolding and leaf fall in the analysis of the species response to the different scenarios, historical phenological observations for a 14-year period were used. Phenological observations of *Betula pubescens*, *Fagus sylvatica* and *Quercus robur* in The Netherlands were available for every year from 1940 until 1953, except for 1945. For 1945 the average value of the phenological events was used. The phenological events monitored were leaf unfolding, full leaf and leaf fall. The observers had been provided with detailed instructions for each species, including pictures, of the exact event to observe, and instructions on how to select the trees (Anonymous 1950). The shifts of these events with either mean winter or summer temperature, based on an extensive data set containing phenological observations of clones relocated over a large latitudinal throughout Europe (Kramer 1995a, Chapter 4), are presented in Table 5.1. When the temperature was increased according to a scenario, the observed dates of leaf unfolding, full leaf and leaf fall were adjusted according to the known responses of *Betula, Fagus* and *Quercus* (Table 5.1). The shift in full leaf with winter temperature was assumed to be similar to leaf unfolding.

Scenarios

Daily meteorological measurements for the period 1940 to 1953 were available for De Bilt (52°N, 6°E), located in the centre of The Netherlands, and used as input to the models. In all calculations, this series was adjusted according to a scenario. The variable evaluated was the annual rate of gross photosynthesis, $P_{g,a}$ (t CH_2O ha^{-1} yr^{-1}), averaged over the simulation period.

To evaluate the importance of phenology, the CO_2 concentration was set at 700 μmol mol^{-1}, and the temperature was increased uniformly by a maximum of 7°C in steps of 1°C. The benchmark scenario (no change in temperature) was also examined. The response of $P_{g,a}$ for *Betula, Fagus* and *Quercus* to these scenarios was calculated according to the three models. The results were expressed relative to the scenario with $[CO_2]$ = 350 μmol mol^{-1}, without an increase in temperature.

The sensitivity of the response of $P_{g,a}$ to a change of ±25% in parameter value was evaluated by comparing the response to the scenario with $[CO_2]$ = 700 μmol mol^{-1} and a uniform 2°C rise in temperature with the reference scenario with $[CO_2]$ = 350 μmol mol^{-1} and no increase in temperature.

These scenarios will be referred to as C_{700}/T_2 and C_{350}/T_0, respectively. The phenology of *Betula* (Table 5.1) was used for this analysis.

Table 5.1. Phenological characteristics of *Betula*, *Fagus* and *Quercus*. *U*, average date of leaf unfolding; *G*, date of the stage full leaf; *F*, date of leaf fall; $\delta U/\delta T_w$, change in date of leaf unfolding with mean winter temperature (T_w, 1 November until leaf unfolding); $\delta G/\delta T_w$, change in date of full leaf; $\delta F/\delta T_s$, change in date of leaf fall with mean summer temperature (T_s, 1 May until leaf fall). *I*, average cumulative irradiance from date of leaf unfolding to date of leaf fall, in The Netherlands (MJ m^{-2} growing season^{-1}); $\delta I_U/\delta T_w$ change in *I* caused by advancement of leaf unfolding (MJ °C^{-1}), $\delta I_F/\delta T_s$, change in *I* caused by advancement of leaf fall (MJ °C^{-1})

	Betula	*Fagus*	*Quercus*
U	22 April	1 May	5 May
G	2 May	8 May	15 May
F	4 October	16 October	20 October
I	2504	2468	2413
$\delta U/\delta T_w$	-3	-2	-2
$\delta G/\delta T_w$	-3	-2	-2
$\delta I_U/\delta T_w$	44 (1.8%)	28 (1.1%)	32 (1.3%)
$\delta F/\delta T_s$	-3	0	-5
$\delta I_F/\delta T_s$	-24 (-1.0%)	0 (0%)	-28 (-1.1%)

Models

Three models with different levels of detail of photosynthesis and allocation were used, i.e. FORGRO, PGEN and the ITE-Edinburgh model. Briefly, FORGRO (Mohren 1987, 1994) is a process-based model suitable for predicting the growth of an even-aged monoculture of coniferous tree species. The photosynthesis-light response curve is modelled using a negative exponential function. An increase in the external CO_2 concentration alters both the initial light use efficiency and the CO_2-limited rate of gross photosynthesis (Goudriaan et al. 1985). Allocation of assimilates is modelled using fixed allocation keys. PGEN (Friend 1993) is a model aiming to predict the rate of photosynthesis at the biochemical level (Farquhar and Von Caemmerer 1982), and the optimization of stomatal conductance given a set of environmental and biological parameters. The ITE-Edinburgh model (Thornley 1991) is a transport-resistance model of forest growth and partitioning based on counter-gradients of carbon and nitrogen substrate between foliage and roots. In the foregoing account the processes in which the models differ and those parts which were adjusted to calculate the growth of deciduous trees have been emphasised: see also Appendices 5.1 and 5.2.

FORGRO. Figure 5.1 presents a simplified scheme of FORGRO. For photosynthesis, the minimum was taken of the rate of photosynthesis limited by either CO_2 or the maximum value measured at light saturation (Figures 5.2 and 5.3, and Equations 5.1 to 5.4 in Appendix 5.2). Mesophyll resistance was calculated using: $r_m = (C_i - \Gamma)/F_{m,m}$ (Figure 5.2), assuming a constant ratio of internal to external CO_2 concentration (Goudriaan et al. 1985). The boundary layer conductance was set at a constant value, and the stomatal conductance depends solely on temperature. The temperature dependence of the CO_2 compensation point is described using a multiplier (Equation 5.5). To relate the light-saturated rate of gross photosynthesis, a temperature multiplier was obtained by linear interpolation of literature data, using a broad plateau of near-unity in the range 10 to 30°C, and declining to zero outside this temperature range. A similar approach was taken to determine the actual mesophyll resistance as a function of temperature, with values similar to the photosynthesis-temperature relationship. Daily gross canopy photosynthesis was calculated by integrating hourly over both sunlit and shaded leaf layers using a Gaussian integration scheme (Goudriaan 1986), dividing the canopy into five shaded and sunlit leaf layers. Growth and maintenance respiration were calculated using the approach of Penning de Vries, which is based on the costs of biosynthetic processes and the biochemical composition of the structural biomass (Penning de Vries et al. 1974). Fixed allocation keys were used for the growth rates of the different organs, with the exception of the allocation to the foliage and the reserve pool, for which saturation curves relative to maximum values were used (Equations 5.6 and 5.7).

The level of reserves was modelled using a minimum equal to 5% of the biomass of each organ, and a maximum which is four times as high. Allocation of assimilates to the reserves has priority over all the other organs, once the full leaf stage has been reached. Daily values of the meteorological variables irradiance, minimum and maximum temperatures, humidity, wind speed and rainfall are required to run FORGRO, which uses a fixed time step of one day.

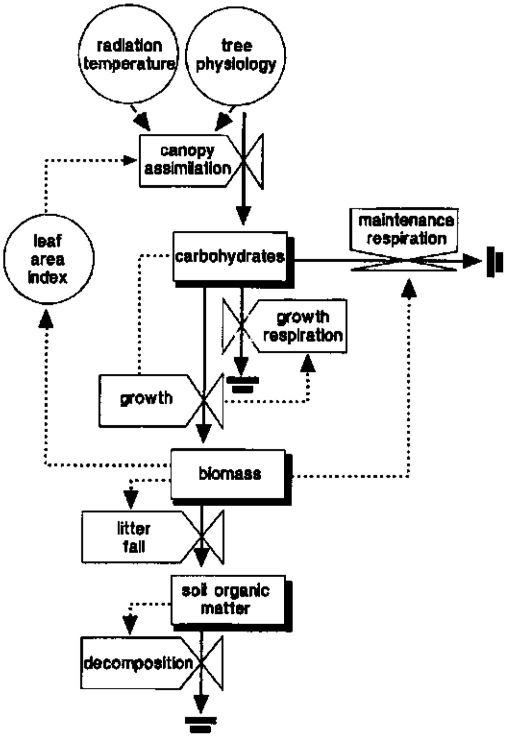

Figure 5.1. Simplified diagram of the structure of FORGRO. Boxes: state variables; valves: rate variables; arrows: flows of carbon (solid lines) or information (dotted lines) (Figure redrawn from Mohren 1994).

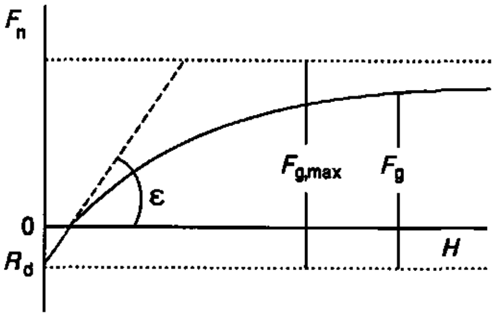

Figure 5.2. Net CO_2 assimilation rate in relation to light absorption by the leaf surface. See Appendix 5.2 for an explanation of the symbols, with their units (Figure redrawn from Goudriaan and Van Laar 1994).

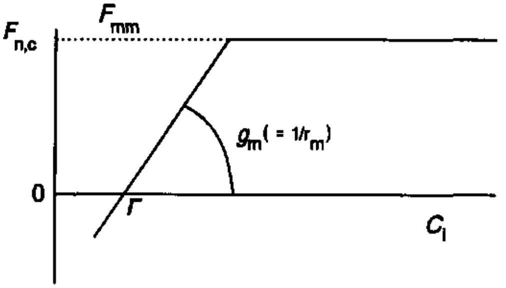

Figure 5.3. Net CO_2 assimilation rate in relation to internal CO_2 concentration. See Appendix 5.2 for an explanation of the symbols, with their units (Figure redrawn from Goudriaan and Van Laar 1994).

PGEN. PGEN is a photosynthesis model which aims at predicting stomatal conductance and photosynthesis with a minimal use of empirical parametrization. It is based on the assumption that a leaf instantaneously optimises its stomatal conductance as a trade-off between CO_2 gain and water loss. CO_2 gain affects photosynthesis according to the biochemical photosynthesis model of Farquhar and Von Caemmerer (1982).

The demand for CO_2 is determined either by carboxylation limitation of Rubisco (Equation 5.9), or by regeneration limitation of RuBP (Equation 5.10), while the supply of CO_2 depends on the difference of CO_2 concentration outside the leaf boundary layer and inside the leaf air spaces (Equation 5.11). Whether the CO_2 supply meets the photosynthetic demands depends on the resistance to CO_2 along the pathway from outside the leaf boundary layer to the mesophyll cells (Equation 5.17). Explicit functions for $r_{c,a}$ and $r_{c,i}$ are presented in PGEN, while $r_{c,s}$ is the resistance which is optimised numerically. Equations 5.14 to 5.22 provide more detail on how the variables in Equations 5.9 to 5.12 are calculated.

The leaf temperature is calculated from the leaf energy balance (Jones 1992). Temperature influences photosynthesis by altering the solubilities of CO_2 and O_2, and alters the Michaelis-Menten constants of the carboxylation and oxygenation of Rubisco following the law of Arrhenius. The influence of temperature on dark respiration is modelled by a Q_{10} approach.

PGEN was coupled to FORGRO by substituting it for the calculations of the gross photosynthesis ($F_{g,max}$) in the canopy module and adjusting it so that input to PGEN was: CO_2 and O_2 concentration in the air, relative humidity, wind speed, incidence of short wave irradiance, atmospheric pressure, air temperature and the absorbed photosynthetic active radiation at a given leaf layer. Incidence of short wave radiation was set at twice the photosynthetic active radiation available at a given leaf layer. Output of PGEN is daily gross photosynthesis.

ITE-Edinburgh model. This model presents a mechanistic approach to assimilate partitioning based on the transport of labile carbon and nitrogen, and the size and activity of meristem (Figure 5.4; Equations 5.23 to 5.29). The transport of C and N substrate is driven by concentration differences and resistances between the organs. Counter-gradients of carbon and nitrogen substrate are formed because the foliage is the only source of C substrate, the roots are the only source of N substrate, and the growing organs act as sinks of carbon and nitrogen. A functional root-shoot balance is attained because the acquisition of carbon depends on the level N substrate of the foliage, and the acquisition of N depends on the level of C substrate in the fine roots. The growth of each organ is determined by the activity and potential size of the meristem, which depends on both the C and N substrate concentrations of the organ. Temperature dependence of parameters was described using a parabolic-shaped multiplier, which equals zero at 0°C, and is maximum at 30°C (Equation 5.30).

The ITE-Edinburgh model was coupled to FORGRO (ITE-FORGRO) by using the modules of FORGRO which calculate light interception, photosynthesis and stomatal conductance. A reserve pool was required to start leaf growth after budburst, and to allow for maintenance respiration in the leafless period. Therefore, a reserve pool was added for each organ. The growth rate of each reserve pool was set at a fixed fraction (0.05) of the growth rate of the structural biomass of the organ. Furthermore, it was assumed that the utilization of carbon and nitrogen and the respiration of the reserve pool are similar to the respiration of the structural biomass. During the build up of the canopy (the period from budburst until full leaf), reserves are mobilised from all organs, i.e. converted into labile C and N, according to a first-order process.

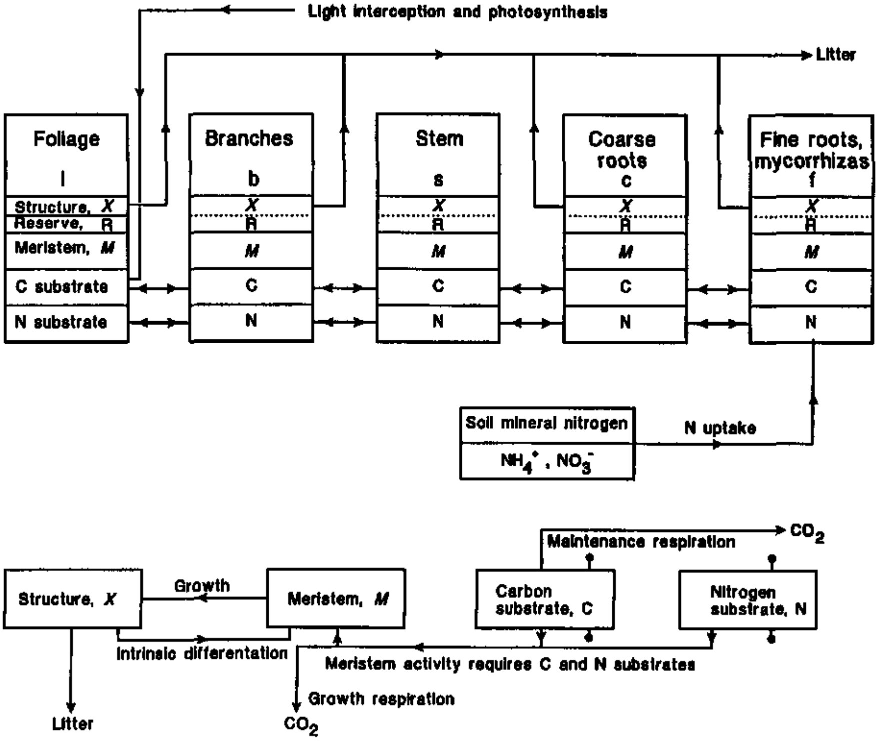

Figure 5.4. Simplified diagram of the structure of ITE-FORGRO. Light interception and photosynthesis are described as in FORGRO (Figure redrawn from Thornley 1991).

During this phase the foliage is the only organ allowed to grow. Consequently, a gradient of both C and N substrate from the fine roots to the foliage develops, since the foliage acts as the only sink. The leaves start to photosynthesise immediately, which causes the C substrate gradient to reverse as soon as the carbon production exceeds carbon utilization, or when the full leaf stage is reached. During the leafless period, the costs of maintenance respiration are directly compensated for from the reserve pool of each organ. The leaf area index was truncated to the same maximum value as used in FORGRO.

The ITE-FORGRO model was developed using SENECA v1.5, a Simulation ENvironment for ECological Application (De Hoop et al. 1992). The integration method was Eulerian with variable time steps. Preliminary runs indicated that it takes approximately three years for the ITE-FORGRO model to attain stable gradients of labile carbon and nitrogen. Therefore, runs were started at 1937, using average values for the phenological events, but output of the 1940 to 1953 period is presented.

Results

Phenology

An impression of the importance of the differences between the phenological types can be obtained by examining the amount of light available on average during the growing period, and how this changes with a rise in temperature (Table 5.1). On average, most irradiance is available for *Betula*. *Fagus* and *Quercus* have respectively 1.4% and 3.6% less. When the temperature changes, the net result is a gain in the average available irradiance of 0.8 for *Betula*, 1.1% for *Fagus* and 0.2% for *Quercus*, per degree temperature rise, relative to the total cumulative irradiance available on average during the growing season for each of these phenological types. In The Netherlands, the irradiance gained on average when leaf unfolding is advanced by one day is more than twice what is lost when leaf fall advances one day (e.g. 15 MJ m^{-2} d^{-1} on 1 May and 6 MJ m^{-2} d^{-1} on 15 October).

Table 5.2 presents the results of FORGRO, FORGRO-PGEN and ITE-FORGRO for the C_{350}/T_0 scenario. Clearly, the differences in phenology only cause small differences in growth and radiation use efficiency, and are consistent with the pattern between the phenological types found in Table 5.1. For this parametrization of the models the $P_{g,a}$ calculated by FORGRO is similar to ITE-FORGRO, but higher than that of FORGRO-PGEN.

Table 5.2. Results of FORGRO, FORGRO-PGEN and ITE-FORGRO for the C_{350}/T_0 scenario for the 1940-1953 situation using default parameter values. RUE, radiation use efficiency: ratio of annual total dry matter production and absorbed PAR (g DM MJ^{-1}). See Appendix 5.1 for the explanation of the other symbols and their units

	FORGRO			FORGRO-PGEN			ITE-FORGRO		
	Betula	*Fagus*	*Quercus*	*Betula*	*Fagus*	*Quercus*	*Betula*	*Fagus*	*Quercus*
$P_{g,a}$	35.7	34.1	32.9	23.1	22.2	22.1	33.1	31.8	31.5
R_m	10.6	10.3	10.2	8.3	8.0	8.0	3.7	3.6	3.6
R_g	3.8	3.6	3.5	2.3	2.2	2.2	7.5	7.2	7.1
RUE	1.6	1.6	1.5	0.9	0.9	0.9	1.5	1.5	1.4

For this parameterisation of ITE-FORGRO, more carbon is respired by growth respiration than by maintenance respiration, whereas in FORGRO the opposite is true. Furthermore, the growth rates of the organs differ because of the different mechanism of allocation (results not presented).

The results of the three models when [CO$_2$] = 700 μmol mol^{-1} are that differences in the response of $P_{g,a}$ between *Betula*, *Fagus* and *Quercus* increase with temperature (Figures 5.5 to 5.7). The difference in the response between *Fagus* and *Quercus* increases by approximately 4% in the C_{700}/T_2 scenario and by approximately 20% in the C_{700}/T_7 scenario, for FORGRO and FORGRO-PGEN, but the corresponding increases according to ITE-FORGRO are 4% and 13%, because of the different mechanism of allocation.

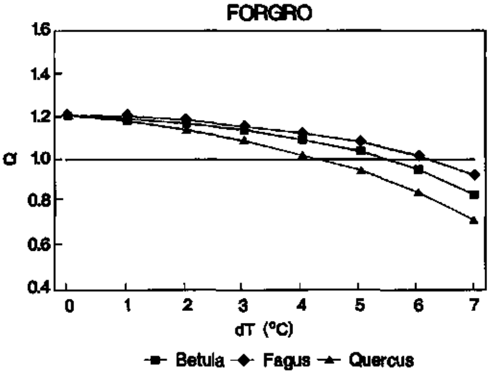

Figure 5.5. Response of $P_{g,a}$ to 2 x [CO $_2$] with increasing temperature, relative to the current climate (Q), according to FORGRO. Annual average over 1940-1953.

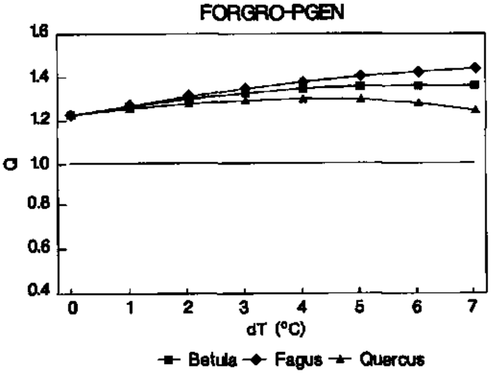

Figure 5.6. Response of $P_{g,a}$ to 2 x [CO $_2$] with increasing temperature, relative to the current climate (Q), according to FORGRO-PGEN. Annual average over 1940-1953.

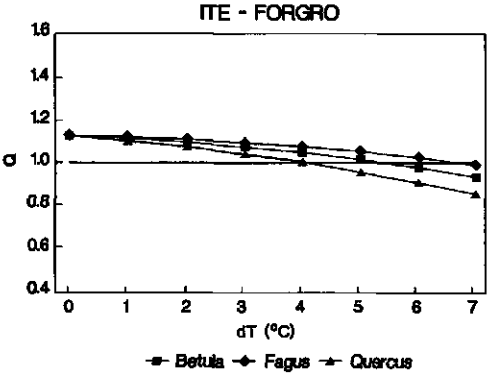

Figure 5.7. Response of $P_{g,a}$ to 2 x [CO $_2$] with increasing temperature, relative to the current climate (Q), according to ITE-FORGRO. Annual average over 1940-1953.

This is consistent with the differences between the phenological types based on the change in average available irradiance with temperature (Table 5.1). Figures 5.5 to 5.7 further show that the response of $P_{g,a}$ to a doubled [CO_2] is greatest according to FORGRO-PGEN, and least in ITE-FORGRO, and that the response increases with temperature according to FORGRO-PGEN (Figure 5.6), but decreases with temperature according to both FORGRO and ITE-FORGRO (Figures 5.5 and 5.7).

The differences in annual gross photosynthesis between FORGRO and FORGRO-PGEN are the results of the response of the daily gross photosynthesis (P_g, kg CH_2O ha^{-1} d^{-1}) to the external CO_2 concentration (Figures 5.8 and 5.9).

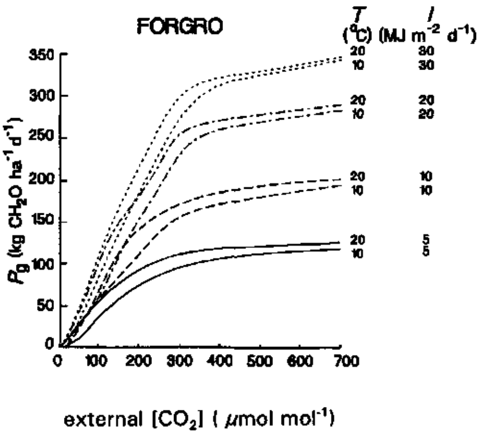

Figure 5.8. Response of P_g to CO_2 at different temperature and light levels, according to FORGRO.

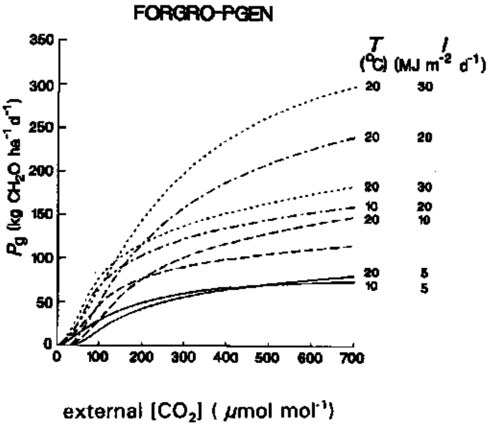

Figure 5.9. Response of P_g to CO_2 at different temperature and light levels, according to FORGRO-PGEN.

For the current parameterisation of FORGRO and FORGRO-PGEN it can be seen that: (1) FORGRO yields a higher P_g than FORGRO-PGEN for any CO_2 , temperature and light combination, (2) the sensitivity of P_g to CO_2 at a constant light level increases with temperature according to FORGRO-PGEN, but decreases slightly according to FORGRO, (3) the sensitivity of P_g to CO_2 at 10°C increases with irradiance similarly in FORGRO and FORGRO-PGEN, and (4) there is a temperature and light interaction for the sensitivity of P_g to CO_2 according to FORGRO-PGEN, but not according to FORGRO. The consequence of these differences between FORGRO and FORGRO-PGEN are that in FORGRO and thus ITE-FORGRO, the increase in respiration with temperature is not compensated for by an increase in photosynthesis (Figures 5.5 and 5.7), whereas this is the case in FORGRO-PGEN (Figure 5.6).

Sensitivity analysis

A sensitivity analysis was performed to evaluate which parameters are most important in determining the response of the annual gross photosynthesis, $P_{g,a}$, to an increase of both CO_2 and temperature.

The response of $P_{g,a}$ to the C_{700}/T_2 scenario relative to the C_{350}/T_0 scenario was used to compare the sensitivities of the parameters. The general trend which can be seen for FORGRO is that when a parameter is set so that $P_{g,a}$ is lower than the default parameter value, then the response to the C_{700}/T_2 scenario is greater (Figure 5.10). For example, a high ratio between internal and external CO_2 concentration, C_i/C_a, reduces the $P_{g,a}$ relative to a low ratio, consequently P_g is increased more by the C_{700}/T_2 scenario compared with the low ratio (24% versus 18%). High values of C_i/C_a, the CO_2 compensation point, and stomatal resistance, and low values of the initial light use efficiency, the light extinction coefficient and specific leaf area reduce $P_{g,a}$, and thus show the large response to C_{700}/T_2. However, for P_{max} the opposite is true: the largest response to C_{700}/T_2 is at the high value of P_{max}, which clearly gives high values of $P_{g,a}$. This was caused by the fact that at low P_{max} , this asymptote was met more frequently than at high P_{max}, thus the sensitivity to the scenarios is less. In general it can be concluded that response of $P_{g,a}$ in FORGRO to the C_{700}/T_2 scenario is similar over a wide range of values of the main parameters which determine light interception and photosynthesis.

A clear effect of the PGEN formulation is that the response of $P_{g,a}$ to the scenarios increases or decreases, depending on the value assigned to a parameter. This is especially true for the parameters describing the temperature response of a parameter (ΔS, m, n, E_a, E_d). The reason for this can be seen from Equations 5.20 to 5.22: a change of one unit in a parameter in the exponent is equivalent to leaf temperature changing by approximately 0.03°C, because the temperature is presented in Kelvin. Thus, these parameters need to be estimated accurately, although a change of 25% in the values of these parameters may exceed the range which is found experimentally.

For the ITE-FORGRO model, the most pronounced effect was found for the total leaf nitrogen ($N_{l,tots}$) and the fraction nitrogen in meristem and structural biomass of all organs (f_{NiM} and f_{NiX}). However, the magnitude of the response of $P_{g,a}$ to the scenario is only slightly affected by a large change in the values of these parameters. The absolute response of the other parameters of the ITE-FORGRO model tested in this manner was much less than that of the nitrogen parameters, whilst only the coefficient determining the potential meristem size showed a $P_{g,a}$ response which differed more than 2% between the scenarios.

Discussion and conclusions

Both FORGRO and FORGRO-PGEN showed that the difference in the response of gross photosynthesis to a doubled CO_2 concentration between the phenological types ranges from 4 to 20% if the corresponding temperature rises by 2 to 7°C, respectively. However, these models diverge in the degree of the

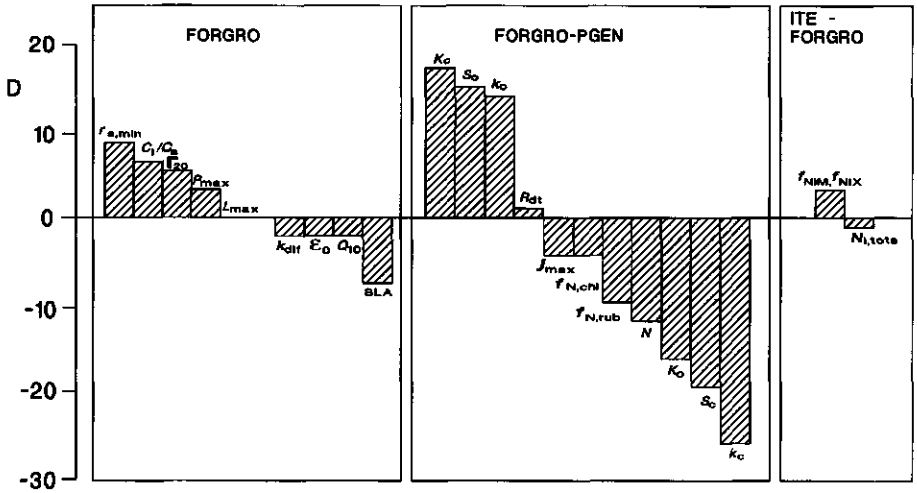

Figure 5.10. Difference (D) between the responses of $P_{g,a}$ to the C_{700}/T_2 scenario relative to the benchmark scenario at high (+25%) and low (-25%) value of the parameter indicated.

response of $P_{g,a}$ to doubled CO_2 scenarios: in FORGRO this response ranges on average from +20% when there is no temperature rise to -16% when the rise is 7°C, while the corresponding range according to FORGRO-PGEN is +22% to +36%. These differences can be attributed to differences in the response of $P_{g,a}$ to [CO_2]. In FORGRO-PGEN this response enhances when temperature and irradiance increase, whilst in FORGRO this interaction is weaker (Figures 5.8 and 5.9). Consequently, in FORGRO-PGEN the increase in photosynthesis exceeds the increase in respiration, whereas in FORGRO and ITE-FORGRO the break-even point lies at or above a temperature increase of 5°C. The CO_2 x temperature interaction is frequently reported in the literature, and is stressed as an important aspect for the study of climate change effects (e.g. Kirschbaum 1994, Idso and Idso 1994). However, the absence of a response or a decline of the relative stimulation of biomass of perennial plants at high CO_2 as temperature increases has also been reported (Ziska and Bunce 1994, and literature therein).

According to the transport-resistance mechanism of allocation (Thornley 1991) the response of $P_{g,a}$ to the scenarios with doubled [CO_2] is less compared with FORGRO and FORGRO-PGEN: relative to the C_{350}/T_0 scenario it is +13% for no temperature rise and -6% for a rise of 7°C. Callaway et al. (1994) presented experimental evidence for a reduced response of growth to enhanced CO_2 because of an altered allocation pattern. They found that the initial stimulating effect of CO_2 on the growth of *Pinus ponderosa* seedlings, and its enhancement by increased temperature, disappeared after 2 months because of an increased allocation of biomass to the roots and other non-photosynthesizing tissues. Furthermore, the differences in the response of $P_{g,a}$ to a 2 x [CO_2] scenario between the phenological types are less than FORGRO and FORGRO-PGEN: 4% if the corresponding temperature rises by 2°C and 13% if it rises by 7°C (Figure 5.6). These features of the transport-resistance model make it worthwhile validating this model for a number of tree species.

Figures 5.5 to 5.7 can be used to evaluate the temperature increase predicted by general circulation models (GCMs). Four well-known GCMs are OSU, GISS, GFDL and UMKO, which predict that mean annual temperature will increase by 3.0, 4.0, 5.3 and 6.5°C, respectively (Leemans 1992). However, these models use CO_2 *equivalents* to calculate the increase in radiative forcing due to an increase in greenhouse gasses. Approximately half of these greenhouse gasses is carbon dioxide, the other half consists of methane, CFCs etc. (Houghton et al. 1990). Furthermore, according to the GCM scenarios the temperature increases more during winter than during summer, rather than uniformly over the year (Leemans 1992). Consequently, the GCM scenarios affect the timing of leaf unfolding more than the timing of leaf fall, and respiration during the growing season is less for the GCM scenarios than for the uniform temperature scenarios. Thus, the equivalent uniform temperature scenario involves a somewhat higher increase in temperature than the annual mean temperature increase of the GCM scenario.

The sensitivity analysis of the parameters of the models affecting photosynthesis showed that for FORGRO and FORGRO-ITE there is generally little interaction between the value of a parameter and the degree of the response of growth to the C_{700}/T_2 climate change scenario, although many parameters strongly affect the response in absolute terms (Figure 5.10). Typically, this sensitivity over a broad range of parameter values is similar in magnitude to the difference between the phenological types in the C_{700}/T_2 scenario (Figures 5.5 and 5.7). For FORGRO-PGEN, however, the degree of the response of $P_{g,a}$ to the C_{700}/T_2 scenario depends on the value of a parameter (Figure 5.10). This was especially the case for the parameters describing the Michaelis-Menten kinetics of Rubisco, and the effect of temperature on these parameters. Also the effect of nitrogen is such that at low values of the nitrogen parameters the response of $P_{g,a}$ to the C_{700}/T_2 scenario is greater than at high values of these parameters (Figure 5.10). For these parameters, this sensitivity is greater than the difference between the phenological types in the C_{700}/T_2 scenario (Figure 5.6). The sensitivity of the response to a variation in the parameter values in FORGRO-PGEN indicates that these parameters must be determined accurately in order to evaluate the effects of CO_2 and temperature on growth. Currently, they are available for only a few species. Furthermore, some of the parameters of the PGEN formulation vary considerably both between and within species (Wullschleger 1993).

An analysis of uncertainty propagation in FORGRO showed that variation in $P_{n,max}$, Q_{10}, ε_0 and SLA within 95% of their uncertainty limits, yielded uncertainties of 19, 9, 9 and 2%, respectively, of the relative standard deviation of the annual growth rate (Van der Voet and Mohren 1994). In a sensitivity analysis of PGEN it was found that the sensitivity indices (ratio of the relative change in a parameter to the relative change in net photosynthesis) of k_c, K_c, N, K_o, $f_{n,rub}$, k_O, $f_{N,chl}$ and j_{max} were 0.7, 0.6, 0.6, 0.4, 0.4, 0.3, 0.2 and 0.2, respectively (Friend 1995). Thus, the uncertainty or sensitivity of these output variables to a small variation in a parameter is not directly applicable for inferring the importance of this parameter on the effects of a climate change scenario on the output variable.

In this study, only the direct effect of temperature on phenology was taken into account. However, nutrients and CO_2 are known to interact with temperature. Murray et al. (1994) showed that for some *Picea sitchensis* clones, an increased CO_2 yields a delayed budburst and an advanced bud set under low nutrient supply. This could shorten the growing season by three weeks. Under high nutrient supply this effect was much less. Increasing temperature counteracted the CO_2 effect, resulting in an advanced budburst, which was less compared to the situation where only temperature was increased. Such complex interacting effects, which are clone specific, greatly complicate the evaluation of the effects of climate change on the growth of trees.

Appendix 5.1. Symbols of variables and parameters with their dimensions. The value indicates the default value for the parameter

Symbol	Definition	Units	Value
	Variables		
$P_{g,a}$	gross photosynthesis	t CH_2O ha^{-1} yr^{-1}	
P_g	gross photosynthesis	kg CH_2O ha^{-1} d^{-1}	
R_m	maintenance respiration	t CH_2O ha^{-1} yr^{-1}	
R_g	growth respiration	t CH_2O ha^{-1} yr^{-1}	
G_i	growth, $i=l$, leaves; $i=b$, branches; $i=s$, stem; $i=c$, coarse roots; $i=f$, fine roots	t DM ha^{-1} yr^{-1}	
	Parameters		
SLA	specific leaf area	m^2 kg^{-1}	20
L_{max}	maximum leaf area index	m^2(leaf) m^{-2} (ground)	6
$P_{n,max}$	maximum rate of net photosynthesis	mg CO_2 m^{-2} s^{-1}	0.56
Γ_{20}	CO_2 compensation point at 20°C	μmol mol^{-1}	50
ε_0	initial light use efficiency	kg CO_2 J^{-1}	0.45
C_i/C_a	ratio internal to external [CO_2]		0.7
k_{dif}	light extinction coefficient of canopy		0.65
R_{d20}	dark respiration at 20°C	mg CO_2 m^{-2} s^{-1}	0.028
Q_{10}	increase of respiration rate given 10°C temperature increase		2.0

Appendix 5.2. Equations

FORGRO

Leaf photosynthesis

$$F_n = F_{g,max}(1 - e^{\frac{-\epsilon H_{abs}}{F_{g,max}}}) - R_d \qquad 5.1$$

$$F_{g,max} = \mathrm{MIN}(F_{n,c}, F_{n,max}) + R_d \qquad 5.2$$

$$F_{n,c} = \frac{C_a - \Gamma}{r_m + 1.6 r_s + 1.4 r_b} \qquad 5.3$$

$$\epsilon = \epsilon_{20} \frac{C_a - \Gamma}{C_a + 2\Gamma} \qquad 5.4$$

$$\Gamma = \Gamma_{20}\, e^{0.07(T-20)} \qquad 5.5$$

Allocation

$$a_{re} = \frac{R - R_{max}}{R_{max}} \qquad 5.6$$

$$a_l = \frac{L - L_{max}}{L_{max}} \qquad 5.7$$

$$a_{st} = 1 - (a_l + a_b) \qquad 5.8$$

a_{re}, a_l, a_b, a_{st}	allocation of assimilates to the reserve pool, leaves, branches and stem	
C_a	ambient CO_2 concentration	μmol mol^{-1}
$F_{g,max}$	max. gross photosynthesis	mg CO_2 m^{-2} s^{-1}
F_n	net rate of photosynthesis	mg CO_2 m^{-2} s^{-1}
$F_{n,c}$	CO_2 limited net photosynthesis	mg CO_2 m^{-2} s^{-1}
$F_{n,max}$	maximum net photosynthesis at high CO_2 and light levels	mg CO_2 m^{-2} s^{-1}
$F_{m,m}$	maximum endogenous rate of gross photosynthesis at high CO_2 and light levels	mg CO_2 m^{-2} s^{-1}
H_{abs}	absorbed PAR	J m^{-2} s^{-1}
R, R_{max}	reserve pool, and maximum level of reserve pool	kg CH_2O ha^{-1}
R_d	dark respiration rate	mg CO_2 m^{-2} s^{-1}
r_m, r_s, r_b	mesophyll, stomatal and boundary layer resistance	s m^{-1}
T	temperature	°C
L, L_{max}	leaf area index, and maximum leaf area index	m^2 (leaf) m^{-2} (ground)
Γ, Γ_{20}	CO_2 compensation point, and CO_2 compensation point at 20°C	μmol mol^{-1}
ϵ, ϵ_{20}	initial light use efficiency, and initial light use efficiency at 20°C	μg CO_2 J^{-1}

PGEN

Leaf photosynthesis

$$A_{n,c} = \frac{V_{c,max}\,(C_i - \Gamma_*)}{C_i + K_c\,(1 + \frac{O_i}{K_o})} - R \qquad 5.9$$

$$A_{n,r} = \frac{J\,(C_i - \Gamma_*)}{4.5\ C_i + 10.5\ \Gamma_*} - R_d \qquad 5.10$$

$$A_{n,s} = \frac{C_a - C_i}{r_c} - \frac{C_a + C_i}{2}\,\frac{E R \overline{T}}{P} \qquad 5.11$$

$$\Gamma_* = \frac{0.5\ V_{o,max}\ K_c\ O_i}{V_{c,max}\ K_o} \qquad 5.12$$

$$J = \frac{J_{max}\ H_{abs}}{2.1\ J_{max} + H_{abs}} \qquad 5.13$$

$$V_{i,max} = k_i\ E_t,\ \text{i: c, o} \qquad 5.14$$

$$J_{max} = \frac{j_{max}\ f_{N,chl}\ N}{0.056} \qquad 5.15$$

$$E_t = 0.0909\ f_{N,rub}\ N \qquad 5.16$$

$$r_c = r_{c,a} + r_{c,s} + r_{c,i} \qquad 5.17$$

$$R_d = R_{dT}\ N \qquad 5.18$$

$$K_i = \frac{K_{i,chl}\ D}{S_i},\ \text{i: c, o} \qquad 5.19$$

Temperature functions

$$x = a\,e^{\frac{E_a}{RT_l}},\ x{:}k_c, k_o, K_{c,chl}, R_{dT} \qquad 5.20$$

$$j_{max} = a\,\frac{e^{\frac{-E_a}{RT_l}}}{1 + e^{\frac{\Delta S T_l - E_d}{RT_l}}} \qquad 5.21$$

$$S_i = \frac{m}{e^{\frac{-n}{RT_l}}}\,\frac{P}{P_0},\ \text{i: c,o} \qquad 5.22$$

$A_{n,c}$, $A_{n,r}$, $A_{n,s}$	carboxylation-limited, RuBP regeneration-limited, and stomatal resistance-limited rate of net photosynthesis	mol CO_2 m^{-2} s^{-1}
C_i, C_a	$[CO_2]$ in leaf air spaces, and in air outside the leaf boundary layer	mol m^{-3}
D	concentration of air in leaf internal air spaces	mol m^{-3}
E	transpiration	mol H_2O m^{-2} s^{-1}
E_a	activation energy	J mol^{-1}
E_d	deactivation energy	J mol^{1}
E_t	leaf Rubisco catalytic site content in leaf	mol m^{-2}
$f_{N,rub}$, $f_{N,chl}$	fraction nitrogen in Rubisco, and chlorophyll	-
H_{abs}	absorbed PAR	mol quanta m^{2} s^{1}
J	potential electron transport rate	mol e^- m^{-2} s^{-1}
j_{max}	PAR-saturated potential electron transport rate (temperature dependent)	mol e^- mol chl^{-1} s^{-1}
J_{max}	PAR-saturated electron transport rate	mol e^- m^{-2} s^{-1}
k_c, k_o	Rubisco carboxylation, and oxygenation turnover number	mol mol $site^{-1}$ s^{-1}
K_c, K_o	M-M constant for carboxylation, and oxygenation of Rubisco (air space equivalents)	mol m^{-3}
$K_{c,chl}$, $K_{o,chl}$	M-M constant for carboxylation, and oxygenation of Rubisco (temperature dependent)	mol m^{-3}
N	leaf nitrogen content	kg m^{-2}
O_i	O_2 concentration in leaf air spaces	mol O_2 m^{-3}
P, P_o	atmospheric pressure, and standard atmospheric pressure	Pa
R	gas constant	J K^{-1} mol^{-1}
r_c	resistance to CO_2 from air outside the leaf boundary layer to the mesophyll surface	s m^{-1}
$r_{c,a}$	resistance to CO_2 transfer across leaf boundary layer	s m^{-1}
$r_{c,i}$	resistance to CO_2 from inside leaf surface to mesophyll surface	s m^{-1}
$r_{c,s}$	resistance to CO_2 across leaf surface	s m^{-1}
R_d	mitochondrial respiration	mol CO_2 m^{-2} s^{-1}
R_{dT}	mitochondrial respiration, temperature dependent)	mol CO_2 kg N^{-1} s^{-1}
S_c, S_o	solubility of CO_2, and O_2 in water	mol m^{-3}
T, T_l	average of leaf and air temperature, and leaf temperature	K
$V_{c,max}$, $V_{o,max}$	maximum rate of carboxylation, and oxygenation of Rubisco	mol CO_2 m^{-2} s^{-1}
Γ_*	photosynthesis compensation $[CO_2]$ in leaf air spaces in absence of mitochondrial respiration	mol CO_2 m^{-3}
ΔS	entropy parameter	J K^{-1} mol^{-1}
a, m, n	empirical constants	

ITE-Edinburgh model

Differential equations

$$\frac{\mathrm{d}M_{\mathrm{iM}}}{\mathrm{d}t} = G_{\mathrm{MiM}} - L_{\mathrm{MiMdif}} \qquad 5.23$$

$$\frac{\mathrm{d}M_{\mathrm{iR}}}{\mathrm{d}t} = G_{\mathrm{MiR}} - L_{\mathrm{MiRlit}} - M_{\mathrm{MiR}} \qquad 5.24$$

$$\frac{\mathrm{d}M_{\mathrm{iX}}}{\mathrm{d}t} = G_{\mathrm{MiX}} - L_{\mathrm{MiXlit}} + L_{\mathrm{MiMdif}} \qquad 5.25$$

$$\frac{\mathrm{d}M_{\mathrm{iC}}}{\mathrm{d}t} = T_{\mathrm{C(i+1)li}} - T_{\mathrm{Cli(i-1)}} - R_{\mathrm{iXm}} - U_{\mathrm{CiG}} + M_{\mathrm{CiR}} \qquad 5.26$$

$$\frac{\mathrm{d}M_{\mathrm{iN}}}{\mathrm{d}t} = T_{\mathrm{N(i-1)li}} - T_{\mathrm{Nli(i+1)}} - U_{\mathrm{NiG}} + M_{\mathrm{NiR}} \qquad 5.27$$

leaves (l) :

$$\frac{\mathrm{d}M_{\mathrm{lC}}}{\mathrm{d}t} = P_{\mathrm{C}} - T_{\mathrm{Cllb}} - R_{\mathrm{lXm}} - U_{\mathrm{ClG}} + M_{\mathrm{ClR}} \qquad 5.28$$

fine roots (f) :

$$\frac{\mathrm{d}M_{\mathrm{fN}}}{\mathrm{d}t} = U_{\mathrm{N}} - T_{\mathrm{Nflc}} - U_{\mathrm{NfG}} + M_{\mathrm{NfR}} \qquad 5.29$$

Temperature function

$$f(T) = \frac{(T - T_l)\ (2\,T_a - T_l - T)}{(T_r - T_l)\ (2\,T_a - T_l - T_r)} \qquad 5.30$$

G_{miM}	growth rate meristem	kg dm ha^{-1} d^{-1}
G_{MiR}	growth rate reserves	kg dm ha^{-1} d^{-1}
G_{MiX}	growth rate structure	kg dm ha^{-1} d^{-1}
L_{MiMdif}	loss in meristem to intrinsic differentiation	kg dm ha^{-1} d^{-1}
L_{MiRlit}	loss reserves to litter	kg dm ha^{-1} d^{-1}
L_{MiXlit}	loss structure to litter	kg dm ha^{-1} d^{-1}
M_{CiR}	mobilization of carbon from reserves	kg C ha^{-1} d^{-1}
M_{NiR}	mobilization of nitrogen from reserves	kg N ha^{-1} d^{-1}
P_C	canopy gross photosynthesis rate	kg C ha^{-1} d^{-1}
R_{iXm}	maintenance respiration	kg dm ha^{-1} d^{-1}
T_{Cij}	carbon transport flux	kg C ha^{-1} d^{-1}
T_{Nij}	nitrogen transport flux	kg C ha^{-1}
T, T_i, T_a, T_r	temperature, minimum, maximum and reference temperature	°C
U_{CiG}	utilization C for growth	kg C ha^{-1} d^{-1}
U_{NiG}	utilization N for growth	kg N ha^{-1} d^{-1}
U_N	uptake N from soil	kg N ha^{-1} d^{-1}

Chapter 6

Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forests

Introduction

Phenology of trees is the study of the timing of annually recurring events such as leaf unfolding and leaf fall, related to climatic and other environmental factors (Leith 1974). It can be assumed that this timing is such that the growing period is optimally synchronised with the period favourable for growth, by either natural selection or management. If a significant climate change occurred within the life span of a tree, then this synchronization may be disrupted. In earlier studies, the effects of temperature increase on phenology and the occurrence of spring frost damage, (Kramer 1994b, Chapter 3), and its consequences on growth of monospecies stands were evaluated (Kramer 1995b, Chapter 5). Species were found to respond differently to the imposed climate change scenarios. Consequently, the competitive relationships between these species, when grown in mixture, will alter due to climate change. The term competition is used as the reduction in growth of a target species, caused by the presence of another species, requiring the same limiting resource. Only differences affecting competition for light were considered.

With respect to phenology and spring frost damage, species differed: (1) in the advancement of the date of leaf unfolding with increasing winter temperature, and (2) in the frequency of freezing temperature around this date. Species that unfold their leaves during the end of April appear to respond more strongly to temperature change than species that unfold their leaves during the first weeks of May (Kramer 1994b, Chapter 3). Such a differential response enhances existing differences between species if temperature increases. This is important to assess climate change impacts on the geographical distribution of a species. Usually the correlation between the distribution of a species and the absolute minimum winter temperature is used (Sakai and Larcher 1987, Woodward 1992). This may only be valid if the vegetation is in equilibrium with its local climate. If the absolute minimum winter temperature rises, and trees attain the same level of frost hardiness during dormancy, then any shift of the boundaries of the distribution must be determined by other competitive factors. Thus by evaluating the relationship between temperature and both leaf unfolding and leaf fall, and the progression of frost hardiness, both the direct effects of the climatic warming (on frost damage), and indirect effects (on competitive ability), are accounted for. The available phenological models are, however, not very accurate (Kramer 1995a, Chapter 4). Therefore, in this study both a regression approach and a modelling approach were taken, enabling evaluation of the inaccuracy of the models for growth in a mixed-species stand.

With respect to growth of a monospecies stand, the difference in the response of gross photosynthesis between phenological types, to temperature scenarios given a doubled CO_2 concentration, ranged from 4 to 20% if the corresponding temperature rose by 2 to 7°C, respectively (Kramer 1995b, Chapter 5). These differences may be enhanced when grown in mixture, especially in combination with an altered occurrence of spring frost damage.

The aims of this study were: (1) to evaluate the effects of differences between species in both phenological response and occurrence of spring frost damage, on growth in mixed-species deciduous forest stands, in relation to increased temperature and atmospheric CO_2 concentration, and (2) to evaluate the importance of inaccuracy of the phenological and frost hardiness models on this evaluation.

This was done by comparison of the annual net primary productivity predicted by the models FORGRO and HYBRID, based on a range of climate change scenarios. Both FORGRO and HYBRID are mechanistic models describing ecophysiological processes in detail. FORGRO (Mohren 1987, 1994) aims to predict forest productivity of managed stands based on information of the species, site and management regime considered. HYBRID (Friend 1993, Friend et al. submitted) aims to predict vegetation types on climate and ecophysiological features of General Plant Types. The species dynamics is described by establishment of seedlings and subsequent growth of individual trees in a gap, which occurs when a large tree dies. The rationale of such a model comparison is that, if models emphasizing different aspects of forest growth yield similar results, then more confidence is gained in these results. If not, then the differences may be explained by further analysis of the processes in which the models differ.

Material and methods

Phenology and frost hardiness

Two approaches were used to describe the timing of both leaf unfolding and the level of frost hardiness: (1) a regression approach, by which mean dates were taken for both leaf unfolding. A fixed threshold was taken for the level of frost hardiness, assuming that frost hardiness is at its lowest level from the date of leaf unfolding onwards, and (2) a modelling approach, using models to predict the date of both leaf unfolding and the progression of frost hardiness. Frost damage occurs in both approaches when the daily minimum temperature is less than the level of frost hardiness. For the date of leaf fall, only the regression approach was used.

Regression approach. Three types of phenological responses to temperature increase were discerned based on the analysis of an extensive data set containing phenological observations on clones relocated over a large latitudinal range throughout Europe: (1) a similar advance of both leaf unfolding and leaf fall; (2) an advance of leaf unfolding, but no change in leaf fall; and (3) a larger advance of leaf fall than of leaf unfolding (Kramer 1995a, Chapter 4). These three phenological types correspond to *Betula*, *Fagus*, and *Quercus*, respectively. Table 6.1 presents the characteristics of these phenological types. The dates of both leaf unfolding and leaf fall are kept constant during the entire simulation period. If the temperature was increased according to a scenario, then the mean dates of both leaf unfolding and leaf fall were adjusted according to the responses of *Betula*, *Fagus*, and *Quercus* (Table 6.1). The level of frost hardiness was assumed to be constant throughout the year, and was set at a value of -2.3°C (Friend et al. submitted)

Modelling approach. Sarvas (1974) discerned two phases during dormancy of woody plants: (1) rest, in which growth-arresting conditions in the bud itself prevent the bud to burst, even when brought in conditions that are normally favourable for development and growth. The growth-arresting factors can be removed by exposing the buds to chilling temperatures for a prolonged period, and (2) quiescence, in which only unfavourable external conditions prevent the buds to burst. When brought in favourable temperature conditions, the buds are readily forced to burst. Hänninen (1990) formalised this approach by defining a state of chilling, S_c, determining how far rest has progressed, and the state of forcing, S_f, determining how far quiescence has progressed. Sarvas (1974) postulated that these phases occur sequentially in time, thus the state of forcing increases only when the chilling requirements are met, i.e. when the state of chilling attains the critical state of chilling, S_c^*. Budburst is predicted to occur when S_f attains the critical state of forcing, S_f^*. For the rate of chilling, R_c, a triangular function with temperature is assumed, and for the rate of forcing, R_f, a logistic function with temperature. The values of the parameters of these functions estimated by Kramer (1995a, Chapter 4) were used. Table 6.1 presents the phenological features of the sequential model.

For the timing of leaf fall, no model could be found that explained the variance of this date better than the mean (Kramer 1995a, Chapter 4). Therefore, the regression approach was used for the date of leaf fall.

Table 6.1. Phenological characteristics of *Betula, Fagus,* and *Quercus*. *U*, average date of leaf unfolding, according to either the regression or the modelling approach for leaf unfolding (*Kramer 1994b, Tables 3.1, 3.4 and 3.6*); *F, date of leaf fall*; P_0, *probability of sub-zero* temperature in a symmetric 11-day period around the date of leaf unfolding. $\delta U/\delta T_w$, change in date of leaf unfolding with mean winter temperature (d °C^{-1}. T_w, 1 November until leaf unfolding); $\delta F/\delta T_s$, change in date of leaf fall with mean summer temperature (d °C^{-1}. T_s, 1 May until leaf fall); R^2, percentage of the variance explained of the date of leaf unfolding by the sequential model

	Betula	*Fagus*	*Quercus*
	Regression approach		
U	22 April	1 May	6 May
F	4 October	16 October	20 October
P_0	0.58	0.37	0.18
$\delta U/\delta T_w$	-3	-2	-2
$\delta F/\delta T_s$	-3	0	-5
	Modelling approach		
U	22 April	1 May	6 May
P_0	0.53	0.30	0.12
$\delta U/\delta T_w$	-5	-4	-5
R^2	86	68	82

Frost hardiness is the freezing temperature a plant can sustain without being damaged. To describe the progression of frost hardiness, the model developed by Leinonen et al. (1995) for *Pinus sylvestris* in Finland was used. Empirical results indicate that plants kept in a constant environment attain a stationary level of frost hardiness. If the environment changes, then the actual level of frost hardiness gradually adjusts to the new situation, at a rate that is proportional to the difference between the stationary and the actual level of frost hardiness. However, the competence to adjust to a changed environment is not constant throughout the year but depends on the plant's state of development. The main environmental factors driving the change in the stationary level of frost hardiness are temperature and photoperiod, which appear to operate additively.

Leinonen et al. (1995) formalised these empirical findings by defining a stationary level of frost hardiness, $\hat{S}_h$ (°C), which may change either due to a change in temperature, $\Delta\hat{S}_h(\mathrm{T})$, or due to a change in photoperiod, $\Delta\hat{S}_h(\mathrm{P})$, or both, starting from a minimum level of frost hardiness, $\hat{S}_{h,min}$, when the plant is completely dehardened:

$$\hat{S}_h(t) = \hat{S}_{h,min} + \Delta\hat{S}_h(T) + \Delta\hat{S}_h(P) \qquad 6.1$$

The rate of change of the actual level of frost hardiness, R_h, can be described as:

$$R_h = C_h(S_f) \cdot \frac{1}{\tau} \cdot (\hat{S}_h - S_h) \qquad 6.2$$

With: $C_h(S_f)$, the plant's hardening competence as a function of the state of forcing which is determined by the sequential model; τ, a time coefficient determining how fast the actual level of frost hardiness adjusts to the stationary level when the environment changes; and S_h, the actual state of frost hardiness. The explicit functions and parameter values for $\Delta\hat{S}_h(\mathrm{T})$, $\Delta\hat{S}_h(\mathrm{P})$, and C_h presented by Leinonen et al. (1995) were used.

Forest growth models

FORGRO (Mohren 1987, 1994; Kramer 1995b) is a process-based primary production model aiming to predict growth of managed stands, using species, site and climatological information. It uses thinning regimes commonly applied in managed forests. FORGRO contains detailed descriptions for light interception, photosynthesis and respiration. To describe light interception in a canopy with a mixture of species, the leaf areas, weighted by the extinction coefficients, are summed over the species (Kropff and Van Laar 1993):

$$I_h = (1-\rho)\, I_0\, e^{-\Sigma k_j L_{h,j}} \tag{6.3}$$

With: I_h, the net flux of radiation at height h (J m^{-2} ground s^{-1}); I_0, the net flux of radiation at the top of the canopy (J m^{-2} ground s^{-1}); ρ, reflection coefficient (-); k_j, extinction coefficient of species j; $L_{h,j}$, cumulative leaf area index of species j above height h (m^2 leaf m^{-2} ground). Canopy photosynthesis is calculated by integration over five shaded and sunlit leaf layers, assuming a rectangular distribution of the leaf area over the canopy height. The photosynthesis-light response curve is modelled using a negative exponential curve. CO_2 affects both the initial light-use efficiency and the asymptote of the light response curve. The temperature dependence of the rate of photosynthesis is based on linear interpolation of experimental data, whereas an exponential function is used for the temperature dependence of the CO_2 compensation point. More details of this approach can be found in Goudriaan and Unsworth (1990), and Goudriaan and Van Laar (1994). Respiration of living biomass depends on its biochemical composition (Penning de Vries et al. 1974), and depends on temperature according to an exponential function ($Q_{10}=2.1$). Allocation of assimilates to the different organs is done daily, based on empirical allocation keys, and saturation curves for allocation to the foliage and the reserve pool (Kramer 1995b, Chapter 5). To focus on light interception and competition for light between species, this version of FORGRO does not take into account the effects of nitrogen and water, thus calculating potential growth (Goudriaan and Van Laar 1994).

HYBRID (Friend 1993, Friend et al. submitted) is an individual-based gap model aiming to predict ecosystem structure and population dynamics based on the cycling of carbon, nitrogen and water, and the exchange of heat fluxes between vegetation and the atmosphere, driven by climate and atmospheric concentrations of CO_2 and O_2. It captures establishment of seedling, growth, mortality, litter production and feedbacks through soil processes to predict transient responses of structure, population dynamics and replacement of vegetation types to a changing climate. The intercepted light is distributed over the crowns of the individual trees that form the canopy, weighted by the leaf area of each individual per leaf layer and the extinction coefficient. To calculate total canopy photosynthesis, it is assumed that the photosynthetic capacity is distributed optimally with respect to radiation over the crown. Thus, the physiological properties of the foliage such as nitrogen and Rubisco content take the same profile over the crown as the attenuation of photosynthetic active radiation (PAR). The rate of net photosynthesis of the crown is then linearly related to that of the uppermost leaf layer (Sellers et al. 1992, Friend et al. submitted). The rate of net photosynthesis is calculated based on the biochemical model of Farquhar and Von Caemmerer (1982), using a simplified version of the model PGEN (Friend et al. 1993, 1995). In this model, the demand for CO_2 is determined either by carboxylation limitation of Rubisco, or by regeneration limitation of RuBP, which is a substrate of Rubisco. Whether the CO_2 supply meets the photosynthetic demands depends on the resistance to CO_2 along the pathway from outside the leaf boundary layer to the mesophyll cells. Explicit functions for the boundary layer and mesophyll resistance were used. For the stomatal conductance an empirical function was used instead of the original optimization approach (Friend 1995, Friend et al. submitted).

Table 6.2. Outline of the features of FORGRO and HYBRID.

Process	FORGRO	HYBRID
light interception & photosynthesis	allows for diurnal course over sunlit and shaded foliage layers	daily integration over crown, optimal distribution of foliage physiological properties, crown photosynthesis scales linearly with photosynthesis of uppermost leaf layer
	neg.-exponential light response	Farquhar biochemistry (PGEN)
stomatal conduct.	empirical	Jarvis' equation
respiration	fixed biochemical composition, Q_{10} function for temperature	depends on [N] of organs (dynamical), exponential temperature function
allocation	*daily, fixed keys, saturation* curves for allocation to leaves and reserves	*annual, optimization of amount of* foliage, sapwood and heartwood area based on allometry (pipe model)
competition	stand level model, species compete for light, homogeneous canopy, photosynthesis weighted per layer for each species	gap model, individuals compete for light, vertically explicit, horizontally homogeneous
population dynamics	thinning by management	annual establishment of all General Plant Types, death if annual carbon gain is insufficient for formation of leaf area
height / diameter	empirical function	allometric relationship
nutrients	(not used)	demand / supply hypothesis
water	(not used)	single layer bucket
soil	(not used)	Century model, 1 layer, 4 litter pools
frost damage	complete defoliation	reduction of photosynthetic capacity during growing season

For respiration an empirical approach is used too, using an exponential temperature function equivalent to a Q_{10} of 2.1. Allocation is done annually based on: (1) allometric relationships between diameter at breast height, tree height and total tree biomass, (2) a fixed ratio between living sapwood area and foliage area, and (3) a fixed ratio between foliage biomass and fine root biomass. Based on these constraints, an iterative procedure is used to distribute the annual net photosynthesis giving priority to: (1) foliage, (2) storage, (3) sapwood, after a fixed amount has been allocated to the sapwood. Table 6.2 outlines the main features of both FORGRO and HYBRID.

The impact of frost damage on growth is described in FORGRO *by complete* defoliation if the daily minimum temperature is less than the state of frost hardiness. From that point onwards, the tree has to rebuild its canopy from the pool of reserves. This method is not possible in HYBRID because of the annual allocation method used. Therefore in HYBRID, the photosynthetic capacity is reduced by 50% each time frost damage occurs. This reduction affects photosynthesis during the entire growing season (Friend et al, submitted).

Scenarios and initialization

Both FORGRO and HYBRID require daily input of the meteorological variables: minimum and maximum temperature, radiation, precipitation, vapour pressure, and wind speed. The variable evaluated was the annual net primary production, NPP (t C ha^{-1} yr^{-1}) per species, averaged over the simulation period. To evaluate the importance of phenology with respect to climate change, the atmospheric CO_2 concentration was set at 700 μmol mol^{-1}, and the observed temperature series was increased uniformly by a maximum of 7°C in steps of 1 °C ($C_{700}/T_{0...7}$). The benchmark scenario (C_{350} / T_0), i.e. ambient CO_2 concentration without a change in temperature, was also examined.

For FORGRO, observations of the period 1940 to 1990 for De Bilt (52°N, 6°E), located in the centre of The Netherlands, were used as input. FORGRO was initialised for a 30-year old stand similar to Kramer (1995b, Chapter 5). HYBRID was initialised with seedlings of a cold-deciduous General Plant Type (Friend et al. submitted). Thus the simulation period is from 1910 to 1990 in HYBRID. The initialization of the biomass and number of trees of a species in a mixed-species stand was one-third of that of the monospecies stand, for both FORGRO and HYBRID.

Results

Phenology and spring frost damage

The differences in the mean date of leaf unfolding, and in the response to an increase in temperature between the phenological types (Table 6.1) affects the duration of the growing season. This results in differences in available radiation during the growing season with increasing temperature (Figure 6.1). Both the regression and the modelling approach show that during the growing season of *Quercus,* less radiation is available than during the growing season of both *Fagus* and *Betula.* Furthermore, for *Fagus* the available radiation exceeds that of *Betula* if the temperature increases by more than about 3°C. However, the increase of the available radiation with temperature is larger according to the modelling approach than based on the regression approach, because the sequential model predicts a larger advancement of leaf unfolding with temperature than observed (Table 6.1).

The differences in the mean date of leaf unfolding, and in the response to an increase in temperature between the phenological types (Table 6.1) result furthermore in differences in the occurrence of frost around the date of leaf unfolding when they unfold their leaves (Figure 6.2). The earlier a species unfolds its leaves, the higher the probability of being damaged by spring frost.

Thus for the phenological types considered, *Betula* has the highest probability of frost damage and *Quercus* the lowest one, whereas *Fagus* takes an intermediate position. With increasing temperature this probability quickly decreases for these phenological types (Figure 6.2).

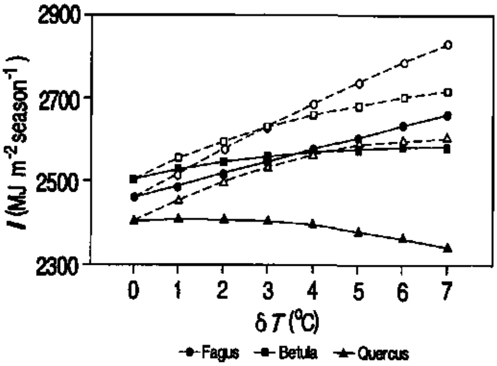

Figure 6.1. Global radiation available during the growing season (*I*). Mean of 1940-1990 in The Netherlands. Solid lines and closed symbols, regression approach; dotted lines and open symbols, modelling approach.

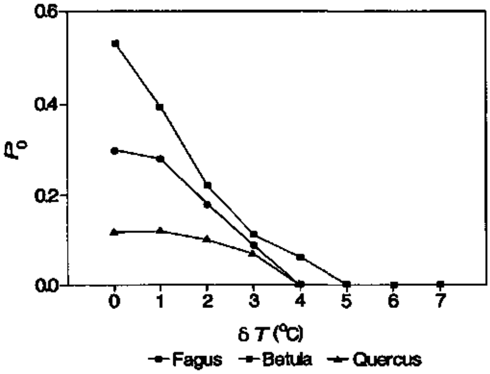

Figure 6.2. Probability of sub-zero temperature in a symmetrical 11-day interval around the date of leaf unfolding (P_0) according to the sequential model.

δ*T*, temperature scenario imposed on the observed values for the period 1940-1990 in The Netherlands.

Growth

Both available radiation and frost damage influence photosynthesis and consequently growth. In the following, the results of both the regression and the modelling approach for phenology and frost hardiness are presented, using the models FORGRO and HYBRID.

FORGRO. Based on the regression approach, without the impacts of frost damage, the pattern of gross primary production (GPP), net primary production (NPP), and respiration is similar to that of the amount of radiation available during the growing season (Figures 6.1 and 6.3). Thus, GPP, NPP and respiration of *Fagus* exceeds that of *Betula* if the increase in temperature is larger than about 3°C, whereas these values for *Quercus* are consistently lower than for both *Fagus* and *Betula.*

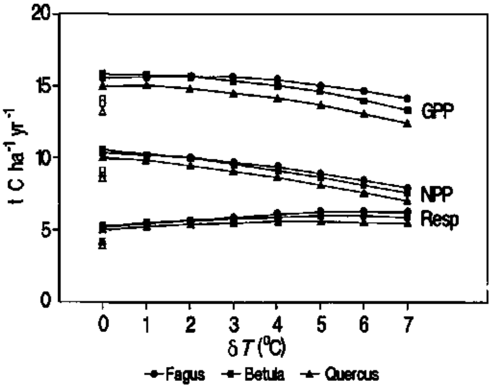

Figure 6.3. Gross primary production (GPP), net primary production (NPP), and respiration of a monospecies stand according to FORGRO, using the regression approach. No effect of frost damage. Open symbols, results of benchmark scenario.

δ*T*, temperature scenario imposed on the observed values for the period 1940-1990 in The Netherlands.

The effect of frost damage on the results of the C_{700}/T_0 scenario, using the fixed frost damage threshold, is a reduction of the NPP of *Betula* in the monospecies stands with 4%, but virtually no change of the NPP of *Fagus* and *Quercus* (Figure 6.4). In mixed-species stands, however, the effect of the same level of frost damage results in much larger differences between the phenological types (Figure 6.4). The reduction of the NPP of *Betula,* compared with the non-damaged situation, leads to an increase of the NPP of *Fagus* and *Quercus*. Frost damage affects the NPP if the temperature increase is less than 3°C, although the probability of sub-zero temperature is then still approximately 10% for each of the phenological types (Figure 6.2).

Both the regression and the modelling approach yield similar responses of NPP with increasing temperature (Figures 6.4 and 6.5). The differences between the approaches are: (1) the NPP of the phenological types diverges more in case of the modelling approach, because of the larger divergence of the amount of available radiation during the growing season (Figure 6.1), and (2) the impact of frost damage on NPP of the mixed-species stands is less in case of the modelling approach for frost hardiness.

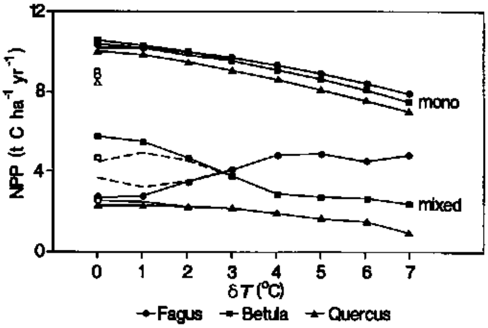

Figure 6.4. Net primary production of a mono- and mixed-species stand according to FORGRO, using the regression approach.

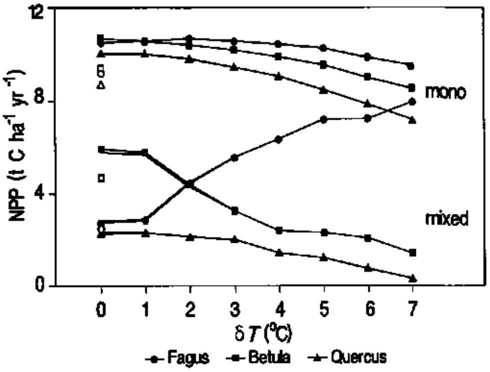

Figure 6.5. Net primary production of a mono- and mixed-species stand according to FORGRO, using the modelling approach.

Solid lines, no effect of frost damage; dotted lines, effect of frost damage. Open symbols, results of benchmark scenario without frost damage.

δ*T*, temperature scenario imposed on the observed values for the period 1940-1990 in The Netherlands.

The reason that the modelling approach for frost hardiness affects NPP less than the constant hardiness threshold is depicted in Figure 6.6: the occurrence of frost damage is larger based on the constant threshold than according to the modelling approach. Based on the parametrization of Leinonen et al. (1995) of the frost hardiness model, the minimum level of frost hardiness is attained after the moment of leaf unfolding. Furthermore, the period between the date of leaf unfolding and the date that the minimum level of frost hardiness is attained, increases with rising temperature, thus reducing the frequency of frost damage.

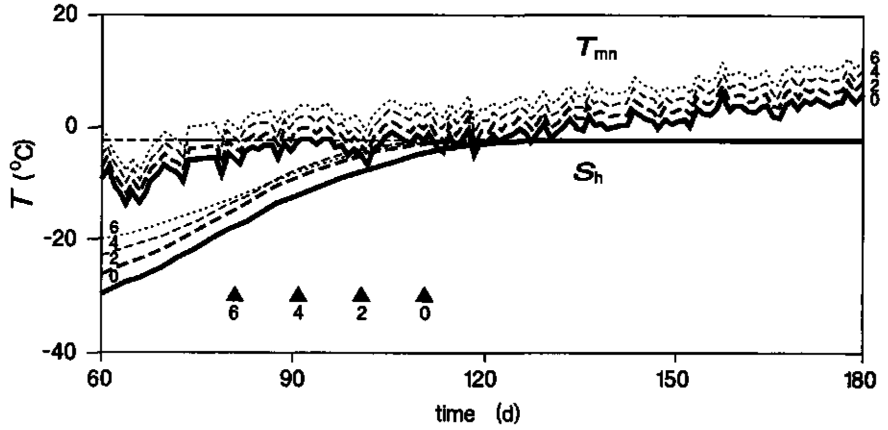

Figure 6.6. Effect of a rise in temperature by 2, 4, and 6°C on frost damage of *Betula*. Frost damage occurs when the minimum daily temperature is less than the level of frost hardiness. T_{mn}, lowest daily minimum temperature in the period 1940-1990; S_h , mean of the actual state of frost hardiness during the same period; horizontal dotted line at -2.3°C: constant level of frost hardiness; triangles, mean date of leaf unfolding, according to the modelling approach.

HYBRID. If population dynamics are taken into account also to assess the importance of phenology with respect to intercepted radiation and frost damage, then a complex picture emerges (Figure 6.7). The progression of the leaf area index in a monospecies stand of *Betula* differs considerably between the scenarios, because of the mortality of trees, and the establishment of new seedlings. For example, the C_{700}/T_0 scenario results in one big tree in the gap (of 400 m^2) after about 30 years. When this tree dies, the build up of the stand starts again. The same pattern is found if the temperature rises by 1 °C (not shown), but not within the selected simulation period if the temperature rises more. Frost damage, using the modelling approach, affects the dynamics of *Betula* if the temperature increase is less than 3 °C, but especially reduces the formation of leaf area on seedlings in the C_{350}/T_0 and C_{700}/T_0 scenarios. Characteristically, the annual net primary production is highest during the build up phase. The average NPP depends therefore, on the period over which this average is calculated, because in some cases the simulation period covers two cycles of forest succession, and in other cases less than one cycle (Figure 6.7). This makes it difficult to choose a period over which the NPP can be averaged best. Averaging the NPP over the entire 80-year simulation period, *Quercus* yields the lowest NPP, *Fagus* the highest NPP when the temperature rise exceeds 2 °C, and *Betula* is affected most by frost damage (Figures 6.8 and 6.9).

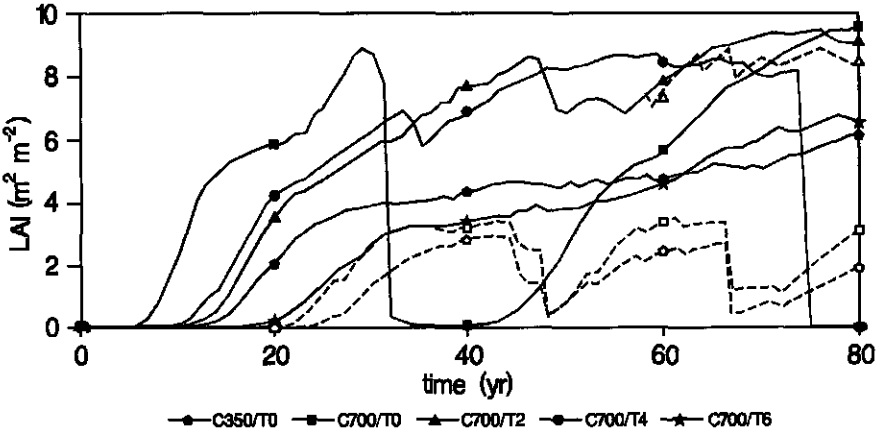

Figure 6.7. Progression of the leaf area index (LAI) of a monospecies stand of *Betula* according to HYBRID, using the modelling approach for phenology and frost hardiness. Solid lines and closed symbols, no effects of frost damage; dotted lines and open symbols, effect of frost damage, using a constant frost hardiness threshold (-2.3 °C).

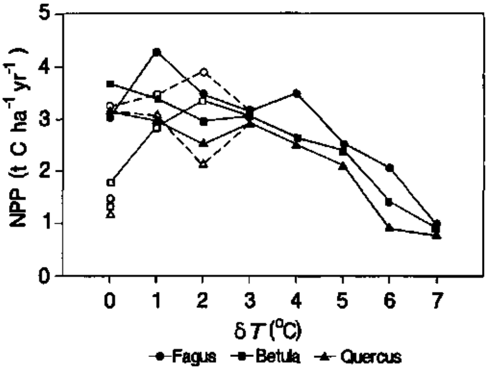

Figure 6.8. Net primary production of a monospecies stand according to HYBRID, using the modelling approach.

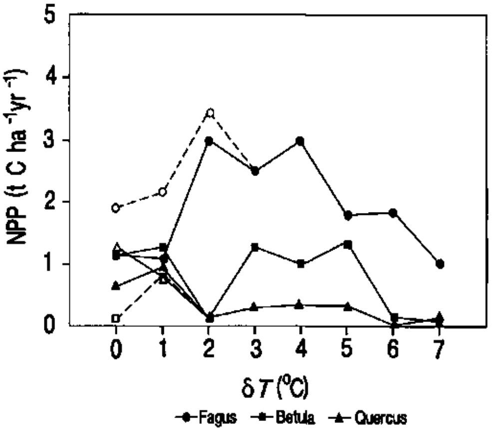

Figure 6.9. Net primary production of a mixed-species stand according to HYBRID, using the modelling approach.

Solid lines and closed symbols, no effect of frost damage; dotted lines and open symbols, effect of frost damage, using a constant frost hardiness threshold (-2.3 °C). Single closed symbols, results of benchmark scenario without frost damage.

δ*T*, temperature scenario imposed on the observed values for the period 1940-1990 in The Netherlands.

For a more detailed analysis, however, also the pattern of forest dynamics is required. Then it can be seen why including frost damage in some cases causes an increase of the NPP of a phenological type: this can be either because of competition, or because of the selected simulation period. An example of the first mechanism is shown in Figure 6.10. *Betula* is affected most by frost damage. Thus, a reduction of the NPP of *Betula* results in an increase of the NPP of both *Fagus* and *Quercus*. An example of the second mechanism is shown in Figure 6.11. The advancement of the death of a tree

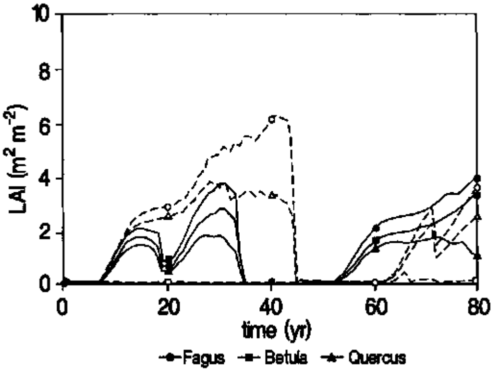

Figure 6.10. Progression of the leaf area index (LAI) of a mixed-species stand based of the C_{700}/T_0 scenario according to HYBRID, using the modelling approach for phenology and frost hardiness.

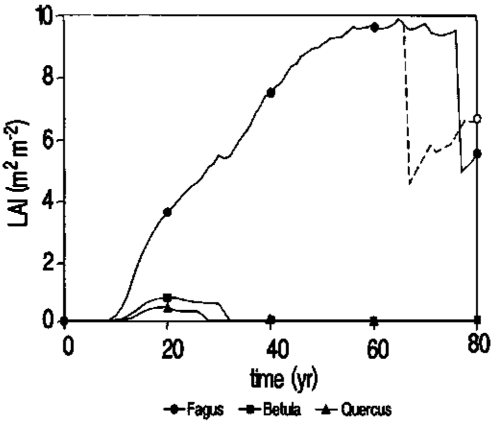

Figure 6.11. Progression of the leaf area index (LAI) of a mixed-species stand based of the C_{700}/T_2 scenario according to HYBRID, using the modelling approach for phenology and frost hardiness.

Solid lines and closed symbols, no effect of frost damage; dotted lines and open symbols, effect of frost damage.

due to frost damage causes a reduction in biomass and thus in the costs for respiration which exceeds the loss in photosynthesis because of a reduction in LAI. Since the LAI is still rather high for a deciduous species (Figure 6.11), the NPP of the last 15 years simulated including frost damage, exceeds the NPP without the effects of frost damage (Figure 6.9).

The sensitivity of the NPP on the simulation period can be circumvented by averaging over several plots that are in a different stage of succession, and using a longer simulation period. Friend et al. (submitted) advises to use ten plots, then a quasi-equilibrium is attained after 250 years, based on synthetic weather series. This is not done here because the focus is on the importance of phenology and spring frost damage on short-term forest dynamics, to evaluate transient responses of forests to climate change.

Discussion and conclusions

This study addressed the consequences of differences between species in phenology on growth of mixed deciduous tree stands, with respect to both the amount of radiation intercepted during the growing season and the occurrence of spring frost damage, in the context of climate change. The direct effect of an increase of the atmospheric CO_2 concentration that can be expected, is an increased rate of photosynthesis. This effect could be counteracted by an increased respiration, if the temperature rose due to the increased atmospheric CO_2 concentration. Temperature further influences growth by its effect on the date of both leaf unfolding and leaf fall, and thus on the duration of the growing season and on the occurrence of frost damage. The consequences of these combined effects on growth in mixed species stands were analysed with the models FORGRO, which highlights potential growth in managed forests, and HYBRID, which highlights feedbacks of carbon, water and nitrogen cycles on soil-vegetation-atmosphere dynamics.

With respect to the effects of differences between species in both phenological response and spring frost damage on growth in mixed species deciduous forests, in relation to an increased temperature and atmospheric CO_2 concentration, both FORGRO and HYBRID show: (1) that the differences in NPP of the three phenological types considered are enhanced when grown in mixed-species stands compared to monospecies stands. These differences increase with rising temperature, because the differences in the duration of the growing season between the phenological types increase with temperature. (2)

that the consequences of frost damage on growth is more prominent in mixed-species stands than in monospecies stands, because in the latter, a reduction in leaf area due to frost damage is quickly obviated by a rebuilding of the canopy, whereas in a mixed-species stand the rebuilding of the canopy is hampered by the presence of foliage of the trees which were less affected by the frost damage. The NPP is higher according to FORGRO, because of the dynamics of the number of trees simulated by HYBRID. NPP is low during the seedling phase, with a low leaf area index, and when there is one mature tree only, and is highest during the build-up phase. In FORGRO, the NPP is more constant during the entire simulation period.

Considering the accuracy of the modelling approach compared to the regression approach for the timing of leaf unfolding, both approaches show similar values and responses of NPP to the scenarios, for the monospecies and the mixed-species stand according to FORGRO (Figures 6.4 and 6.5). Although more light is available during the growing season according to the modelling appraoch, photosynthesis still can not compensate for the increase in respiration, if the temperature increases more than 3°C. The differences between the phenological types in NPP are, however, enhanced according to the modelling approach because the differences in the increase of the duration of the growing season, compared to the regression approach.

Considering the accuracy of the modelling approach compared to the regression approach for frost hardiness, the regression approach shows a greater frequency of frost damage, because according to the model the minimum level of frost hardiness is attained after the date of leaf unfolding, thus reducing this frequency (Figure 6.6). According FORGRO, NPP is reduced more in case of the regression approach, especially in mixed-species stands (Figures 6.4 and 6.5) However, both approaches do not qualitatively affect the outcome of competition. The impact of frost damage on growth is less according to in FORGRO than according to HYBRID. In FORGRO the canopy is quickly rebuilt, if there are sufficient reserves. In HYBRID, especially the seedling stage is affected by frost damage, and delays the moment when the build-up phase starts (Figure 6.7). This delay reduces consequently the mean NPP of the simulation period (Figure 6.8). Thus, it is important to assess the degree of injury brought about by frost to evaluate climate change impacts on the transient dynamics of temperate-zone deciduous forests. This is, however, not constant but depends on the freezing rate, phenological stage, tissue hydration, solute in sap, and external wetness (Santibanez 1994). Furthermore, the dehardening of *Pinus sylvestris* not only depends on temperature, but was found to be hastened with elevated CO_2 (Repo et al. in press).

The results of this study can be used to evaluate the transient responses of the geographical distribution of species to climate change. Usually close correlations are found between the geographical distribution of a species and climatic variables such as absolute minimum temperature, precipitation, mean annual temperature is used (Sakai and Larcher 1987, Woodward 1992). These correlations can, however, not be used to predict the responses of the species to climate change scenarios, because these correlations may not indicate the cause of the distributions (Woodward and McKee 1991). They state further that the absolute minimum temperature, perse, does not limit the distribution of boreal trees, because these trees can endure temperture below -90°C, but the length and temperature of the growing season is an important limit. Consequently, competition limits the expansion of vegetation types in equatorial direction (Woodward 1992). This study confirms that differences in the duration of the growing season, in combination with spring frost damage, has profound impacts on competition between tree species.

Chapter 7

General discussion

Phenology and scale

Phenology links the functioning of a tree to the climate of its environment. In seasonal climates, selective pressure synchronises growth to the period favourable for growth. Therefore, phenology influences both *capacity adaptation*, the ability to metabolise, grow and develop in a specific environment, and *survival adaptation*, the ability to survive the physical extremes which the environment imposes on trees. Both aspects determine the competitive ability of a species. Here the term *competition* is used to mean the reduction in growth of a species caused by the presence of another species that requires the same limiting resource. In the research described in this thesis, only species differences affecting competition for light were considered, by evaluating the growth of homogeneous, even-aged forest stands under conditions of non-limiting water and nutrient supply. This competitive ability has direct consequences both for the species composition of forests and for the geographical distribution of a species if climatological conditions change.

Phenology further links vegetation to the atmosphere by influencing the exchange of water, carbon dioxide, and energy. The timing and rate of the 'green wave' in spring and the 'brown wave' in autumn modify the surface energy and moisture balances of the lower atmosphere (Schwartz 1994). Thus, phenology affects vegetation-atmosphere interactions that must be accounted for in General Circulation Models, to predict climate and its impacts on vegetation.

The scientific challenge lies in analysing the relationship between climate and tree phenology at the individual, ecosystem, regional and global scales, and in assessing the consequences for forest management. This study focused on the analysis at the scale of individual trees and ecosystems. The relevance of phenology to capacity adaptation was evaluated by several forest growth models, while its relevance for survival adaptation was assessed by evaluating the impacts of frost damage.

Phenology: models and data

To answer the questions posed in this study, I relied on phenological models developed, and data collected by other researchers, and assumed that the information compiled elsewhere and integrated in recent decades can be used to assess climate change impacts on phenology and growth of forests. The models and data both have merits and limitations, as outlined below.

Models

In population genetics, two general types of model are discerned to evaluate the consequences of selection pressure caused by a changing environment. Firstly, there are *character state* models, which describe the causes that lead to the value attained by a character of a genotype in a specific environment. Secondly, there are *reaction norm* models, which describe the functional response of such a character to different environments (De Jong 1995). (A functional response is the meaningful change in physiology and/or morphology caused by different environmental conditions: Bradshaw 1965). Reaction norms thus represent the phenotypic plasticity of a character of a genotype for an environmental factor. The character state model I selected for the date of leaf unfolding is the sequential model. As the reaction norm model I selected the linear regression through the dates of leaf unfolding of the clones as function of the mean winter temperature. I assumed that the reaction norm represents the response of the species to a future climate. This enabled the response of the sequential model to temperature scenarios to be tested against the reaction norm of the data. The results showed that the response of the sequential model to a rising mean winter temperature, using uniform climate change scenarios, exceeds the reaction norm of the clones to the mean winter temperatures. This is the consequence of the way the sequential model describes the rate of development during dormancy. This rate can only be measured indirectly as the reciprocal of the period between leaf fall and leaf unfolding, since a generally applicable mechanism is not known. However, experimental evidence has shown that dormancy consists of two phases that cannot be distinguished by eye: rest, affected by chilling temperatures, and quiescence, affected by forcing temperatures (Sarvas 1974). Consequently, the parameter values estimated numerically for the rate of chilling during rest correlate with the rate of forcing during quiescence, based on the dormant period. This implies that several combinations of parameter values exist, all predicting the same date of leaf unfolding. The estimation procedure yielded parameter values that give little variation in the duration of rest. Thus, most variation in the dates of leaf unfolding results from variation in the quiescent period. This was accounted for by a logistic function, mapping the variation of the temperature series to the variation of the date of leaf unfolding. Based on these functions and parameter values, independent observations were predicted accurately. However, when I used the sequential model for extrapolation in climate change studies, the advancement of leaf unfolding with temperature exceeded the reaction norm of the clones. The importance of this inaccuracy for growth of mixed-species forests was evaluated by the forest growth models. The results showed that this inaccuracy yields values for the annual net primary production, that arre higher than those attained with the reaction norm model. However, the competitive balance between the phenological types considered did not change.

Experiments have shown that temperature as well as photoperiod may affect the timing of phenological events (Vegis 1964). A rapid climate change could thus disturb the coordinated response to the photoperiodic signal, which remains unaltered, and the temperature signal (Reich 1995). The general pattern found is that photoperiod may be a substitute for chilling, whereas a threshold value of photoperiod may trigger leaf fall. Incorporating photoperiod additively to the rate of chilling increases the number of correlated parameters of the sequential model, and this made the model more difficult to calibrate. Thus, the impact of photoperiod on leaf unfolding could not be verified from the observations of the clones relocated over Europe. The results of the clones relocated over Europe show for both leaf unfolding and leaf fall, that there is no photoperiodic threshold that triggers these events.

Data

The phenological observations of the clones from the International Phenological Gardens proved very valuable for the evaluation the phenological model, and for studying the possible impacts of increased temperature on the duration of the growing season. The principal shortcoming of this data set is that it consists of annual means, and therefore no within-clone variance could be calculated and the data could not be rigorously statistically evaluated. The other shortcomings of the data were the non-adjacency of the temperature and phenological observations, and the variation in the number of phenological observations per location and year. Only one sufficiently long temperature series was available for The Netherlands, and the phenological observations were obtained from locations throughout the country. In addition, the varying number of observations per year resulted in an unequal distribution over the country. Hence, the differences between years were affected by site and genotypic differences too. Nevertheless, approximately 80% of the variation in leaf unfolding in the phenological types discerned in this study could be explained by temperature only.

Forest growth models and climate change scenarios

Whether an increase in atmospheric carbon dioxide and in temperature leads directly to increased forest growth, depends on the impacts on photosynthesis and respiration, assuming the absence of acclimation of photosynthesis to increased CO_2 by down-regulation of the amount and/or activity of Rubisco (Ceulemans and Moussau 1995), and provided that nutrients and water are available in non-limiting amounts. The photosynthesis models consistently showed an increase in annual gross photosynthesis of approximately 20% if the CO_2 concentration doubles. Thus, the sensitivity of photosynthesis and respiration to temperature is crucial to assess climate change impacts on growth. At a certain break-even temperature, the increased gains by photosynthesis are counteracted by the increased cost of respiration, because photosynthesis depends on temperature according to an optimum curve, whereas respiration increases exponentially with temperature (Goudriaan and Van Laar 1994). The Farquhar approach to photosynthesis uses Arrhenius equations to describe the effect of temperature on photosynthesis (Farquhar and Von Caemmerer 1982). Since these are exponential equations, they are very sensitive to errors in the measurement of the exponents. The empirical approach to photosynthesis involves using a temperature multiplier based on linear interpolation of experimental data, which is less sensitive to measurements errors. However, the empirical approach ignores the interaction between CO_2 and temperature, whereas the Farquhar approach takes account of it in accordance with experimental evidence (Kirschbaum 1994). Consequently, the Farquhar approach to photosynthesis yields a higher value for the break-even temperature than the empirical approach.

However, the break-even temperature depends on the climate change scenarios and the forest growth models used. Both have their merits and limitations, as outlined below.

Scenarios

Two aspects of the scenarios may result in a lower break-even temperature: (1) The 'doubling of CO_2' used in General Circulation Models, in fact refers to all greenhouse gases, expressed in the equivalent radiative power of an atmospheric CO_2 concentration of 700 μmol mol^{-1}. However, CO_2 constitutes only half of the greenhouse gases. Nevertheless, in physiological experiments, plant growth at a CO_2 concentration of 700 μmol mol^{-1} is usually compared to that at 350 μmol mol^{-1}. So, the response of gross photosynthesis to the GCM scenarios may in fact be half of the measured response. In the present study, the photosynthesis response to 700 μmol mol^{-1} was used, enabling comparisons to to be made with experimental results.

(2) The GCMs predict that temperature will increase mainly in winter, and observations indicate that the temperature increase in summer is mainly due to an increase in nocturnal temperature (Houghton et al. 1990). As a consequence of these points, photosynthesis may be overestimated and respiration underestimated, thus reducing the break-even temperature.

However, because the atmospheric CO_2 concentration rises gradually, instead of doubling instantaneously, it is likely to affect the climate gradually. Assuming a transient climate change scenario, in which the CO_2 concentration rises linearly to 700 μmol mol^{-1}, and the temperature increases linearly over a 100-year period, then the break-even temperature increases by approximately 1 °C, because the impact of temperature on respiration is delayed compared to the effect of CO_2 on photosynthesis.

Another assumption was that the incidence of extreme events would remain unchanged. If, however, the incidence of hurricanes and periods of drought were to increase, this would affect forest growth more dramatically than the direct impacts of increased CO_2 and temperature.

Models

The forest growth models used in this study had various limitations. The version of FORGRO used, did not take nutrients or water into account. In the ITE-FORGRO and HYBRID models the species did not differ in nutrient and water use. Despite these limitations, the models consistently showed that differences in phenology result in significant differences in capacity adaptation.

The relevance of phenology for survival adaptation was considered by introducing a model describing the progression of frost hardiness, and by evaluating the possible effects of frost damage on photosynthesis. It was found that frost damage affects the competitive ability of a species, and thus the growth and dynamics of mixed-species forest.

In summary, it could be concluded that the differences between the phenological types in both capacity adaptation (characterised by the forest growth models) and survival adaptation (characterised by the frost hardiness model) significantly affect competition between these types.

Forest management

If the climate changes, then the growth of forests may be affected. This study indicates that the growth of monospecies forests in Europe will be boosted by 15 to 30%, if the CO_2 concentration doubles and the temperature increases by 2°C, providing that nutrients and water are available in non-limiting amounts. Furthermore, the different responses of species affect their competitive ability. Forest dynamics will therefore change, and possibly so will species composition. This implies that climate change may affect both the forest type that a forest manager is aiming at, and the silvicultural treatment required to achieve the management goals. This poses practical problems for forest management that cannot be solved from historical experience. In this study, a mechanistic approach for analysing future forest growth was used instead of empirical estimates of growth and yield. Using this approach, appropriate future forest types can be derived from models such as HYBRID which consider environmental influences on the competition and dynamics of natural forests, such as the model HYBRID. The appropriate silvicultural treatment can be derived using models such as FORGRO, which explicitly account for silvicultural options and for changed competitive relations between tree species

Forestry research has a long history of analysing and optimizing phenological characters of plantation species through selection programmes and provenance trials. The results reported in this study indicate that species may be phenotypically capable of a significant plastic response to an altered environment. Traditionally, such a response was considered to counteract selection pressure (Thomson 1991). The current idea, however, is that phenotypic plasticity is itself an adaptive character, which is genetically controlled (Sultan 1992). As a result, selection on characters that show a plastic response to an environmental factor will only succeed if there is genetic variation for the reaction norm. For selection on phenological characters this implies that for those species or genotypes for which these characters are strictly photoperiodically controlled have no reaction norms to temperature. Selection must therefore be directed to adjusting the mean of the character. If the phenological characters are mainly driven by temperature, then it should be confirmed that genetic variation for the reaction norm exists.

Summary

Research topics

The relationships between climate and both phenology and growth of some important European tree species were studied to evaluate the potential impacts of climate change on trees and forests in Europe. In order to make such assessments, insight is required on the mechanisms how climatic variables interact with plant processes. The topics addressed in this study were: (1) the modelling of phenology, (2) the consequences of climate change on spring frost damage, (3) the importance of phenotypic plasticity, (4) the importance of phenology on the effects of climate change on growth of monospecies deciduous forests, and (5) the importance of phenology on the effects of climate change on growth of mixed-species deciduous forests.

Modelling phenology

To evaluate the impacts of climate change on growth of temperate deciduous tree species, the onset and cessation of the growth must be accurately described. A review is presented on eight models predicting the date of leaf unfolding depending on temperature. These models were fitted using 57 years of observations on the date of leaf unfolding of *Fagus sylvatica* in The Netherlands, and used to predict 40 years of similar observations collected in Germany. As conflicting experimental evidence exist on the role of photoperiod on leaf unfolding of *Fagus sylvatica*, photoperiod was incorporated into each of these models.

The timing of leaf unfolding could best be described by a model in which the effects of chilling temperatures (-5 to +10°C) and forcing temperatures (>0°C) operate sequentially in time, according to a triangular and logistic

function, respectively. Including photoperiod reduced the predicting power of this model.

Spring frost damage

Two studies presented in literature evaluate the effect of increasing winter temperature on the probability of spring frost damage to trees. However, one study predicted an increase, while the other predicted a decrease in the probability of spring frost damage. It is unclear whether the disparity is because: (1) different models were used, (2) different climatic warming scenarios used, or (3) the tree species at the different locations respond differently to warmer winters. To evaluate the effects of climatic warming to *Larix decidua, Betula pubescens, Tilia platyphylla, Fagus sylvatica, Tilia cordata, Quercus rubra, Quercus robur, Fraxinus excelcior, Quercus petraea, Picea abies* and *Pinus sylvestris* in The Netherlands and in Germany, both models were fitted to long series of observations on the date of leaf unfolding of these tree species. The impact of the two scenarios (uniformly and non-uniformly changing winter temperature) on the date of leaf unfolding and on the probability of freezing temperature around that date was evaluated. To test the importance of adaptation to local climate, hypothetical provenance transfers were analysed.

For tree species in The Netherlands and Germany the probability of spring frost damage will decrease, provided the variability in temperature does not change. The contradictory results found in literature could be ascribed to differences among provenances adapted to their local climate, rather than to differences between either the models or the climatic warming scenarios used in these studies.

Plasticity

To evaluate the potential response of individual trees to climatic warming, phenological observations of clones of *Larix decidua, Betula pubescens, Tilia cordata, Populus canescens, Quercus robur, Fagus sylvatica*, and *Picea abies* transferred over a large latitudinal range in Europe were analysed. The magnitude of the clone's response was compared to that of genetically different trees of the same species along a part of the latitudinal range, which were assumed to have adapted to their local climate.

The responses of the date of leaf unfolding and leaf fall of the clones to temperature are similar in magnitude to those of the genetically different trees. This demonstrates that trees possess a considerable plasticity and are able to respond phenotypically to a major change in their local climate. For the clones of *Larix decidua* and *Quercus robur* the growing season may shorten with increasing temperature, because leaf fall is advanced more than leaf unfolding. In *Betula pubescens* and *Populus canescens*, leaf unfolding and leaf fall are advanced equally, whereas in *Tilia cordata* and *Fagus sylvatica* the date of leaf fall seems to be unaltered but leaf unfolding advances with increasing temperature. These differences in the duration of the growing season in response to increasing temperature may alter the competitive balance between the species in mixed stands.

Descriptive dynamic models showed that most of the variance of the date of leaf unfolding can be accounted for by temperature. However, a generally applicable model of leaf fall based on temperature and/or photoperiod could not improve the null model, i.e. the mean date of leaf fall, because of variability in other environmental factors.

The lowest temperature around the date of leaf unfolding and leaf fall differed among the clones. The hypothesis that the survival of the clones is curtailed by spring frosts was supported. Thus, these lowest temperatures around leaf unfolding may represent thresholds below which the species cannot survive.

It is argued that these thresholds may be a particularly sensitive means to evaluate the impacts of climatic warming on the geographical distribution of tree species.

Growth of monospecies forests

The importance of three phenological types of deciduous tree for the effects of climate change on growth of monospecies forests was evaluated using the model FORGRO. The climate change scenarios used were a doubling of the CO_2 concentration (700 μmol mol^{-1}) and an increase in temperature ranging from 0 to 7°C. To elucidate the relative importance of photosynthesis and allocation for this evaluation, models with different levels of mechanistic detail of photosynthesis and allocation were used. The photosynthesis approach of FORGRO was compared to the Farquhar and Von Caemmerer approach as formulated in PGEN (FORGRO-PGEN). Similarly, the allocation approach of FORGRO was compared to the transport-resistance approach, as formulated in the ITE-Edinburgh model (ITE-FORGRO). A sensitivity analysis was performed to ascertain whether the response of gross photosynthesis to a climate change scenario depends on the value assigned to parameters in these models, and to compare this sensitivity with the differences found between the phenological types. The differences in the response of annual gross photosynthesis ($P_{g,a}$) to the climate change scenarios between the phenological types were smaller according to ITE-FORGRO as compared to FORGRO. These differences are of a similar magnitude when comparing the two photosynthesis models. Furthermore, FORGRO-PGEN showed that the response of $P_{g,a}$ to a 2 x $[CO_2]$ increases with rising temperature, thus compensating for the increase in respiration. For both FORGRO and ITE-FORGRO, this CO_2 and temperature interaction was not found. Consequently, in these models the increase in respiration exceeded the increase in gross photosynthesis at the higher range of temperature rise. The sensitivity analysis showed that the models differ in the sensitivity of the response of $P_{g,a}$ to a 2 x $[CO_2]$ scenario combined with a temperature rise of 2°C (C_{700}/T_2), when parameter values change by ±25%. In FORGRO-PGEN, the magnitude of the response of $P_{g,a}$ depended on the values of some of its parameters, especially those determining the Michaelis-Menten kinetics of Rubisco, which for these parameters exceeded the differences between the phenological types in this scenario. In both FORGRO and ITE-FORGRO, this sensitivity is similar to or less than the difference between the phenological types in the C_{700}/T_2 scenario.

Growth of mixed-species forests

Using the same three phenological types and climate change scenarios, the effects of differences in phenology and spring frost damage on growth in mixed-species stands were evaluated using the models FORGRO and HYBRID. FORGRO highlights potential growth in managed forests, whereas HYBRID highlights feedbacks of carbon, water and nitrogen cycles in General Vegetation Types, based on gap model theory. Furthermore, the importance of inaccuracy of the phenological model for growth in mixed-species stands was evaluated by comparing the modelling approach with a regression approach.

The results of the climate change scenarios indicate for both FORGRO and HYBRID that: (1) the differences in NPP of the three phenological types considered are enhanced when grown in a mixed-species stand compared to a monospecies stand; and (2) the consequences of frost damage on growth is more prominent in mixed-species stands than in monospecies stands.

Considering the accuracy of the modelling approach compared to the regression approach for the timing of leaf unfolding and spring frost damage, the sequential model of leaf unfolding shows a similar response of the NPP as the regression approach, both for the monospecies and the mixed-species situation. The modelling approach yields, however, larger differences in the NPP between the phenological types because the model predicts a greater advancement of leaf unfolding than the regression model. Comparing the regression approach to the modelling approach for frost hardiness, the regression approach shows a greater frequency of frost damage, because according to the model, the minimum level of frost hardiness is attained after the date of leaf unfolding, thus reducing this frequency.

The differences in phenological response to temperature can be used to evaluate the consequences of climate change on the geographical distributions of species.

Samenvatting

Klimaatverandering

Verbranding van fossiele brandstoffen en grootschalige ontbossing heeft een snelle toename van de koolstofdioxideconcentratie in de atmosfeer tot gevolg. Atmosferisch CO_2 laat de kortgolvige straling door die van de zon komt, maar absorbeert de langgolvige straling die de aarde uitzendt. CO_2 zendt vervolgens deze geabsorbeerde straling weer uit, dus ook richting de aarde. Dit heeft tot gevolg dat de warmtebalans van de aarde verandert. Het is dus mogelijk dat als gevolg van de gewijzigde atmosferische samenstelling het klimaat op aarde verandert. Algemene circulatiemodellen die de weerpatronen op aarde simuleren, geven een toename aan van de gemiddelde temperatuur met 2 tot 5 °C, en een verandering in neerslag bij een verdubbeling van de CO_2-concentratie in de atmosfeer. Er bestaat echter nog veel onzekerheid over de mate van deze verandering omdat het klimaat uiteindelijk door zeer veel factoren wordt bepaald. Wel is duidelijk dat er grote regionale verschillen in klimaatverandering bestaan.

Methodologie

Experimenten kunnen niet direct uitsluitsel geven hoe een toekomstig klimaat de groei en ontwikkeling van bomen en bossen zal beïnvloeden, vanwege de grootte en levensduur van bomen, en door de complexiteit van de betrokken processen. Numerieke simulatiemodellen bieden de mogelijkheid om de ruimtelijke en temporele schaal te overbruggen door de relevante processen te integreren. Toekomstprojecties van groei in een klimaat dat tot dusverre nog niet is voorgekomen, zijn alleen dan mogelijk indien de relaties tussen de processen die groei en ontwikkeling bepalen en het klimaat, op een mechanistische manier worden beschreven. Experimenten die deze relaties verhelderen, bieden de essentiële informatie hoe de modellen ontworpen dienen te worden. Dus de mechanistische modellering van de groei van het bos, op een solide experimentele basis, in combinatie met realistische klimaatveranderingsscenario's, is de enige mogelijkheid om een indruk te krijgen van de toekomstige groei van het bos.

Wegens onvoldoende kennis omtrent het functioneren van het klimaat is het echter moeilijk in te schatten of klimaatveranderingsscenario's realistisch zijn. Bovendien bestaan er veel onzekerheden over de modellering van de relevante processen. Om met onzekerheden in het toekomstige klimaat om te gaan is ervoor gekozen om historische meetreeksen te gewijzigen volgens een bepaald scenario. Dit met de gedachte dat voor locale studies de toekomstige weerpatronen zoals die door de algemene circulatiemodellen worden voorspeld waarschijnlijk minder betrouwbaar zijn dan een -aangepaste- continuering van vroegere weerpatronen. Verder zijn steeds de effecten van een reeks scenario's onderzocht. Om met onzekerheden over de modellering van de relevante processen om te gaan, zijn steeds modellen vergeleken die verschillen in de mate van detail waarin ze kritieke groeibepalende processen beschrijven. Als er een consistent resultaat wordt gevonden, geeft deze benadering meer vertrouwen in dit resultaat. Is dit niet het geval, dan biedt nadere analyse van de modellen de mogelijkheid om de verschillen te verklaren. Iedere uitspraak die in deze studie gedaan wordt over de gevolgen van klimaatverandering op fenologie en groei van bomen en bossen moet daarom met enige voorzichtigheid gehanteerd geworden, gezien de onzekerheid in zowel de klimaatveranderingsscenario's en sommige aspecten van de modellen.

Fenologie en groei

Deze studie behandelt de effecten van klimaatverandering op fenologie en groei van enkele belangrijke Europese boomsoorten. Fenologie van bomen is de studie hoe jaarlijks terugkerende gebeurtenissen zoals bladontplooiing, bloei, vruchtzetting en bladval, beïnvloed worden door klimaat- en andere omgevingsfactoren. Een nauwkeurige synchronisatie tussen de periode waarin een boom groeit en de periode die klimatologisch gunstig is om te groeien is van belang om niet verdrongen te worden door soorten die beter gesynchroniseerd zijn. Als hij te vroeg uitloopt, bestaat de kans dat door late nachtvorst het blad beschadigd wordt. Als hij te laat uitloopt, wordt de periode die gunstig is voor groei, niet optimaal benut. Temperatuur is hierbij het belangrijkste omgevingsignaal om deze synchronisatie te bewerkstelligen. Om niet uit te lopen gedurende een warme periode in de winter, hebben bomen in gematigde en boreale gebieden eerst een periode met koele temperatuur nodig, voordat zij gevoelig zijn voor de warme voorjaarstemperatuur die tot het uitlopen van het blad leidt. Als het klimaat zou veranderen gedurende het leven van een boom, kan de synchronisatie verstoord worden. Daar staat tegenover dat individuele bomen mogelijk de plasticiteit bezitten om fenotypisch de synchronisatie te herstellen, m.a.w. om de timing van fenologische gebeurtenissen aan te passen aan een wijziging in hun omgeving. Als soorten verschillend reageren op een klimaatverandering, veranderen de concurrentie verhoudingen tussen deze soorten wanneer zij gezamelijk voorkomen. Op de lange termijn verandert daardoor de samenstelling van een natuurlijk bos.

Deze gedachtengang heeft geleid tot de volgende vragen die in deze studie aan de orde zijn gekomen: (1) hoe is de relatie tussen klimaatfactoren en de timing van fenologische gebeurtenissen zoals bladontplooiing en bladval te modelleren? (2) wat zijn de gevolgen van een klimaatverandering voor de kans op voorjaarsvorstschade? (3) bezitten bomen plasticiteit wat betreft bladontplooiing en bladval om zich fenotypisch aan een wijziging van het klimaat in hun omgeving aan te passen? (4) wat is het belang van fenologie voor de groei van ongemengde bossen? en (5) wat is het belang van fenologie en voorjaarsvorstschade voor groei van gemengde bossen?

Modellering van fenologie

Een overzicht is gepresenteerd van acht modellen die de datum van bladontplooiing voorspellen op grond van temperatuur. De parameterwaarden van deze modellen zijn geschat op grond van waarnemingen van de datum van bladontplooiing van beuk in Nederland gedurende de periode 1901 tot en met 1968 ($n=57$). Deze modellen zijn getoetst met gelijksoortige waarnemingen in Duitsland gedurende de periode 1951 tot en met 1990 ($n=40$). Omdat experimenten elkaar tegenspreken wat betreft de invloed van fotoperiode op bladontplooiing van beuk, is in elk van deze modellen eveneens het mogelijke effect van fotoperiode betrokken.

Het bleek dat de datum van bladontplooiing van beuk het best beschreven kan worden met een model waarin een periode met koele temperatuur gevolgd wordt door een periode met warme temperatuur, volgens respectievelijk een driehoeks- en een logistische functie. Toevoeging van fotoperiode verslechterde het voorspellend vermogen van dit model.

Voorjaarsvorstschade

In de literatuur zijn twee studies gepresenteerd die het effect van een toename in wintertemperatuur op de kans op voorjaarsvorstschade onderzoeken. De ene studie voorspelde echter een toename van deze kans, en de andere een afname. Het was onduidelijk of dit tegengestelde resultaat het gevolg was van het feit dat verschillende modellen waren gebruikt, of dat verschillende klimaatveranderingsscenario's waren gebruikt, of dat de boomsoorten op de lokaties verschillend reageren op warme winters. De parameterwaarden van beide modellen zijn geschat op grond van langjarige waarnemingen van bladontplooiing aan Europese lariks, zachte berk, zomerlinde, beuk, winterlinde, Amerikaanse eik, zomereik, es, wintereik, fijnspar en grove den in Nederland en Duitsland. Vervolgens is het effect onderzocht van beide klimaat-

veranderingsscenario's (een uniforme en een niet-uniforme temperatuurstijging) op de datum van bladontplooiing en op de kans op vorst rondom die datum. Om het belang van aanpassing aan het lokale klimaat te onderzoeken zijn hypothetische herkomstproeven geëvalueerd door middel van simulatie.
De conclusie was dat voor deze soorten de kans op voorjaarsvorstschade zal afnemen zowel in Nederland als in Duitsland. De tegengestelde resultaten uit de literatuur konden toegeschreven worden aan verschillen tussen de herkomsten. Zij zijn niet het gevolg van het feit dat verschillende modellen en klimaatveranderingsscenario's waren gebruikt.

Plasticiteit

Om de fenologische reactie te onderzoeken van individuele bomen op een klimaatverandering zijn bladontplooiing en bladval geanalyseerd van klonen die over een groot bereik van breedtegraden binnen Europa zijn aangeplant. Het betrof klonen van Europese lariks, zachte berk, winterlinde, grauwe abeel, zomereik, beuk en fijnspar. De mate waarin deze klonen reageren op verschillen tussen en binnen deze locaties werd vergeleken met dezelfde gegevens van genetisch ongelijke bomen van dezelfde soorten langs een deel van dit bereik. Van de genetisch ongelijke bomen werd verondersteld dat ze aangepast zijn aan het klimaat waar ze voorkomen. Dit is niet het geval voor de klonen omdat die van enkele locaties binnen Europa afkomstig zijn.
Wat betreft de datum van bladontplooiing bleek dat de respons op temperatuur van de klonen van dezelfde orde van grootte is als die van de genetisch ongelijke bomen. Opvallend was dat de kans op vorst rondom deze datum zowel bij de klonen als bij de genetisch verschillende bomen vrijwel gelijk is, en ook dat deze kans tamelijk constant is tussen de locaties, ondanks grote verschillen in temperatuur. Daarmee ondersteunen deze resultaten de veronderstelling dat de soorten een aanzienlijke plasticiteit bezitten wat betreft de datum van bladontplooiing, en dat de mate van verschuiving

begrensd wordt door vorst rondom genoemde datum. Toepassing van het eerder geselecteerde model maakte duidelijk dat de meeste variatie in de datum van bladontplooiing verklaard kan worden door de invloed van temperatuur. Het model overschat echter de respons van de datum van bladontplooïng op temperatuur. Bovendien is het model te flexibel aangezien de uiteindelijke respons het gevolg kan zijn van geheel verschillende reacties van de perioden waarin de boom gevoelig is voor koele en warme temperatuur.

Wat betreft de datum van bladval bleek de respons met temperatuur en de kans op vorst rondom deze datum veel minder duidelijk te zijn. Er werd geen duidelijk verband gevonden tussen de klonen en de genetisch ongelijke bomen. Bovendien kon er geen model gevonden worden dat de datum van bladval goed beschrijft, hoewel de datum van bladval van sommige soorten wel vervroegd wordt door een temperatuurstijging.

De gedachte dat sommige soorten uitlopen ofwel hun blad laten vallen als de daglengte een bepaalde duur bereikt, was voor de onderzochte klonen met zekerheid niet juist.

Voorts lijken er drie typen van fenologische reactie te zijn op een stijging in temperatuur: (1) de vervroeging van de datum in bladval is groter dan de vervroeging in bladontplooiing, dit is gevonden voor Europese lariks en zomereik, (2) de vervroeging van de datum van bladval en bladontplooiing is ongeveer even groot, dit is gevonden voor zachte berk en grauwe abeel, en (3) de vervroeging van de datum van bladontplooiing is groter dan die van de datum van bladval, zoals gevonden voor beuk en winterlinde. Op grond van dergelijke verschillen kunnen de groei en de concurrentieverhouding tussen soorten veranderen als gevolg van klimaatverandering.

Groei van ongemengde bossen

Het belang van de deze verschillende fenologische typen voor het effect van klimaatverandering op groei van ongemengde bossen is onderzocht met behulp van het bosgroeimodel FORGRO. De gebruikte klimaatveranderingsscenario's waren een verdubbeling van de atmosferische CO_2-concentratie in combinatie met een temperatuurstijging van 0 tot 7°C. Om het belang van fotosynthese en allocatie van assimilaten in deze analyse te verhelderen, zijn versies van FORGRO met elkaar vergeleken waarin deze processen met een verschillende mate van detail beschreven werden. De fotosynthesebenadering van FORGRO werd vergeleken van die van Farquhar en Von Caemmerer zoals beschreven in PGEN (FORGRO-PGEN). Op dezelfde manier werd de allocatiebenadering van FORGRO vergeleken met die van het transport-weerstand-model zoals beschreven in het ITE-Edinburgh model (ITE-FORGRO). Een gevoeligheidsanalyse was uitgevoerd om vast te stellen of de respons van de jaarlijkse brutofotosynthese ($P_{g,a}$) op een klimaatveranderingsscenario afhangt van de waarde van de parameters van deze modellen, en om deze gevoeligheid te vergelijken met de verschillen die veroorzaakt worden door de fenologische typen.

Het bleek dat de verschillen in de respons van $P_{g,a}$ op de klimaatveranderingsscenario's tussen de fenologische typen van ITE-FORGRO kleiner waren dan die van FORGRO. Deze verschillen zijn van eenzelfde orde van grootte volgens de twee fotosynthesemodellen. Volgens FORGRO-PGEN neemt de respons van $P_{g,a}$ op de 2 x $[CO_2]$ scenario's toe met stijgende temperatuur, en compenseert daarmee de toename in ademhalingskosten. FORGRO en ITE-FORGRO vertoonden deze interactie tussen CO_2 en temperatuur niet. Dit had tot gevolg dat volgens deze modellen de respiratie hoger was dan de fotosynthese bij een temperatuurstijging van meer dan ongeveer 4°C.

De gevoeligheidsanalyse toonde aan dat de modellen eveneens verschillen in de gevoeligheid van de respons van $P_{g,a}$ op de 2 x $[CO_2]$ scenario's in combinatie met een stijging van de temperatuur met 2°C (C_{700}/T_2), als de waarde van een parameter met plus en minus 25% gevarieerd werd. In FORGRO-PGEN was de respons van $P_{g,a}$ met name afhankelijk van die parameters die de Michaelis-Menten-kinetiek van Rubisco beschrijven. De verschillen in $P_{g,a}$

waren groter door deze parameters over dit bereik te variëren, dan door de fenologische typen. Voor zowel FORGRO als ITE-FORGRO was deze gevoeligheid gelijk of kleiner dan de verschillen tussen de fenologische typen voor het C_{700}/T_2 scenario.

Groei van gemengde bossen

Het belang van verschillen in zowel fenologie als het optreden van voorjaarsnachtschade voor de groei van gemengde bossen is onderzocht op grond van dezelfde fenologische typen en klimaatveranderingsscenario's. Verder is onderzocht wat de gevolgen zijn van de onnauwkeurigheid van het fenologische model, aangezien het de respons van de datum van bladontplooïng op temperatuur overschat. Dit is gedaan met behulp van de bosgroeimodellen FORGRO en HYBRID. FORGRO is voor deze studie aangepast om groei in gemengde opstanden te simuleren, met name van beheerde bossen waarin regelmatig dunningen worden uitgevoerd. HYBRID benadrukt groei van natuurlijke bossen, waarin zich zaailingen vestigen en verder ontwikkelen in een 'gap' die ontstaat als er een volwassen bomen sterft.

Beide modellen voorspellen dat de verschillen in zowel fenologie als het optreden van voorjaarsvorstschade, tot grotere verschillen in groei tussen de fenologische typen leiden, als ze in een gemengde opstand groeien, ten opzichte van een opstand die uit één soort bestaat.

Het fenologische model voorspelt een sterkere vervroeging van bladontplooiing met stijgende temperatuur dan de waargenomen respons. Dit leidt tot een sterkere toename van de groei, door de snellere toename van de duur van het groeiseizoen volgens het model. Deze onnauwkeurigheid van het model beïnvloedt echter de concurrentieverhoudingen tussen de fenologische typen in gemengde opstanden niet.

Curriculum vitae

Koen Kramer is op 28 december 1961 geboren te Meppel. Na het behalen van het HAVO diploma aan de Openbare Scholengemeenschap in Diever, en het VWO diploma aan het Nassau College in Assen, ging hij in 1981 biologie studeren aan de Rijksuniversiteit Groningen. Daar voltooide hij de studie in 1988 (oude stijl) met als afstudeerrichtingen Plantenoecologie en Populatiegenetica, en met als bijvakken Theoretische Biologie en Bio-informatica. Na zijn militaire dienst was hij werkzaam bij het Rijksinstituut voor Natuurbeheer te Arnhem, waar hij een model ontwikkelde voor de effecten van graslandgebruik op de weidevogelstand. Vervolgens heeft hij bij de Dienst Getijdenwateren van Rijkswaterstaat de invloed van organische belasting en temperatuur op het zuurstofgehalte van de Westerschelde gemodelleerd. Sinds 1991 werkt hij op het Instituut voor Bos- en Natuuronderzoek te Wageningen aan de effecten van klimaatverandering op groei en ontwikkeling van bossen.

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Listing of FORGRO 3.5

```
*======================================================================*
*                                                                      *
*                          FORGRO 3.5                                  *
*                                                                      *
* Based on:                                                            *
* Mohren G.M.J, 1987.                                                  *
*     Simulation of forest growth applied to Douglas Fir stands in The *
*     Netherlands, thesis, 184 pp.                                     *
* Simulation model for forest growth of mixed species stands, based on *
* Mohren, G.M.J., I.T.M Jorritsma, J.P.G.G.M. Florax, H.H. Bartelink   *
* J.R. van der Veen & K. Kramer (in prep.)                             *
*    FORGRO 3.0: A basic forest growth model. Model documentation and  *
*    listing.                                                          *
* Kropff, M.J. & Van Laar H.H, 1993.                                   *
*    Modelling crop-weed interactions, IRRI, CAB International, 274 pp.*
*                                                                      *
* The model is programmed, using the FORTRAN Simulation Environment    *
* for Crop Growth Models (FSE), developed by D.W.G. van Kraalingen     *
* Simulation Report CABO-TT, no 23, July 1991, 77 pp.                  *
* Department of Theoretical Production Ecology and                     *
* Centre for Agrobiological Research, Wageningen, The Netherlands      *
*                                                                      *
* External files needed:  TIMER.DAT                                    *
*                         SPEC<nr>.DAT                                 *
*                         SITE.DAT                                     *
*                         weather files                                *
*                         RERUNS.DAT (only when reruns are needed)     *
*                                                                      *
*======================================================================*

      PROGRAM MAIN

      INCLUDE 'FORGRO.CMN'

*     Common blocks for PGEN (Friend, 1993):
      INCLUDE 'inits.cmn'
      INCLUDE 'env.cmn'
      INCLUDE 'biol.cmn'
      INCLUDE 'outs.cmn'
      INCLUDE 'nits.cmn'

*     WTRMES flags any messages from the weather system and the filenames
      DATA WTRMES /.FALSE./

*---- Open output file, read number of rerun sets
      CALL FOPEN  (IUNITO, FILEO,  'NEW', 'DEL')
      CALL COPFIL (IUNITT, FILET, IUNITO)
      CALL RDSETS (IUNITR, IUNITO, FILER, INSETS)
      IF (INSETS.GT.0) CALL COPFIL (IUNITR+1, FILER, IUNITO)

*======================================================================*
*                                                                      *
*                  Main loop and reruns begins here                    *
*                                                                      *
*======================================================================*

      DO 10 I1=0,INSETS

      IRUN = I1+1
      IYR  = 1
      WRITE (*,'(A)') ' '

*---- Select data set
      CALL RDFROM (I1, .TRUE.)
```

```
*=====================================================================*
*                                                                     *
*                       Initialization section                        *
*                                                                     *
*=====================================================================*
      ITASK  = 1

      TERMNL = .FALSE.

*---- Read variables from TIMER.DAT file
      CALL RDINIT (IUNITT  , IUNITO, FILET)
      CALL RDSCHA ('WTRDIR', WTRDIR)
      CALL RDSCHA ('CNTR'  , CNTR)
      CALL RDSREA ('STTIME', STTIME)
      CALL RDSREA ('FINTIM', FINTIM)
      CALL RDSREA ('PRDEL' , PRDEL)
      CALL RDSINT ('IYEAR' , IYEAR)
      CALL RDSINT ('ISTN'  , ISTN)
      CALL RDSINT ('ITABLE', ITABLE)
      CALL RDSINT ('IDTMP' , IDTMP)
      CALL RDSREA ('FRGR'  , FRGR)
      CALL RDSREA ('PGN'   , PGN)
      CLOSE (IUNITT, STATUS='DELETE')

      NYRS  = (FINTIM - STTIME + 1) / 365

*---- Initialise TIMER and OUTDAT routines
      CALL TIMER  (ITASK, STTIME,   DELT, PRDEL, FINTIM,
     &             IYEAR,   TIME,    DAY,  IDAY,  TERMNL, OUTPUT)
      CALL OUTDAT (ITASK, IUNITO, 'TIME',  TIME)

*---- Open weather file and read station information and return
*---- weather data for start day of simulation
      CALL STINFO (1101   , WTRDIR, ' ', CNTR, ISTN, IYEAR,
     &             ISTAT1, LONG  , LAT,  ELV,   A1,    B1)

      CALL WEATHR (IDAY   , ISTAT2, DRAD, TMN,  TMX, VAPOUR, WIND, RAIN)

      CALL METEO

      WTRMES = WTRMES .OR. (ISTAT1.NE.0) .OR. (ISTAT2.NE.0)
      WTROK  = (ISTAT1.EQ.0).AND.((ISTAT2.GE.0).OR.(ISTAT2.LT.-111111))
      TERMNL = TERMNL.OR..NOT.WTROK

      CALL PLANT

*---- Read input data required for PGEN
      IF (PGN.EQ.1.) CALL INIPGN

*=====================================================================*
*                                                                     *
*                     Dynamic simulation section                      *
*                                                                     *
*=====================================================================*

20    IF (.NOT.TERMNL) THEN

        PRINT '(''+'',A,I3,A,I5,A,F7.2)',
     &       ' Run:', IRUN,', Year:', IYEAR
     &       ,', Day:', DAY

*---------------------------------------------------------------------*
*                    Integration of rates section                     *
*---------------------------------------------------------------------*

      IF (ITASK.NE.1) THEN
         ITASK = 3

         CALL PLANT

      END IF
```

```
      ITASK = 2

*----------------------------------------------------------------------*
*              Calculation of driving variables section                *
*----------------------------------------------------------------------*

*---- Open weather file
      CALL STINFO (1101   , WTRDIR, ' ', CNTR, ISTN,  IYEAR,
     &             ISTAT1, LONG   , LAT,  ELV,   A1,    B1)

      CALL WEATHR (IDAY   , ISTAT2, DRAD, TMN,  TMX, VAPOUR, WIND, RAIN)

      IF (OUTPUT.OR.TERMNL) THEN
         CALL OUTDAT (ITASK, IUNITO, 'TIME', TIME)
         CALL OUTDAT (ITASK, IUNITO, 'DAY' , DAY)
      END IF

      CALL METEO

      WTRMES = WTRMES .OR. (ISTAT1.NE.0) .OR. (ISTAT2.NE.0)
      WTROK  = (ISTAT1.EQ.0).AND.((ISTAT2.GE.0).OR.
     &         (ISTAT2.LT.-111111))
      TERMNL = TERMNL.OR..NOT.WTROK

*----------------------------------------------------------------------*
*                    Calculation of rates section                      *
*----------------------------------------------------------------------*

      CALL PLANT

*---- Time update, check for FINTIM and OUTPUT
      CALL TIMER  (ITASK, STTIME, DELT, PRDEL, FINTIM,
     &             IYEAR,   TIME,  DAY,  IDAY, TERMNL, OUTPUT)

      IF (IDAY.EQ.365) IYR = IYR + 1

      GOTO 20
      END IF

*======================================================================*
*                                                                      *
*                          Terminal section                            *
*                                                                      *
*======================================================================*

      ITASK = 4

*---- Generate output file dependent on option from timer file
      IF (ITABLE.GE.4) CALL OUTDAT (ITABLE, 20, ' ',0.)

      CALL PLANT

*---- Delete temporary output file dependent on switch from timer file
      IF (IDTMP.EQ.1) CALL OUTDAT (99, 0, ' ', 0.)

*---- loop over number of reruns
10    CONTINUE

*---- Delete temporary rerun file if reruns were carried out
      IF (INSETS.GT.0) CLOSE (IUNITR, STATUS='DELETE')
      IF (WTRMES) THEN
         WRITE (*,'(A,/,A)')
     &      ' There have been errors and/or warnings from',
     &      ' the weather system, check file WEATHER.LOG'
         WRITE (IUNITO,'(A,/,A)')
     &      ' There have been errors and/or warnings from',
     &      ' the weather system, check file WEATHER.LOG'
         WRITE (*,'(A)') ' Press <RETURN>'
         READ (*,'(A)') DUMMY
      END IF
      STOP
      END
```

```
*=====================================================================*
*                                                                     *
* SUBROUTINE PLANT                                                    *
*                                                                     *
* Purpose: This subroutine simulates potential growth of competing    *
*          species                                                    *
*                                                                     *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time)  *
* name   type description                               units  class *
* ----   ---- -----------                               -----  ----- *
* ITASK   I4  determines action of the subroutine,        -     C,I  *
*             1=initialization, 2=rate calculation,                   *
*             3=integration, 4=terminal                               *
* IUNITT  I4  unit number of timer data file              -     C,I  *
* IUNITP  I4  unit number of plant data file              -     C,I  *
* IUNITO  I4  unit number of output file                  -     C,I  *
* FILET   C*  file name for time variables                -     C,I  *
* FILEP   C*  file name for plant variables               -     C,I  *
* OUTPUT  L4  flag that indicates if output to file is    -     C,I  *
*             required                                                *
* TERMNL  L4  flag that indicates if simulation should    -    C,I,O *
*             terminate                                               *
* DAY     R4  daynumber since 1 January                   d      T   *
* IDAY    I4  integer variable for DAY                    d      T   *
* DELT    R4  time interval of integration                d      T   *
* LAT     R4  latitude of weather station              degrees I     *
* AVRAD   R4  daily incoming total global radiation    J/m2/d  I     *
* TMN     R4  daily minimum temperature         degrees Celsius I     *
* TMX     R4  daily maximum temperature         degrees Celsius I     *
* VAPOUR  R4  average vapour pressure                  mbar    I     *
* WIND    R4  daily average wind speed                 m/s     I     *
*                                                                     *
* FATAL ERROR CHECKS (execution terminated, message)                  *
* DELT < 1.0                                                          *
* Certain sequences of ITASK, see subroutine CHKTSK                   *
*                                                                     *
* SUBROUTINES and FUNCTIONS called: CHKTSK, OUTCOM, ERROR, RDINIT,    *
*      RDAREA, RDSREA, COPFIL, ASTRO, TOTASS, TOTRAN, OUTARR, OUTDAT  *
*      OUTPLT, LINT, INTGRL, RES                                      *
*                                                                     *
* FILE usage: - time variables file IUNITT, FILET                     *
*             - plant data file with unit IUNITP, FILEP               *
*             - output file with unit IUNITO for output and warnings  *
*                                                                     *
*=====================================================================*

      SUBROUTINE PLANT

      INCLUDE 'FORGRO.CMN'

      SAVE

      DATA ITOLD /4/,INITP /.FALSE./

      CALL CHKTSK ('PLANT', IUNITO, ITOLD, ITASK)

*=====================================================================*
*                         Initialization                              *
*=====================================================================*

      IF (ITASK.EQ.1) THEN

*------- Send title to output file
         CALL OUTCOM ('FORGRO: Competition model for trees')

         CALL RDINIT (IUNITT, IUNITO, FILET)

*------- Initialization of run characteristics
         CALL RDSINT ('IRUNLA', IRUNLA)
         CALL RDSREA ('CO2E'  , CO2E  )
         CALL RDSREA ('TMPSCN', TMPSCN)
         CALL RDAINT ('IPSPEC', IPSPEC, IMNS, INS )
```

```
         CALL RDAINT ('IPLTYP', IPLTYP, IMNS, INS2)

         IF (INS.NE.INS2) CALL ERROR('PLANT',
     &      'Inconsistent initialization in TIMER.DAT')

         LAITOT = 0.

         CALL ASTRO

         CALL PHENO

         CALL PHOTO

         CALL STAND

         DO 30 IS=1,INS

            FILEP = 'SPEC'//CHAR(IPSPEC(IS)+48)//'.DAT'
            CALL OUTCOM ('Spec ('//CHAR(IPSPEC(IS)+48)//')')

            IF (.NOT.INITP) THEN
              CALL COPFIL (IUNITP, FILEP, IUNITO)
              INITP = .TRUE.
            ENDIF
            CALL RDINIT (IUNITP, IUNITO, FILEP)

*---------- Reading species-file:
            CALL RDSCHA ('SPNAME', SPNAME(IS))
*---------- State variables
            CALL RDAREA('WFLI'  ,WFLI  ,IMNFLC,IFLCL(IS))
            CALL RDSREA('WBRI'  ,WBRI  )
            CALL RDAREA('WSWI'  ,WSWI  ,IMNSWC,ISWCL(IS))
            CALL RDSREA('WHWI'  ,WHWI  )
            CALL RDSREA('WCRI'  ,WCRI  )
            CALL RDSREA('WFRI'  ,WFRI  )
            CALL RDSREA('WLTI'  ,WLTI  )
*---------- Model parameters
                         < SEE EXAMPLE OF SPEC<NR>.DAT FILE >
*           Photosynthesis and respiration
*           Light interception
*           Death rates
*           Reserve level
*           Mineral content
*---------- AFGEN functions

            CLOSE (IUNITP, STATUS='DELETE')

*---------- Initializing states
            WFLT(IS) = 0.
            DO 31 I=1,IFLCL(IS)
               WFL(IS,I) = WFLI(I)  * NTR(IS)/NTRT
               WFLT(IS)  = WFLT(IS) + WFL(IS,I)
31          CONTINUE
            WSWT(IS) = 0.
            DO 32 I=1,ISWCL(IS)
               WSW(IS,I) = WSWI(I)  * NTR(IS)/NTRT
               WSWT(IS)  = WSWT(IS) + WSW(IS,I)
32          CONTINUE
            WBR   (IS) = WBRI       * NTR(IS)/NTRT
            WHW   (IS) = WHWI       * NTR(IS)/NTRT
            WCR   (IS) = WCRI       * NTR(IS)/NTRT
            WFR   (IS) = WFRI       * NTR(IS)/NTRT
            WST   (IS) = WHW (IS) + WSWT(IS)
            WSH   (IS) = WFLT(IS) + WBR (IS) + WST(IS)
            WRT   (IS) = WCR (IS) + WFR (IS)
            WTT   (IS) = WSH (IS) + WRT (IS) + WRS(IS)
            WLT   (IS) = WLTI
            WRSMN (IS) = CRSFL(IS)*WFLT (IS)+CRSBR(IS)*WBR(IS)+
     &                   CRSSW(IS)*WSWT (IS)+CRSHW(IS)*WHW(IS)+
     &                   CRSCR(IS)*WCR  (IS)+CRSFR(IS)*WFR(IS)
            WRSMX (IS) = CRSNX(IS)*WRSMN(IS)
```

```
            WRSI       = (WRSMN(IS) + WRSMX(IS)) / 2.
            WRS   (IS) = WRSI

*---------- Initializing array parameters
            DO 35 I=1,IFLCL(IS)
               CDFL(IS,I) = CDFL2(I)
35          CONTINUE

30        CONTINUE

          CALL ANNTOT

*=====================================================================*
*                      Rate calculation section                       *
*=====================================================================*

      ELSE IF (ITASK.EQ.2) THEN

         CALL ASTRO

         CALL PHENO

         CALL PHOTO

         CALL STAND

         CALL TOTASS

         RESET = 0.
         IF (IDAY.EQ.365) RESET = 1.

         DO 50 IS=1,INS

            IF (WRS(IS).LT.1.) GO TO 57

*---------- Maintenance respiration

*           effective air and soil temperature
            TEFFA      = Q10(IS)**((DATMP-REFTMP(IS))/10.)
            TEFFS      = Q10(IS)**((TSOIL-REFTMP(IS))/10.)

*           reduction on maintenance respiration when reserve level is below minimum value
            RESRED     = AMIN1 (1., AMAX1 (0., WRS(IS)/WRSMN(IS)))

*           coefficients for maintenance respiration
            CMRFL (IS) = 0.25*NFL(IS) +
     &                   0.08*(PFL(IS)+KFL(IS)+CFL(IS)+MFL(IS))
            CMRBR (IS) = 0.25*NBR(IS) +
     &                   0.08*(PBR(IS)+KBR(IS)+CBR(IS)+MBR(IS))
            CMRSW (IS) = 0.25*(NSW(IS)+NHW(IS))/2.     +
     &                   0.08*(PSW(IS)+KSW(IS)+CSW(IS)+MSW(IS) +
     &                         PHW(IS)+KHW(IS)+CHW(IS)+MHW(IS))/2.
            CMRHW (IS) = 0.
            CMRCR (IS) = 0.25*NCR(IS) +
     &                   0.08*(PCR(IS)+KCR(IS)+CCR(IS)+MCR(IS))
            CMRFR (IS) = 0.25*NFR(IS) +
     &                   0.08*(PFR(IS)+KFR(IS)+CFR(IS)+MFR(IS))

            MRFL  (IS) = TEFFA*CMRFL(IS)*WFLT(IS)*(24.-DAYL)/24.
            MRBR  (IS) = TEFFA*CMRBR(IS)*WBR (IS)
            MRSW  (IS) = TEFFA*CMRSW(IS)*WSWT(IS)
            MRHW  (IS) = TEFFA*CMRHW(IS)*WHW (IS)
            MRCR  (IS) = TEFFS*CMRCR(IS)*WCR (IS)
            MRFR  (IS) = TEFFS*CMRFR(IS)*WFR (IS)

            MRT   (IS) = RESRED *
     &                   (MRFL(IS)+MRBR(IS)+MRSW(IS)+MRHW(IS)+MRCR(IS)+MRFR(IS))+
     &                    0.1 * GPHOT(IS)

*           dark respiration:
            IF (LAIT(IS) .GT. 0.01) THEN
              DRESP (IS) = (44./30.)*RESRED*CMRFL(IS)+0.025*GPHOT(IS)) /
```

```
     &                     (24.*LAIT(IS))
            ELSE
              DRESP (IS) = 0.
            ENDIF

*---------- Allocation

            FRT   (IS) = LINT (FRTTB (1,IS),ILFRT (IS), DVS(IS))
            FSH   (IS) = 1. -  FRT   (IS)
*           alocation to foliage dependent on maximal LAI for deciduous trees
            IF (IPLTYP(IS).EQ.1.) THEN
              FFL (IS) = AMIN1(1.,
     &            AMAX1(0.,(LAIMAX(IS) - LAIT(IS)) / LAIMAX(IS)))
*           allocation to foliage according to LINT-function for coniferous trees
            ELSE
              FFL (IS) = LINT (FFLTB (1,IS),ILFFL (IS), DVS(IS))
            ENDIF
            FBR   (IS) = LINT (FBRTB (1,IS),ILFBR (IS), DVS(IS))
            FST   (IS) = 1. - (FFL   (IS) + FBR   (IS))
            FFR   (IS) = LINT (FFRTB (1,IS),ILFFR (IS), DVS(IS))
            FCR   (IS) = 1. -  FFR   (IS)
*           allocation to reserves dependent on maximal reserve pool for deciduous trees
            IF (IPLTYP(IS).EQ.1.) THEN
              FRS (IS) = AMIN1(1.,
     &            AMAX1(0.,(WRSMX(IS) - WRS(IS)) / WRSMX(IS)))
            ELSE
*           allocation to reserves according to LINT-function for coniferous trees
              FRS (IS) = LINT (FRSTB (1,IS),ILFRS (IS), DVS(IS))
            ENDIF

*---------- Growth: rate of increase

*           Energy for leaf flush from reserves

            PFLUSH = 0.
            IF ((WRS(IS).GT.0.).AND.(DVS(IS).GE.1.).AND.(DVS(IS).LE.1.25)) THEN
              PFLUSH = FFL(IS) * CFLUSH(IS) * WRS(IS)
            ENDIF

*           If Net Supply of Assimilates (NSA) is negative: supply from reserves
            PMAINT = 0.
            NSA    = GPHOT(IS) - MRT(IS)
            IF ((WRS(IS).GT.0.).AND.(NSA.LT.0.)) PMAINT = -NSA

*           Gross Total Dry Matter
            GTDM  (IS) = AMAX1(0., (GPHOT(IS)-MRT(IS)+PMAINT) / ASRQ(IS))

*           Reserve level considered as dry matter
            GRS   (IS) = FRS (IS) * GTDM(IS) -
     &                   (PFLUSH + PMAINT)  / ASRQ(IS)

            GTDM  (IS) = (1.-FRS(IS)) * GTDM(IS)
            GSH   (IS) = FSH (IS) * GTDM(IS)
            GFL   (IS) = FFL (IS) * GSH (IS) + PFLUSH / ASRQ(IS)
            GBR   (IS) = FBR (IS) * GSH (IS)
            GST   (IS) = FST (IS) * GSH (IS)
            GSW   (IS) = GST (IS)
            GHW   (IS) = CLSW(IS) * WSW (IS,ISWCL(IS)) / 365.
            GRT   (IS) = FRT (IS) * GTDM(IS)
            GCR   (IS) = FCR (IS) * GRT (IS)
            GFR   (IS) = FFR (IS) * GRT (IS)

            GLT   (IS) = DSH (IS) + DRT (IS) + DRS(IS) +
     &                   RESET*WFL(IS,IFLCL(IS))


*---------- Death: rate of decrease (Decomposition in case of litter)

*           Coefficient of Leaf Fall in case of deciduous trees
            CLF = 0.
            IF ((IPLTYP(IS).EQ.1).AND.(DVS(IS).GE.2.)) CLF = CLFFL(IS)
```

```
            DFLT(IS) = 0.
            DO 51 I = 1, IFLCL(IS)
               DFL(IS,I) = (CLF + CDFL(IS,I)) * WFL(IS,I) / 365.
               DFLT(IS)  = DFLT(IS) + DFL(IS,I)
51          CONTINUE
            DSWT(IS) = 0.
            DO 52 I = 1, ISWCL(IS)
               DSW(IS,I) = CDSW(IS) * WSW(IS,I) / 365.
               DSWT(IS)  = DSWT(IS) + DSW(IS,I)
52          CONTINUE

            DBR   (IS) = CDBR (IS) * WBR (IS) / 365.
            DHW   (IS) = CDHW (IS) * WHW (IS) / 365.
            DCR   (IS) = CDCR (IS) * WCR (IS) / 365.
            DFR   (IS) = CDFR (IS) * WFR (IS) / 365.
            DST   (IS) = DSWT (IS) + DHW (IS)
            DSH   (IS) = DFLT (IS) + DBR (IS) + DST(IS)
            DRT   (IS) = DFR  (IS) + DCR (IS)
            DLT   (IS) = CDLT (IS) * WLT (IS)
            DRS   (IS) = CRSFL(IS) * DFLT(IS) + CRSBR(IS) * DBR(IS) +
     &                   CRSSW(IS) * DSWT(IS) + CRSHW(IS) * DHW(IS) +
     &                   CRSCR(IS) * DCR (IS) + CRSFR(IS) * DFR(IS)

*---------- Thinning: fraction removed by management,
            TFLT(IS) = 0.
            DO 53 I  = 1, IFLCL(IS)
               TFL(IS,I) = FTHIN(IS) * WFL(IS,I)
               TFLT(IS)  = TFLT(IS)  + TFL(IS,I)
53          CONTINUE

            TSWT(IS) = 0.
            DO 54 I  = 1,ISWCL(IS)
               TSW(IS,I) = FTHIN(IS) * WSW(IS,I)
               TSWT(IS)  = TSWT(IS)  + TSW(IS,I)
54          CONTINUE

            TBR   (IS) = FTHIN(IS) * WBR(IS)
            THW   (IS) = FTHIN(IS) * WHW(IS)
            TCR   (IS) = FTHIN(IS) * WCR(IS)
            TFR   (IS) = FTHIN(IS) * WFR(IS)
            TRS   (IS) = FTHIN(IS) * WRS(IS)
            TLT   (IS) = TFLT(IS)  + TBR(IS) + TSWT(IS) + THW(IS) +
     &                   TCR (IS)  + TFR(IS) + TRS (IS)

*---------- Rates of change: differential equations
*           foliage
            IF (IPLTYP(IS).EQ.2) THEN                                ! Coniferous
               RWFL(IS,1) = GFL(IS) - DFL(IS,1)
     &                      - RESET*WFL(IS,1) - TFL(IS,1)
               DO 55 I=2,IFLCL(IS)
                  RWFL (IS,I) = -DFL(IS,I)
     &                      + RESET*(WFL(IS,I-1)-WFL(IS,I)) - TFL(IS,I)
55             CONTINUE
            ELSE
               RWFL(IS,1) = GFL(IS) - DFL(IS,1) - TFL(IS,1)          ! Deciduous
            END IF
*           sapwood: first, intermediate and last sapwoodclass
            RWSW(IS,1) = GSW(IS) - DSW(IS,1) - RESET*WSW(IS,1) - TSW(IS,1)
            DO 56 I=2,ISWCL(IS)-1
               RWSW(IS,I) = - DSW(IS,I)
     &                      + RESET*(WSW(IS,I-1)-(WSW(IS,I)) - TSW(IS,I)
56          CONTINUE
            RWSW(IS,ISWCL(IS)) = - DSW(IS,ISWCL(IS)) - GHW(IS)
     &                      + RESET*WSW(IS,ISWCL(IS)-1)- TSW(IS,ISWCL(IS)

*           Differential equations
            RWHW  (IS) = GHW(IS) - DHW(IS) - THW(IS)
            RWBR  (IS) = GBR(IS) - DBR(IS) - TBR(IS)
            RWCR  (IS) = GCR(IS) - DCR(IS) - TCR(IS)
            RWFR  (IS) = GFR(IS) - DFR(IS) - TFR(IS)
            RWRS  (IS) = GRS(IS) - DRS(IS) - TRS(IS)
            RWLT  (IS) = GLT(IS) - DLT(IS) + TLT(IS)
```

```
*           Set rates of change at zero if reserve pool approaches zero
57          IF (WRS(IS).LT.1.) THEN
*             foliage
              DO 58 I=1,IFLCL(IS)
                RWFL (IS,I) = 0.
58            CONTINUE
*             sapwood
              DO 59 I=1,ISWCL(IS)
                 RWSW(IS,I) = 0.
59            CONTINUE
              RWHW  (IS) = 0.
              RWBR  (IS) = 0.
              RWCR  (IS) = 0.
              RWFR  (IS) = 0.
              RWRS  (IS) = 0.
              RWLT  (IS) = 0.
            ENDIF

50      CONTINUE

        CALL ANNTOT

*------ Output of states and rates only if it is required

        IF (OUTPUT .OR. TERMNL) THEN
                       < OUTPUT POSSIBLE OF ALL VARIABLES, E.G.: >
*           photosynthesis
            CALL OUTARR('GPHOT' ,GPHOT ,1, INS)
            CALL OUTDAT(2,0,'LAITOT', LAITOT)
*           maintenance
*           biomass
*           growth rates
*           death rates
*           thinning
*           allocation
*           phenology
*           light
*           meteo
*           stand characteristics
*           annual totals

        END IF

*=================================================================*
*                      Integration section                        *
*=================================================================*

      ELSE IF (ITASK.EQ.3) THEN

         CALL ASTRO

         CALL PHENO

         CALL STAND

         LAITOT = 0.
         DO 60 IS=1,INS
            WFLT(IS) = 0.
            DO 61 I=1,IFLCL(IS)
              WFL(IS,I) = INTGRL(WFL(IS,I), RWFL(IS,I),DELT)
              IF (TMN.LE.SHRD(IS)) THEN
                WFL(IS,I) = 0.
              ENDIF
              WFLT(IS)  = WFLT(IS) + WFL(IS,I)
61          CONTINUE
            WSWT(IS) = 0.
            DO 62 I=1,ISWCL(IS)
               WSW(IS,I) = INTGRL(WSW(IS,I), RWSW(IS,I), DELT)
               WSWT(IS)  = WSWT(IS) + WSW(IS,I)
62          CONTINUE
```

```
            WBR   (IS) = INTGRL(WBR (IS), RWBR (IS),DELT)
            WHW   (IS) = INTGRL(WHW (IS), RWHW (IS),DELT)
            WCR   (IS) = INTGRL(WCR (IS), RWCR (IS),DELT)
            WFR   (IS) = INTGRL(WFR (IS), RWFR (IS),DELT)
            WRS   (IS) = INTGRL(WRS (IS), RWRS (IS),DELT)
            WLT   (IS) = INTGRL(WLT (IS), RWLT (IS),DELT)

            WST   (IS) = WHW (IS)+WSWT(IS)
            WSH   (IS) = WFLT(IS)+WBR (IS)+WST (IS)
            WRT   (IS) = WCR (IS)+WFR (IS)
            WTT   (IS) = WSH (IS)+WRT (IS)+WRS (IS)

            WRSMN (IS) = CRSFL(IS)*WFLT(IS)+CRSBR(IS)*WBR(IS)+
     &                   CRSSW(IS)*WSWT(IS)+CRSHW(IS)*WHW(IS)+
     &                   CRSCR(IS)*WCR (IS)+CRSFR(IS)*WFR(IS)
            WRSMX (IS) = CRSMX(IS)*WRSMN(IS)

            LAIT(IS) = 0.
            DO 63 I=1,IFLCL(IS)
               LAI(IS,I) = SLA (IS) * WFL(IS,I) / 10000.
               LAIT(IS)  = LAIT(IS) + LAI(IS,I)
63          CONTINUE
            LAIT(IS) = LAIT(IS) / CANCLO(IS)
            LAITOT   = LAITOT   + LAIT(IS)

60       CONTINUE

      CALL ANNTOT

*=======================================================================*
*                        Terminal section                               *
*=======================================================================*

      ELSE IF (ITASK.EQ.4) THEN

        CALL ANNTOT

        DO 70 IS = 1,INS

          WRITE (IUNITO,'(A10,2F5.0,3F15.2)')
     &           SPNAME(IS),CO2E,TMPSCN,AAGPCN(IS),AAMRT(IS),NPP
          WRITE (*      ,'(A10,2F5.0,3F15.2)')
     &           SPNAME(IS),CO2E,TMPSCN,AAGPCN(IS),AAMRT(IS),NPP

70      CONTINUE

      END IF

      ITOLD = ITASK

      CLOSE (IUNITD, STATUS='DELETE')

      RETURN
      END
```

```
*================================================================*
*                                                                *
*  Subroutine ANNTOT                                             *
*                                                                *
*  Purpose : this subroutine calculates annual totals            *
*                                                                *
*================================================================*

      SUBROUTINE ANNTOT

      INCLUDE 'FORGRO.CMN'

      SAVE

      IF (ITASK.EQ.1) THEN

        DO 10 IS = 1, INS
           AGPHOT(IS) = 0.
           AMRT  (IS) = 0.
           AGTDM (IS) = 0.
           AARCN (IS) = 0.
           AAGPCN(IS) = 0.
           AAMRT (IS) = 0.
           AAGTDM(IS) = 0.
           AAARCN(IS) = 0.
10      CONTINUE

      ELSE IF (ITASK.EQ.2) THEN

*     reset or update annual variables
        IF (IDAY .EQ. 365) THEN

           DO 20 IS = 1, INS
             AAGPCN(IS) = AAGPCN(IS) + AGPHOT(IS)
             AAMRT (IS) = AAMRT (IS) + AMRT  (IS)
             AAGTDM(IS) = AAGTDM(IS) + AGTDM (IS)
             AAARCN(IS) = AAARCN(IS) + AARCN (IS)

             AGPHOT(IS) = 0.
             AMRT  (IS) = 0.
             AGTDM (IS) = 0.
             AARCN (IS) = 0.
20         CONTINUE

        ENDIF

      ELSE IF (ITASK.EQ.3) THEN

        DO 30 IS = 1, INS
*         Photosynthesis and canopy assimilation:
          AGPHOT(IS) = INTGRL(AGPHOT(IS), GPHOT (IS)/1000., DELT)
          AMRT  (IS) = INTGRL(AMRT  (IS), MRT   (IS)/1000., DELT)
          AGTDM (IS) = INTGRL(AGTDM (IS), GTDM  (IS)/1000., DELT)
          AARCN (IS) = INTGRL(AARCN (IS), DARCN (IS)/1.E+6, DELT)
30      CONTINUE

      ELSE IF (ITASK.EQ.4) THEN

        DO 40 IS = 1,INS
          AAGPCN(IS) = AAGPCN(IS) / REAL(NYRS)
          AAMRT (IS) = AAMRT (IS) / REAL(NYRS)
          AAGTDM(IS) = AAGTDM(IS) / REAL(NYRS)
          AAARCN(IS) = AAARCN(IS) / REAL(NYRS)
40      CONTINUE

      END IF

      RETURN
      END
```

```
*=====================================================================*
*                                                                     *
* SUBROUTINE ASSIM                                                    *
*                                                                     *
* Purpose: This subroutine (for two or more species in competition)   *
*          performs a Gaussian integration over the canopy            *
*          for each species, and computes the leaf area index for each *
*          layer (LAIC), and the leaf area density (LD) and local     *
*          assimilation rate at each layer. The integrated variables  *
*          are FGRCN and ARCN.                                        *
*                                                                     *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time)  *
* name   type description                            units  class *
* ----   ---- -----------                            -----  ----- *
* INS     I4  number of species                        -      I   *
* AMAX    R4  actual maximum CO2-assimilation rate   kg/ha/h  I   *
*             for individual leaves                               *
* EFF     R4  initial light use efficiency for    kg/ha/h/J m2 s IN *
*             leaves                                              *
* KDF     R4  extinction coefficient for leaves        -      I   *
* HGHT    R4  total height of a species in the canopy  m      I   *
* CNBASE  R4  crown base of a species in the canopy    m      I   *
* LAI     R4  leaf area index                        ha/ha    I   *
* SINB    R4  sine of solar elevation                m2/m2    I   *
* RADDIR  R4  incoming global direct radiation       J/m/s    I   *
* RADDIF  R4  incoming global diffuse radiation      J/m/s    I   *
* FGRCN   R4  canopy gross assimilation rate         kg/ha/h  O   *
* ARCN    R4  absorbed radiation by canopy of a species J/m2/s O  *
*                                                                     *
* FATAL ERROR CHECKS (execution terminated, message): none            *
*                                                                     *
* SUBROUTINES and FUNCTIONS called: LEAFPA or LEAFRE                  *
*                                                                     *
* FILE usage: none                                                    *
*                                                                     *
*=====================================================================*

      SUBROUTINE ASSIM

      INCLUDE 'FORGRO.CMN'

*     Common blocks for PGEN (Friend, 1993):
      INCLUDE 'inits.cmn'
      INCLUDE 'env.cmn'
      INCLUDE 'biol.cmn'
      INCLUDE 'outs.cmn'
      INCLUDE 'nits.cmn'

      SAVE

      DATA XGAUS /0.1127, 0.5000, 0.8873/
      DATA WGAUS /0.2778, 0.4444, 0.2778/
      DATA XGAUS1 /0.0469101, 0.2307534, 0.5000000, 0.7692465, 0.9530899/
      DATA WGAUS1 /0.1184635, 0.2393144, 0.2844444, 0.2393144, 0.1184635/

*     CO2 in the air (mol m-3), required for PGEN
      CCAIR  = CO2E*PATM*1.E-6 / (8.3144*(DATMP+273.15))

      DO 10 IS = 1,INS

*---- Reflection coefficients of canopy for horizontal (REFH) and
*     spherical (REFS) leaves
        REFH = (1.-SQRT(1.-SCV(IS)))/(1.+SQRT(1.-SCV(IS)))
        REFS = REFH*2./(1.+1.6*SINB)
        KDRDR (IS) = (0.5/SINB)*KDF(IS)/(0.8*SQRT(1.-SCV(IS)))
        KDRT  (IS) = KDRDR(IS)*SQRT(1.-SCV(IS))
        FGRCN (IS) = 0.
        ARCN  (IS) = 0.

10    CONTINUE
```

```
*---- Height within canopy is selected (H, m), leaf area density at height H (LD, m2/m3).
*    Exponents for: diffuse radiation (EXDF), direct component of direct radiation (EXDRDR), and
*    total direct radiation (EXDRT), are calculated in subroutine LEAFPA or LEAFRE
      DO 100 IS  = 1,INS

        IF (LAIT(IS).LT.0.01) GOTO 100

C       Gaussian integration
        DO 50  IG1 = 1,INGP1
          H        = XGAUS1(IG1)*(HGHT(IS)-CNBASE(IS)) + CNBASE(IS)

*----     rectangular (LEAFRE) or parabolic (LEAFPA) leaf area distribution over the canopy
          CALL LEAFRE

*----     Absorbed radiation (J/m2 leaf/s) per species at specified
*         height in the canopy: diffuse (ARDF), total direct (ARDRT,
*         direct component of direct radiation (ARDRDR)
          ARDF  (IS) = (1.-REFH)    * PARDIF*KDF  (IS) * EXP(-EXDF)
          ARDRT (IS) = (1.-REFS)    * PARDIR*KDRT (IS) * EXP(-EXDRT)
          ARDRDR(IS) = (1.-SCV(IS)) * PARDIR*KDRDR(IS) * EXP(-EXDRDR)

*         Rate of gross photosynthesis by shaded leaves (kg CO2/ha leaf/h)
          ARSHD (IS) = ARDF(IS)+ARDRT(IS)-ARDRDR(IS)

          IF (FRGR.EQ.1.) THEN
            IF (AMAX(IS).GT.0.) THEN
              FGRSHD(IS) = AMAX(IS)*(1.-EXP(-ARSHD(IS)*EFF(IS)/AMAX(IS)))
            ELSE
              FGRSHD(IS) = 0.
            ENDIF
          ENDIF
          IF (PGN.EQ.1.) THEN
            IF (ARSHD(IS).GT.2.) THEN
              CALL PGEN(CCAIR,COAIR,RELHUM,WIND,PARDIF*2.,PATM,
     &                 DATMP+273.15,PSIFOL,ARSHD,ACHL)
C              conversion µmol CO2 m-2 s-1 to kg CO2 ha-1 h-1
              FGRSHD(IS)  = AMAX1(0., ACHL * 1.584)
             ELSE
              FGRSHD(IS) = 0.
            ENDIF
          ENDIF

*         Rate of gross photosynthesis by sunlit leaves (kg CO2/ha leaf/h)
*         Direct radiation absorbed by sunlit leaves perpendicular to the
*         direct beam (ARPP); instantaneous assimilation of sunlit
*         leaf area (FGRSUN) integrated over the sine of incidence of
*         direct light, assuming a spherical leaf angle distribution
          ARPP       = (1.-SCV(IS))*PARDIR/SINB
          FGRSUN(IS) = 0.
          ARSUN (IS) = 0.
          VISSUN     = 0.

          DO 30 IG = 1,INGP
            VISSUN = ARSHD (IS) + ARPP * XGAUS(IG)

            IF (FRGR.EQ.1.) THEN
              IF (AMAX(IS).GT.0.) THEN
                FGRS = AMAX(IS)*(1.-EXP(-VISSUN*EFF(IS)/AMAX(IS)))
              ELSE
                FGRS = 0.
              ENDIF
            ENDIF
            IF (PGN.EQ.1.) THEN
              IF (VISSUN.GT.2.) THEN
                 CALL PGEN(CCAIR,COAIR,RELHUM,WIND,PARDIF*2.,PATM,
     &                    DATMP+273.15,PSIFOL,VISSUN,ACHL)
C                conversion µmol CO2 m-2 s-1 to kg CO2 ha-1 h-1
                 FGRS = AMAX1(0., ACHL * 1.584)
               ELSE
                 FGRS = 0.
              ENDIF
            ENDIF
```

```
            FGRSUN(IS) = FGRSUN(IS) + FGRS   * WGAUS(IG)
            ARSUN (IS) = ARSUN (IS) + VISSUN * WGAUS(IG)
30        CONTINUE

*         Fraction sunlit leaf area (FSLLA)
*         gross assimilation rate of current layer (FGRL, kg CO2/ha leaf/h)
*         total gross canopy assimilation rate (FGRCN, kg CO2/ha leaf/h)

          FSLLA      = EXP(-EXDF)
          FGRL  (IS) = (FSLLA*FGRSUN(IS)+(1.-FSLLA)*FGRSHD(IS))*LD(IS)

C         Gaussian integration
          FGRCN (IS) = FGRCN(IS) + FGRL(IS) * WGAUS1(IG1) * (HGHT(IS)-CNBASE(IS))

*         absorbed radiation of current layer (ARL, J/m2 leaf/s),
*         total absorbed radiation by crown (ARCN, J/m2 leaf/s)
          ARL   (IS) = (FSLLA*ARSUN(IS)+(1.-FSLLA)*ARSHD(IS))*LD(IS)
C         Gaussian integration
          ARCN  (IS) = ARCN(IS) + ARL(IS) * WGAUS1(IG1) * (HGHT(IS)-CNBASE(IS))

50      CONTINUE

100   CONTINUE

      RETURN
      END
```

```
*======================================================================*
*                                                                      *
* SUBROUTINE ASTRO                                                     *
*                                                                      *
* Purpose: This subroutine computes daylength (DAYL)                   *
*                                                                      *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time)   *
* name   type description                               units   class *
* ----   ---- -----------                               -----   ----- *
* DAY     R4  daynumber since 1 January                   -       T,I  *
* LAT     R4  latitude of weather station               degrees    I   *
* DAYL    R4  daylength                                   h/d     T,O  *
* DAYLP   R4  photoperiodic daylength                     h/d     T,O  *
* SINLD   R4  intermediate variable in calculating         -        I  *
*             daylength                                                *
* COSLD   R4  intermediate variable in calculating         -        I  *
*             daylength                                                *
*                                                                      *
* FATAL ERROR CHECKS (execution terminated, message): none             *
*                                                                      *
* SUBROUTINES and FUNCTIONS called: none                               *
*                                                                      *
* FILE usage: none                                                     *
*                                                                      *
*======================================================================*

      SUBROUTINE ASTRO

      INCLUDE 'FORGRO.CMN'

      SAVE

*---- Declination of the sun as function of daynumber (DAY)
      DEC   = -ASIN(SIN(23.45*RAD)*COS(2.*PI*(DAY+10.)/365.))

*---- SINLD, COSLD and AOB are intermediate variables
      SINLD = SIN(RAD*LAT)*SIN(DEC)
      COSLD = COS(RAD*LAT)*COS(DEC)
      AOB   = SINLD/COSLD

*---- Daylength (DAYL)
      DAYL  = 12.0*(1.+2.*ASIN(AOB)/PI)

      RETURN
      END
```

```
*=================================================================*
*                                                                 *
* SUBROUTINE LEAFPA                                               *
*                                                                 *
* Purpose: This subroutine assumes a parabolic leaf area          *
*          distribution; height (HGHT), a point H and total leaf area *
*          index (LAIT) are input                                 *
*          the leaf area density (LD) at point H and              *
*          exponents for diffuse, direct component of direct radiation *
*          and total direct radiation are calculated              *
*                                                                 *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time) *
* name   type description                           units  class *
* ----   ---- -----------                           -----  ----- *
* INS     I4  number of species                       -      I    *
* H       R4  selected height                         m      I    *
* HGHT    R4  total height of a species in the canopy m      I    *
* CNBASE  R4  crown base of a species in the canopy   m      I    *
* LAIT    R4  total leaf area index                 ha/ha    I    *
* KDF     R4  extinction coefficient for diffuse                  *
*             radiation                               -      I    *
* KDRDR   R4  extinction coefficient for direct                   *
*             component of direct radiation           -      I    *
* KDRT    R4  extinction coefficient for total                    *
*             direct radiation                        -      I    *
* LD      R4  leaf area density at point H          m2/m3    O    *
* EXDF    R4  exponent for diffuse radiation          -      O    *
* EXDRDR  R4  exponent for direct component of direct             *
*             radiation                               -      O    *
* EXDRT   R4  exponent for total direct radiation     -      O    *
*                                                                 *
*                                                                 *
* FILE usage: none                                                *
*                                                                 *
*=================================================================*

      SUBROUTINE LEAFPA

      INCLUDE 'FORGRO.CMN'

      SAVE

      INTEGER IS2

      EXDF   = 0.
      EXDRDR = 0.
      EXDRT  = 0.

      DO 20 IS2=1,INS
        IF (H.LE.HGHT(IS2)) THEN
          IF (H.GE.CNBASE(IS2)) THEN
            LAIC(IS2) = LAIT(IS2) - ((LAIT(IS2) / HGHT(IS2)**3) *
     &                  H**2 * (3*HGHT(IS2) - 2*H))
            LD  (IS2) = (6.*LAIT(IS2)/HGHT(IS2)**3) * H *
     &                  (HGHT(IS2) - H)
          ELSE
            LAIC(IS2) = LAIT(IS2)
            LD  (IS2) = 0.
          ENDIF
        ELSE
          LAIC  (IS2) = 0.
          LD    (IS2) = 0.
        ENDIF

*----   Weighted exponents for light distribution functions
        EXDF   = EXDF   + KDF   (IS2) * LAIC  (IS2)
        EXDRDR = EXDRDR + KDRDR (IS2) * LAIC  (IS2)
        EXDRT  = EXDRT  + KDRT  (IS2) * LAIC  (IS2)
20    CONTINUE

      RETURN
      END
```

```
*=================================================================*
*                                                                 *
* SUBROUTINE LEAFRE                                               *
*                                                                 *
* Purpose: This subroutine assumes a rectangular leaf area        *
*          distribution; height (HGHT), a point H and total leaf area *
*          index (LAIT) are input                                 *
*          the leaf area density (LD) at point H and              *
*          exponents for diffuse, direct component of direct radiation *
*          and total direct radiation are calculated              *
*                                                                 *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time)  *
* name   type description                           units  class *
* ----   ---- -----------                           -----  ----- *
* INS     I4  number of species                       -      I    *
* H       R4  selected height                         m      I    *
* HGHT    R4  total height of a species in the canopy m      I    *
* CNBASE  R4  crown base of a species in the canopy   m      I    *
* LAIT    R4  total leaf area index                  ha/ha   I    *
* KDF     R4  extinction coefficient for diffuse                  *
*             radiation                               -      I    *
* KDRDR   R4  extinction coefficient for direct                   *
*             component of direct radiation           -      I    *
* KDRT    R4  extinction coefficient for total                    *
*             direct radiation                        -      I    *
* LD      R4  leaf area density at point H           m2/m3   O    *
* EXDF    R4  exponent for diffuse radiation          -      O    *
* EXDRDR  R4  exponent for direct component of direct             *
*             radiation                               -      O    *
* EXDRT   R4  exponent for total direct radiation     -      O    *
*                                                                 *
* FILE usage: none                                                *
*                                                                 *
*=================================================================*

      SUBROUTINE LEAFRE

      INCLUDE 'FORGRO.CMN'

      SAVE

      INTEGER IS2

      EXDF   = 0.
      EXDRDR = 0.
      EXDRT  = 0.

      DO 20 IS2=1,INS

        IF (H.LE.HGHT(IS2)) THEN
          IF (H.GE.CNBASE(IS2)) THEN
            LAIC (IS2) = LAIT(IS2) * (HGHT(IS2)-H) / (HGHT(IS2)-CNBASE(IS2))
            LD   (IS2) = LAIT(IS2) / (HGHT(IS2)-CNBASE(IS2))
          ELSE
            LAIC (IS2) = LAIT(IS2)
            LD   (IS2) = 0.
          ENDIF
        ELSE
          LAIC  (IS2) = 0.
          LD    (IS2) = 0.
        ENDIF

*----   Weighted exponents for light distribution functions
        EXDF   = EXDF   + KDF   (IS2) * LAIC  (IS2)
        EXDRDR = EXDRDR + KDRDR (IS2) * LAIC  (IS2)
        EXDRT  = EXDRT  + KDRT  (IS2) * LAIC  (IS2)

20    CONTINUE

      RETURN
      END
```

```
*=====================================================================*
*                                                                     *
*  Subroutine METEO                                                   *
*                                                                     *
*  Purpose : calculates meteorological conditions                     *
*                                                                     *
*=====================================================================*
      SUBROUTINE METEO

      INCLUDE 'FORGRO.CMN'

      SAVE

*     Total daily radiation from kJ/m2/d to J/m2/d
      AVRAD  = DRAD * 1000.

*     Daily temperature and daytime temperature (Celsius):
      TMX    = TMX + TMPSCN
      TMN    = TMN + TMPSCN
      DATMP  = (TMX + TMN) / 2.0
      DDTMP  = TMX - 0.29  * (TMX - TMN)

*     Soil temperature, as long-term running average of average
*     air temperature:
      TSOIL  = TSUM/60.
      DTSUM  = DATMP - TSOIL
      TSUM   = INTGRL (TSUM  ,DTSUM ,DELT)

*     Vapour pressure from kPa to mbar:
      VAPOUR = VAPOUR * 10.

*     Deficit during the day (mbar):
      SVP    = 6.11 * EXP(17.4*DDTMP/(DDTMP+239.))
      VPD    = AMAX1(0.,SVP - VAPOUR)
      RELHUM = AMIN1(1., AMAX1(0., VAPOUR / SVP))

      RETURN
      END
```

```
*=================================================================*
*                                                                 *
* SUBROUTINE PHENO                                                *
*                                                                 *
* Purpose: This subroutine calculates the development stage of   *
*          coniferous and deciduous tree species.                 *
*                                                                 *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time) *
* name   type description                          units  class  *
* ----   ---- -----------                          -----  -----  *
* ITASK   I4  determines action of the subroutine,   -     C,I   *
*             1=initialization, 2=rate calculation,              *
*             3=integration, 4=terminal                          *
* IUNITT  I4  unit number of timer data file         -     C,I   *
* IUNITP  I4  unit number of plant data file         -     C,I   *
* IUNITO  I4  unit number of output file             -     C,I   *
* FILET   C*  file name for time variables           -     C,I   *
* FILEP   C*  file name for plant variables          -     C,I   *
* OUTPUT  L4  flag that indicates if output to file is -   C,I   *
*             required                                           *
* TERMNL  L4  flag that indicates if simulation should -   C,I,O *
*             terminate                                          *
* IDAY    I4  daynumber since 1 January              d     T     *
* DELT    R4  time interval of integration             -   T,I   *
* DATMP   R4  average day temperature               °C     I     *
* DAYL    R4  daylength                             h/d    I     *
* DVS     R4  development stage                      -     O     *
* SHRD    R4  state of frost hardiness              °C     O     *
*                                                                 *
* SUBROUTINES and FUNCTIONS called:                               *
*                                                                 *
* FILE usage: - time variables file IUNITT, FILET                 *
*             - plant data file with unit IUNITP, FILEP           *
*             - output file with unit IUNITO for output and warnings *
*                                                                 *
*=================================================================*

      SUBROUTINE PHENO

      INCLUDE 'FORGRO.CMN'

      SAVE

      CALL CHKTSK ('PHENO', IUNITO, ITOLD, ITASK)

*=================================================================*
*                         Initialization                          *
*=================================================================*

      IF (ITASK.EQ.1) THEN

*------- Initialization of run characteristics
         CALL RDINIT (IUNITT, IUNITO, FILET)
         CALL RDAINT ('IPSPEC', IPSPEC, IMNS, INS)
         CALL RDAINT ('IPLTYP', IPLTYP, IMNS, INS)
         CLOSE (IUNITT, STATUS='DELETE')

         DAYLMX = 0.

*------- Initialization of species characeristics
         DO 30 IS=1,INS

            FILEP = 'SPEC'//CHAR(IPSPEC(IS)+48)//'.DAT'
            CALL OUTCOM ('Spec ('//CHAR(IPSPEC(IS)+48)//')')

            IF (.NOT.INITP) THEN
              CALL COPFIL (IUNITP, FILEP, IUNITO)
              INITP = .TRUE.
            END IF
            CALL RDINIT (IUNITP, IUNITO, FILEP)
```

```
*---------- States
            CALL RDSREA('SCHLI' ,SCHLI)
            CALL RDSREA('SFRCI' ,SFRCI)
            CALL RDSREA('TMPSMI',TMPSMI)
            CALL RDSREA('SHRDI' ,SHRDI)

*---------- Parameters
                          < SEE EXAMPLE OF SPEC<NR>.DAT FILE >
*           Phenology
*           Frost hardiness

*---------- AFGEN functions
            CALL RDAREA('DVSTB' ,DVSTB (1,IS),IMNP,ILDVS (IS))

            CLOSE (IUNITP, STATUS='DELETE')

*---------- Initializing states
            SCHL  (IS) = SCHLI
            SFRC  (IS) = SFRCI
            TMPSUM(IS) = TMPSMI
            SFRC  (IS) = SFRCI
            SHRD  (IS) = SHRDI
            DVS   (IS) = 0.

*---------- Initializing
            DO 25 I=1,INOBS(IS)
              BDBRST(IS,I) = BDBST2(I)
              FORGRN(IS,I) = FRGRN2(I)
              FOLFLL(IS,I) = FOLFL2(I)
25          CONTINUE

30    CONTINUE

*=======================================================================*
*                      Rate calculation section                         *
*=======================================================================*

      ELSE IF (ITASK.EQ.2) THEN

*------- Reset state of forcing and chilling
         RSTFRC = 0.
         IF (IDAY.EQ.365) RSTFRC = 1.
         RSTCHL = 0.
         IF (IDAY.EQ.304) RSTCHL = 1.

         NL  = 24. - DAYL

         DO 40 IS=1,INS

            IF (SCHL(IS) .LE. SCHLBB(IS)) THEN
              RFRC(IS)    = 0. - RSTFRC * SFRC(IS)
*------------ chilling
              IF ((DATMP.GT.TMINCH(IS)).AND.(DATMP.LT.TMAXCH(IS))) THEN
                 IF (DATMP.LT.TOPTCH(IS)) THEN
                    RCHL(IS) = ((DATMP-TMINCH(IS)) /
     &              (TOPTCH(IS)-TMINCH(IS))) - RSTCHL*SCHL(IS)
                 ELSE
                    RCHL(IS) = ((DATMP-TMAXCH(IS)) /
     &              (TOPTCH(IS)-TMAXCH(IS))) - RSTCHL*SCHL(IS)
                 ENDIF
              ELSE
                 RCHL(IS) = 0. - RSTCHL*SCHL(IS)
              ENDIF
            ELSE
              RCHL(IS)    = 0. - RSTCHL * SCHL(IS)
*------------ forcing
              IF (DATMP .LE. 0.) THEN
                RFRC(IS) = 0. - RSTFRC*SFRC(IS)
              ELSE
                RFRC(IS) = C1FRC(IS) /
     &                    (1.+EXP(C2FRC(IS)*(DATMP+C3FRC(IS))))
```

```
     &                     - RSTFRC*SFRC(IS)
              ENDIF
            ENDIF

*---------- temperature sum
            RTMPSM(IS) = INSW(DATMP-BATMP(IS), 0., DATMP-BATMP(IS))
     &                   - RSTFRC*TMPSUM(IS)

*---------- hardening
            RHRD   (IS) = (SSHRD(IS) - SHRD(IS)) / TAU(IS)

            DHRDDT (IS) = AT(IS)*DATMP + BT(IS)
            IF (DATMP.GT.T1(IS)) DHRDDT(IS) = RTMIN(IS)
            IF (DATMP.LT.T2(IS)) DHRDDT(IS) = RTMAX(IS)

            DHRDDP (IS) = AP(IS)*NL + BP(IS)
            IF (NL.LT.P1(IS)) DHRDDP(IS) = RPMIN(IS)
            IF (NL.GT.P2(IS)) DHRDDP(IS) = RPMAX(IS)

            CR (IS) = 0.
            IF (SCHL(IS) .LE. SCHLBB(IS)) CR(IS) = 1.
            IF (SFRC(IS) .LE. SFRCBB(IS)) CR(IS) = 1. - 0.00294*SFRC(IS)

40       CONTINUE

*====================================================================*
*                      Integration section                           *
*====================================================================*

      ELSE IF (ITASK.EQ.3) THEN

         DO 60 IS=1,INS

*---------- chilling, forcing, temperature sum and hardening
            SCHL  (IS) = INTGRL(SCHL   (IS), RCHL  (IS),DELT)
            SFRC  (IS) = INTGRL(SFRC   (IS), RFRC  (IS),DELT)
            TMPSUM(IS) = INTGRL(TMPSUM (IS), RTMPSM(IS),DELT)
            SHRD  (IS) = INTGRL(SHRD   (IS), RHRD  (IS),DELT)

            SSHRD (IS) = RMIN(IS) + CR(IS)*(DHRDDT(IS)+DHRDDP(IS))

            IF (IDAY.EQ.172) DAYLMX = DAYL

*---------- joint factor model: NOT USED
C            IF (IPLTYP(IS).EQ.1) THEN                           ! deciduous trees
C               IF (IDAY .GE. 172) THEN
C                  JF  (IS) = SFRC(IS) + (DAYLMX - DAYL) /
C     &                        (DAYLMX - DAYLLF(IS)) * DAYLLF(IS)
C                  IF ((IDAY.EQ.365).OR.(IDAY.EQ.366)) JF(IS) = 0.
C                  DVS (IS) = LINT (DVSTB(1,IS), ILDVS(IS), JF(IS))
C               ELSE
C                  DVS (IS) = LINT (DVSTB(1,IS), ILDVS(IS), SFRC(IS))
C               ENDIF
C            ELSE                                                ! coniferous trees
C                  DVS (IS) = LINT (DVSTB(1,IS), ILDVS(IS), TMPSUM(IS))
C            END IF

*           sequential model during for development during winter,
*           temperature sum for developmental stage (DVS) during growing season
            IF (IPLTYP(IS).EQ.1) THEN                            ! deciduous trees
              IF (DVS(IS).LE.1.) THEN
                DVS (IS) = LINT (DVSTB(1,IS), ILDVS(IS), SFRC(IS))
              ELSE
                DVS (IS) = LINT (DVSTB(1,IS), ILDVS(IS), TMPSUM(IS))     ! coniferous trees
              ENDIF
            ENDIF

60       CONTINUE
```

```
*=================================================================*
*                       Terminal section                          *
*=================================================================*

      ELSE IF (ITASK.EQ.4) THEN

      ENDIF

      RETURN
      END
```

```
*===================================================================*
*                                                                   *
* SUBROUTINE PHOTO                                                  *
*                                                                   *
* Purpose: This subroutine calculates the maximal rate of           *
*          photosynthesis, initial light use efficiency and         *
*          dark respiration                                         *
*                                                                   *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time) *
* name    type description                             units  class *
* ----    ---- -----------                             -----  ----- *
* ITASK   I4  determines action of the subroutine,      -      C,I  *
*             1=initialization, 2=rate calculation,                 *
*             3=integration, 4=terminal                             *
* IUNITT  I4  unit number of timer data file            -      C,I  *
* IUNITP  I4  unit number of plant data file            -      C,I  *
* IUNITO  I4  unit number of output file                -      C,I  *
* FILET   C*  file name for time variables              -      C,I  *
* FILEP   C*  file name for plant variables             -      C,I  *
* OUTPUT  L4  flag that indicates if output to file is  -      C,I  *
*             required                                              *
* TERMNL  L4  flag that indicates if simulation should  -     C,I,O *
*             terminate                                             *
* IDAY    I4  daynumber since 1 January                 d      T    *
* DDTMP   R4  average day time temperature              °C     I    *
* CO2E    R4  external CO2 concentration                ppm    I    *
* DVS     R4  development stage                         -      I    *
* IFLCL   I4  number of foliage classes                 -      I    *
* WFLT    R4  total weight of foliage              kg DM ha-1  I    *
* WFL     R4  weight of foliage for each age class kg DM ha-1  I    *
* AMAX    R4  maximum rate of photosynthesis  kg CO2 ha-1 h-1  O    *
* EFF     R4  initial light use efficiency                          *
*                               kg CO2 ha-1 h-1 (J m-2 s-1)-1  O    *
* DRESP   R4  dark respiration                kg CO2 ha-1 h-1  O    *
*                                                                   *
* SUBROUTINES and FUNCTIONS called:                                 *
*                                                                   *
* FILE usage: - time variables file IUNITT, FILET                   *
*             - plant data file with unit IUNITP, FILEP             *
*             - output file with unit IUNITO for output and warnings *
*                                                                   *
*===================================================================*

      SUBROUTINE PHOTO

      INCLUDE 'FORGRO.CMN'

*---- Local variables

      REAL FWFL (IMNFLC)

      SAVE

      CALL CHKTSK ('PHOTO', IUNITO, ITOLD, ITASK)

*===================================================================*
*                         Initialization                            *
*===================================================================*

      IF (ITASK.EQ.1) THEN

*------- Initialization of run characteristics
         CALL RDINIT (IUNITT, IUNITO, FILET)
         CALL RDAINT ('IPSPEC', IPSPEC, IMNS, INS)
         CALL RDAINT ('IPLTYP', IPLTYP, IMNS, INS)
         CLOSE (IUNITT, STATUS='DELETE')

*------- Initialization of species characeristics
         DO 30 IS=1,INS

            FILEP = 'SPEC'//CHAR(IPSPEC(IS)+48)//'.DAT'
            CALL OUTCOM ('Spec ('//CHAR(IPSPEC(IS)+48)//')')
```

```
            IF (.NOT.INITP) THEN
              CALL COPFIL (IUNITP, FILEP, IUNITO)
              INITP = .TRUE.
            END IF
            CALL RDINIT (IUNITP, IUNITO, FILEP)

*---------- States

*---------- Parameters
            CALL RDSREA('AMAXM' ,AMAXM (IS))
            CALL RDSREA('EFF20' ,EFF20 (IS))
            CALL RDSREA('GAMM20',GAMM20(IS))
            CALL RDSREA('IECO2' ,IECO2 (IS))
            CALL RDSREA('DRSP20',DRSP20(IS))
            CALL RDSREA('RSMIN' ,RSMIN (IS))
            CALL RDSREA('RB'    ,RB    (IS))
            CALL RDSREA('RC'    ,RC    (IS))

*---------- AFGEN functions
            CALL RDAREA('AMDVST',AMDVST(1,IS),IMNP,ILADVS(IS))
            CALL RDAREA('AMTMPT',AMTMPT(1,IS),IMNP,ILATMP(IS))
            CALL RDAREA('AMAGET',AMAGET(1,IS),IMNP,ILAAGE(IS))
            CALL RDAREA('GMTMPT',GMTMPT(1,IS),IMNP,ILGTMP(IS))
            CALL RDAREA('GSVPDT',GSVPDT(1,IS),IMNP,ILGVPD(IS))

            CLOSE (IUNITP, STATUS='DELETE')

30    CONTINUE

*======================================================================*
*                     Rate calculation section                         *
*======================================================================*

      ELSE IF (ITASK.EQ.2) THEN

         DO 40 IS=1,INS

*           increase in CO2 compensation point and dark respiration with temperature:
            TEFF       = EXP(0.07 * (DDTMP-20.))
            GAMMA      = GAMM20(IS) * TEFF
            DRESP (IS) = DRESP (IS) * TEFF

*           conversion external CO2 concentration (CO2E) and CO2 compensation point (GAMMA)
*           from µmol mol-1 to mg m-3
            CONV       = PATM  * 1.E-6/(GASCON*(DDTMP+273.15))*44.E+3
            CO2        = CO2E  * CONV
            CO2CMP     = GAMMA * CONV

*           reduction of light use efficiency due to photorespiration
            EFF   (IS) = EFF20(IS) * (CO2E-GAMMA) / (CO2E+2.*GAMMA)

*           conversion from kg CO2 ha-1 leaf h-1 to mg CO2 m-2 leaf s-1
            AMX0       = AMAXM(IS) / (3600 * 10000 * 1.E-6)

*           correction factor mesophyl conductance reduction for temperature (0-1)
            GMTMP (IS) = LINT (GMTMPT(1,IS), ILGTMP(IS), DDTMP)

*           calculation mesophyl resistance at the given temperature
            RM    (IS) = GMTMP(IS) * (IECO2(IS)*CO2 - CO2CMP) / AMX0

*           stomatal resistance dependent on vapour pressure deficit
            GSVPD (IS) = LINT(GSVPDT, ILGVPD(IS), VPD)
            RS    (IS) = AMAX1(RSMIN(IS), 1000./GSVPD(IS))

*           maximum photosynthesis rate determined by CO2 diffusion:
            GASLAW     = (44./24.) * (293. / (273. + DDTMP))
            AMX1       = (CO2E-GAMMA) * GASLAW /
     &                     (RM(IS) + 1.6 * RS(IS) + 1.4 * RB(IS))

*           effect of temperature on maximum photosynthetic rate ("capacity")
            AMTMP (IS) = LINT (AMTMPT,ILATMP(IS), DDTMP)
            AMX2       = AMTMP(IS) * AMX0
```

```
*            calculation weighting factor (FWFL) and correction factor for AMAX for foliage-age (FAMT)
*            dependent of foliage age (FLAGE) and DVS
             FAMT = 0.
             IF (WFLT(IS).GT.0.) THEN
                AMDVS    (IS) = LINT (AMDVST,ILADVS,DVS)
                DO 41 I = 1,IFLCL(IS)
                   FWFL(I)    = WFL(IS,I) / WFLT(IS)
                   FLAGE      = IDAY + (I-1) * 365.
                   AMAGE (IS) = LINT(AMAGET, ILAAGE, FLAGE)
                   FAMT       = FAMT + FWFL(I) * AMAGE(IS) * AMDVS(IS)
41              CONTINUE
             END IF

*            assume similar relationship between dark respiration with DVS
*            as with AMAX
             DRESP (IS) = DRESP(IS) * AMDVS(IS)

*            maximum rate of photosynthesis is limited by either AMX1 or AMX2
*            and conversion from mg CO2 m-2 s-1 to kg CO2 ha-1 h-1
             AMAX  (IS) = FAMT * (AMIN1(AMX1, AMX2))*3600*10000*1.E-6
     &                    + DRESP(IS)

40       CONTINUE

*------ Output of states and rates only if it is required

        IF (OUTPUT .OR. TERMNL) THEN

        END IF

*==========================================================================*
*                        Integration section                               *
*==========================================================================*

      ELSE IF (ITASK.EQ.3) THEN

*==========================================================================*
*                         Terminal section                                 *
*==========================================================================*

      ELSE IF (ITASK.EQ.4) THEN

      END IF

      RETURN
      END
```

```
*==================================================================*
*                                                                  *
* SUBROUTINE RADIAT                                                *
*                                                                  *
* Purpose: This subroutine computes diffuse and direct amount of   *
*          photosynthetically active radiation from average global *
*          radiation (AVRAD), day of the year and hour of the day. *
*                                                                  *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time) *
* name   type description                              units  class *
* ----   ---- -----------                              -----  ----- *
* HOUR    R4  selected hour at which CO2 assimilation    h     T,I  *
*             is calculated                                         *
* DAY     R4  daynumber since 1 January                  d     T,I  *
* DAYL    R4  daylength                                 h/d    T,I  *
* SINLD   R4  intermediate variable                      -      I   *
* COSLD   R4  intermediate variable                      -      I   *
* AVRAD   R4  daily incoming total global radiation   J/m2/d    I   *
* ATMTR   R4  atmospheric transmission coefficient       -      I   *
* SINB    R4  sine of solar elevation                    -      I   *
* PARDIR  R4  instantaneous flux of direct PAR        J/m2/s    O   *
* PARDIF  R4  instantaneous flux of diffuse PAR       J/m2/s    O   *
*                                                                  *
* FATAL ERROR CHECKS (execution terminated, message): none         *
*                                                                  *
* SUBROUTINES and FUNCTIONS called: none                           *
*                                                                  *
* FILE usage: none                                                 *
*                                                                  *
*==================================================================*

      SUBROUTINE RADIAT

      INCLUDE 'FORGRO.CMN'
      SAVE

*---- Sine of solar elevation (SINB), integral of SINB (DSINB)
*     and integral of SINB with correction for lower atmospheric
*     transmission at low solar elevations (DSINBE)
      AOB    = SINLD/COSLD
      SINB   = AMAX1(0.,SINLD+COSLD*COS(2.*PI*(HOUR+12.)/24.))
      DSINB  = 3600.*(DAYL*SINLD+24.*COSLD*SQRT(1.-AOB*AOB)/PI)
      DSINBE= 3600.*(DAYL*(SINLD+0.4*
     &             (SINLD*SINLD+COSLD*COSLD*0.5))+12.0*COSLD*
     &             (2.0+3.0*0.4*SINLD)*SQRT(1.-AOB*AOB)/PI)

*---- Solar constant (SC) and daily extraterrestrial
*     radiation (ANGOT)
      SC     = 1370.*(1.+0.033*COS(2.*PI*DAY/365.))
      ANGOT = SC * DSINB

*---- Diffuse light fraction (FRDIF) from atmospheric
*     transmission (ATMTR)
      ATMTR = AVRAD/ANGOT
      IF (ATMTR.GT.0.75) FRDIF = 0.23
      IF (ATMTR.LE.0.75.AND.ATMTR.GT.0.35)
     &                   FRDIF = 1.33-1.46*ATMTR
      IF (ATMTR.LE.0.35.AND.ATMTR.GT.0.07)
     &                   FRDIF = 1.-2.3*(ATMTR-0.07)**2
      IF (ATMTR.LE.0.07) FRDIF = 1.

*---- Diffuse PAR (PARDIF) and direct PAR (PARDIR)
      PAR    = 0.5*AVRAD*SINB*(1.+0.4*SINB)/DSINBE
      PARDIF = AMIN1(PAR,SINB*FRDIF*ATMTR*0.5*SC)
      PARDIR = PAR-PARDIF
      RADDIF = 2. * PARDIF
      RADDIR = 2. * PARDIR

      RETURN
      END
```

```
*======================================================================*
*                                                                      *
* SUBROUTINE STAND                                                     *
*                                                                      *
* Purpose: This subroutine calculates stand characteristics.           *
*                                                                      *
*                                                                      *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time)   *
* name   type description                             units  class *
* ----   ---- -----------                             -----  ----- *
* ITASK   I4  determines action of the subroutine,      -     C,I  *
*             1=initialization, 2=rate calculation,               *
*             3=integration, 4=terminal                           *
* IUNITT  I4  unit number of timer data file            -     C,I  *
* IUNITP  I4  unit number of plant data file            -     C,I  *
* IUNITO  I4  unit number of output file                -     C,I  *
* FILET   C*  file name for time variables              -     C,I  *
* FILEP   C*  file name for plant variables             -     C,I  *
* OUTPUT  L4  flag that indicates if output to file is  -     C,I  *
*             required                                            *
* TERMNL  L4  flag that indicates if simulation should  -    C,I,O *
*             terminate                                           *
* IDAY    I4  daynumber since 1 January                 d      T   *
* DELT    R4  time interval of integration              d      T   *
* DVS     R4  developmental stage                       -      I   *
* FTHIN   R4  fraction thinned                          -      O   *
* HGHT    R4  height                                    m      O   *
* CANCLO  R4  canopy closure                            -      O   *
*                                                                  *
* FATAL ERROR CHECKS (execution terminated, message)               *
* DELT < 1.0                                                       *
* Certain sequences of ITASK, see subroutine CHKTSK                *
*                                                                  *
* SUBROUTINES and FUNCTIONS called:                                *
*                                                                  *
* FILE usage: - time variables file IUNITT, FILET                  *
*             - plant data file with unit IUNITP, FILEP            *
*             - output file with unit IUNITO for output and warnings *
*                                                                  *
*======================================================================*

      SUBROUTINE STAND

      INCLUDE 'FORGRO.CMN'
      SAVE
      CALL CHKTSK ('STAND', IUNITO, ITOLD, ITASK)

*======================================================================*
*                         Initialization                               *
*======================================================================*

      IF (ITASK.EQ.1) THEN

*------- Send title to output file
         CALL RDINIT (IUNITT, IUNITO, FILET)

*------- Initialization of run characteristics
         CALL RDAINT ('IPSPEC', IPSPEC, IMNS, INS)
         CALL RDAINT ('IPLTYP', IPLTYP, IMNS, INS2)

         NTRT  = 0.
         DBHT  = 0.
*------------- Initialization of species characeristics
         DO 30 IS=1,INS

            FILEP = 'SPEC'//CHAR(IPSPEC(IS)+48)//'.DAT'
            CALL OUTCOM ('Spec ('//CHAR(IPSPEC(IS)+48)//')')

            IF (.NOT.INITP) THEN
              CALL COPFIL (IUNITP, FILEP, IUNITO)
              INITP = .TRUE.
            END IF
```

```
            CALL RDINIT (IUNITP, IUNITO, FILEP)

*---------- States
            CALL RDSREA('NTRI'  ,NTRI  )
            CALL RDSREA('STAGEI',STAGEI)
            CALL RDSREA('HGHTI' ,HGHTI )
            CALL RDSREA('CNRADI',CNRADI)

*---------- Parameters
                                < SEE EXAMPLE OF SPEC<NR>.DAT FILE >
*           Stand characteristics
            CLOSE (IUNITP, STATUS='DELETE')

*---------- Initializing states
            NTR   (IS) = NTRI    / INS
            DBH   (IS) = DBH(IS) / INS
            STAGE (IS) = STAGEI
            HGHT  (IS) = HGHTI
            CNRAD (IS) = CNRADI

*---------- Initial values of auxilary variables
            CP    (IS) = AMIN1(1.,0.0001*NTR(IS)*PI*CNRAD(IS)**2)
            CNLENG(IS) = HGHT(IS) - CNBASE(IS)
            CANCLO(IS) = AMAX1(0.,AMIN1(1.,CP(IS)**
     &                   (1./(CNLENG(IS)/CNRAD(IS)))))

            STVOL (IS) = 0.001*NTR(IS)*CSH1(IS)*(DBH(IS)**CSH2(IS))*
     &                   (HGHT(IS)**CSH3(IS))
            BAREA (IS) = NTR(IS)*PI*(DBH(IS)/200.)**2.
            LAIMAX(IS) = DBH(IS) / DBHLAI(IS)

            CSH1R (IS) = CSH1(IS)**(-1./CSH2(IS))
            CSH2R (IS) = 1./CSH2(IS)
            CSH3R (IS) = -CSH3(IS)/CSH2(IS)

            NTRT       = NTRT + NTR   (IS)
            DBHT       = DBHT + DBH   (IS)

*           Initializing array parameters
            DO 31 I=1,INTH(IS)
              THAGE (IS,I) = THAGE2(I)
              FTHVOL(IS,I) = FTHVL2(I)
              FTHTRE(IS,I) = FTHTR2(I)
31          CONTINUE

30    CONTINUE

*=====================================================================*
*                     Rate calculation section                        *
*=====================================================================*

      ELSE IF (ITASK.EQ.2) THEN

         RESET = 0.
         IF (IDAY.EQ.365) RESET = 1.

         DO 50 IS=1,INS

*           THINNING: fraction of number of trees or volume removed by management
*           thinning occurs at day 365 of year with thinning
            FTHT     = 0.
            FTHV     = 0.
            DO 51 I = 1, INTH(IS)
               IF (INT(THAGE(IS,I)).EQ.INT(STAGE(IS))) THEN
                  FTHT   = RESET * FTHTRE(IS,I)
*                  FTHV   = RESET * FTHVOL(IS,I)
                  GOTO 52
               ENDIF
51          CONTINUE
52          CONTINUE
            FTHIN (IS) = FTHT
```

```
*           number of trees
            RNTR(IS) = -FTHIN(IS) * NTR(IS)

*           stand age
            RSTAGE(IS) = 1./365.

*           height
            IF (DVS(IS) .GT. 1.) THEN
              RHGHT  (IS) =
     &        -0.9*HGHMAX(IS)*((1.-EXP(C1HGHT(IS)*STAGE(IS)))**
     &        (C2HGHT(IS)-1.))*C1HGHT(IS)*C2HGHT(IS)*EXP(C1HGHT(IS)*
     &        STAGE(IS))/100.
            ELSE
              RHGHT  (IS) = 0.
            ENDIF

*           horizontal crown expansion:
            IF (CP(IS) .LT. 0.9) THEN
               RCNRAD(IS) = (RHGHT(IS)/(0.9*HGHMAX(IS))) * MCNRAD(IS)
            ELSE
               RCNRAD(IS) = 0.
            ENDIF

50      CONTINUE

*======================================================================*
*                       Integration section                            *
*======================================================================*

      ELSE IF (ITASK.EQ.3) THEN

         NTRT  = 0.
         DBHT  = 0.
         DO 60 IS=1,INS
            NTR   (IS) = INTGRL(NTR   (IS), RNTR   (IS),DELT)
            STAGE (IS) = INTGRL(STAGE (IS), RSTAGE (IS),DELT)
            HGHT  (IS) = INTGRL(HGHT  (IS), RHGHT  (IS),DELT)
            CNRAD (IS) = INTGRL(CNRAD (IS), RCNRAD (IS),DELT)
            STVOL (IS) = WST(IS) / BADEN(IS)
            TRVOL (IS) = 1000. * STVOL(IS) / NTR(IS)
            DBH   (IS) = CSH1R(IS)*(TRVOL(IS)**CSH2R(IS))*
     &                   (HGHT(IS)**CSH3R(IS))
            BAREA (IS) = NTR(IS)*PI*(DBH(IS)/200.)**2.
            LAIMAX(IS) = DBH(IS) / DBHLAI(IS)
            CNBASE(IS) = AMAX1(0.,AMIN1(0.65,1.-15./STAGE(IS)))
     &                   * HGHT(IS)
            CNLENG(IS) = HGHT(IS) - CNBASE(IS)
            CP    (IS) = AMIN1(1.,0.0001*NTR(IS)*PI*CNRAD(IS)**2)
            CANCLO(IS) = AMAX1(0.,AMIN1(1.,CP(IS)**
     &                   (1./(CNLENG(IS)/CNRAD(IS)))))
            NTRT       = NTRT + NTR   (IS)
            DBHT       = DBHT + DBH   (IS)

60      CONTINUE

*======================================================================*
*                        Terminal section                              *
*======================================================================*

      ELSE IF (ITASK.EQ.4) THEN

      END IF

      RETURN
      END
```

```
*=====================================================================*
*                                                                     *
* SUBROUTINE TOTASS                                                   *
*                                                                     *
* Purpose: This subroutine calculates daily total gross assimilation  *
*          (DTGA) by performing a Gaussian integration over time. At  *
*          three different times of the day, radiation is computed and *
*          used to determine assimilation whereafter integration      *
*          takes place.                                               *
*                                                                     *
* FORMAL PARAMETERS: (I=input, O=output, C=control, IN=init, T=time)  *
* name   type description                               units  class *
* ----   ---- -----------                               -----  ----- *
* DAY     R4  daynumber since 1 January                   d      T,I *
* DAYL    R4  daylength                                  h/d     T,I *
* INS     I4  number  of species                          -       I  *
* AMAX    R4  actual maximum CO2-assimilation rate for  kg/ha/h   I  *
*             individual leaves                                      *
* EFF     R4  initial light use efficiency for     kg/ha/h/J m2 s IN *
*             leaves                                                 *
* KDF     R4  extinction coefficient for leaves           -       I  *
* HGHT    R4  total height of a species in the canopy     m       I  *
* CNBASE  R4  crown base of a species in the canopy       m       I  *
* LAIT    R4  total leaf area index                     ha/ha     I  *
* AVRAD   R4  daily incoming total global radiation     J/m2/d    I  *
* SINLD   R4  intermediate variable in calculating        -       I  *
*             daylength                                              *
* COSLD   R4  intermediate variable in calculating        -       I  *
*             daylength                                              *
* ATMTR   R4  atmospheric transmission coefficient        -       I  *
* FARCN   R4  fraction absorbed incoming global radiation -       I  *
* FRD     R4  fraction global radiation used for drying   -       I  *
*             power in penman evaporation                            *
* DTGA    R4  daily total gross CO2-assimilation        kg/ha/h   O  *
* DARCN   R4  daily absorbed radiation per species  J/m2 ground/d O  *
*                                                                     *
* FATAL ERROR CHECKS (execution terminated, message): none            *
*                                                                     *
* SUBROUTINES and FUNCTIONS called: RADIAT, ASSIM                     *
*                                                                     *
* FILE usage: none                                                    *
*                                                                     *
*=====================================================================*

      SUBROUTINE TOTASS

      INCLUDE 'FORGRO.CMN'
      SAVE
      DATA XGAUS /0.1127, 0.5000, 0.8873/
      DATA WGAUS /0.2778, 0.4444, 0.2778/

*---- Assimilation set to zero and three different times of the day (HOUR)
      DO 10 IS=1,INS
         DTGA  (IS) = 0.
         DARCN (IS) = 0.
10    CONTINUE

      DO 30 IG = 1,INGP
         HOUR = 12.0 + DAYL * 0.5 * XGAUS(IG)

*------- At the specified HOUR, radiation is computed and used to compute assimilation
         CALL RADIAT
         CALL ASSIM

*------- Integration of assimilation rate to a daily total (DTGA)
*        Daily absorbed radiation by the crown (DARCN) and
         DO 20 IS=1,INS
            DTGA  (IS) = DTGA  (IS) + FGRCN (IS) * WGAUS(IG)
            DARCN (IS) = DARCN (IS) + ARCN  (IS) * WGAUS(IG)
20       CONTINUE

30    CONTINUE
```

```
      LAITOT = 0.
      DARCNT = 0.
      DO 40 IS = 1,INS
         DTGA  (IS) = DTGA  (IS) * DAYL
         GPHOT (IS) = DTGA  (IS) * 30./44.

         DARCN (IS) = DARCN (IS) * DAYL * 3600.
         DARCNT     = DARCNT + DARCN(IS)
         LAITOT     = LAITOT + LAIT(IS)
40    CONTINUE

      DO 45 IS = 1,INS
        IF (DARCNT.GT.0.) THEN
           FARCN (IS) = (DARCN (IS)/DARCNT) * (1.-EXP(-0.5*LAITOT))
        ELSE
           FARCN (IS) = 0.
        ENDIF
45    CONTINUE

      RETURN
      END
```

Common blocks used in FORGRO 3.5

```
*=====================================================================*
*                                                                     *
*      Control variables                                              *
*                                                                     *
*=====================================================================*

      IMPLICIT   REAL (A-Z)

      INTEGER    ITASK , ITOLD , INSETS, IRUN  , IRUNLA, I1
      INTEGER    ISTAT1, ISTAT2, ISTN
      INTEGER    ITABLE, IDTMP
      LOGICAL    OUTPUT, TERMNL, INITP , WTRMES, WTROK
      CHARACTER*80 WTRDIR
      CHARACTER*7  CNTR
      CHARACTER*1  DUMMY

*     Unit numbers for rerun (R), timer (T), output (O),
*     plant data (P), site data (S) and debug information (D) files.

      INTEGER      IUNITR, IUNITT, IUNITO, IUNITP, IUNITS
      CHARACTER*80 FILER , FILET , FILEO , FILEP , FILES

      PARAMETER (IUNITR=20,IUNITT=30,IUNITO=40,IUNITP=50,IUNITS=60)
      PARAMETER (FILER ='RERUNS.DAT',FILET='TIMER.DAT',FILEO='RES.DAT',FILES ='SOIL.DAT')

*---- Time variables

      INTEGER    IDAY  , IYEAR , IYR   , NYRS
      REAL       HOUR  , TIME  , DAY
      REAL       STTIME, FINTIM, DELT  , PRDEL
      REAL       FRGR  , PGN

*     Time step of integration
      PARAMETER (DELT = 1.)

      COMMON /CONTRL/
     &           ITASK , ITOLD , INSETS, IRUN  , IRUNLA, I1    ,
     &           ISTAT1, ISTAT2, ISTN  , ITABLE, IDTMP , OUTPUT,
     &           TERMNL, INITP , WTRMES, WTROK , WTRDIR, CNTR  , DUMMY ,
     &           IDAY  , IYEAR , IYR   , NYRS  , HOUR  ,
     &           TIME  , DAY   , STTIME, FINTIM, PRDEL ,
     &           FRGR  , PGN

*=====================================================================*
*                                                                     *
*      Mathematical constants,                                        *
*      (micro-) meteorological and other abiotic variables            *
*                                                                     *
*=====================================================================*

*     Gaussian integration
      INTEGER    IG    , IG1   , INGP  , INGP1
      PARAMETER (INGP=3, INGP1=5)
      REAL       XGAUS  (INGP) , WGAUS (INGP), XGAUS1(IGP1), WGAUS1(IGP1)

*     soil water potential (MPa) and O2 concentration in the air (mol m-3), required in PGEN
      REAL       PSIFOL, COAIR
      PARAMETER (PSIFOL=0., COAIR=8.471)

*     Pi, and conversion factor from degrees to radians
      REAL       PI    , RAD
      PARAMETER (PI    = 3.141592654, RAD   = 0.017453292)

*---- (Micro-) meteorological and other abiotic variables
      REAL       DAYL  , DAYLP , SINLD , COSLD , SINB
      REAL       LONG  , LAT   , ELV
      REAL       DRAD  , TMN   , TMX   , VAPOUR, WIND  , RAIN
      REAL       AVRAD , ATMTR , RADDIR, RADDIF, PARDIR, PARDIF
```

```
      REAL       DATMP , DDTMP , TSOIL , CO2E  , TMPSCN
      REAL       SVP   , VPD   , RELHUM

*     atmospheric pressure and gas constant, used in PHOTO
      REAL       PATM  , GASCON
      PARAMETER (PATM  = 101325., GASCON = 8.3144)

      COMMON /MICMET/
     &           DAYL  , DAYLP , SINLD , COSLD , SINB  ,
     &           LONG  , LAT   , ELV   ,
     &           DRAD  , TMN   , TMX   , VAPOUR, WIND  , RAIN  ,
     &           AVRAD , ATMTR , RADDIR, RADDIF, PARDIR, PARDIF,
     &           DATMP , DDTMP , TMTMX , TSOIL , CO2E  , TMPSCN,
     &           SVP   , VPD   , RELHUM
```

```
*=====================================================================*
*                                                                     *
*     Plant variables                                                 *
*                                                                     *
*=====================================================================*

      INTEGER     I       , I2    , INS   , INS2   , IS    , IL
      REAL        H

*---- Maximum number of species, parameters, foliage classes, sapwood classes,
*     foliate layers, times thinning

      INTEGER     IMNS    , IMNP  , IMNFLC,  IMNSWC, IMNL  , IMNTH
      PARAMETER (IMNS=3  , IMNP=30,IMNFLC=5,IMNSWC=10, IMNL=50,IMNTH=20)
      PARAMETER (IMNOBS=14)
      INTEGER     IPSPEC(IMNS), IPLTYP(IMNS), IFLCL (IMNS), ISWCL (IMNS)
      INTEGER     INTH  (IMNS), INOBS (IMNS)
      CHARACTER*8 SPNAME(IMNS)

*---- Declaration of varables. Syntax:
*---- FL-foliage, BR-branches, SW-sapwood, HW-heartwood, ST-stem
*---- CR-coarse roots, FR-fine roots, RS-reserves, LT-litter, CR-crown
*---- W..-weight, G..-growth rate, D..- death rate, T..-change of weight
*---- due to thinning, R..-rate of change, C..-coefficient
*---- ..I-initial value, ..T-total,
*---- State variables  ,       initial values, rate variables
*     weights
      REAL WFL   (IMNS,IMNFLC), WFLI(IMNFLC), RWFL  (IMNS,IMNFLC)
      REAL WSW   (IMNS,IMNSWC), WSWI(IMNSWC), RWSW  (IMNS,IMNSWC)
      REAL WBR   (IMNS),        WBRI        , RWBR  (IMNS)
      REAL WHW   (IMNS),        WHWI        , RWHW  (IMNS)
      REAL WCR   (IMNS),        WCRI        , RWCR  (IMNS)
      REAL WFR   (IMNS),        WFRI        , RWFR  (IMNS)
      REAL WRS   (IMNS),        WRSI        , RWRS  (IMNS)
      REAL WLT   (IMNS),        WLTI        , RWLT  (IMNS)
*     stand characteristics
      REAL NTR   (IMNS),        NTRI        , RNTR  (IMNS)
      REAL STAGE (IMNS),        STAGEI      , RSTAGE(IMNS)
      REAL HGHT  (IMNS),        HGHTI       , RHGHT (IMNS)
      REAL CNRAD (IMNS),        CNRADI      , RCNRAD(IMNS)
*     phenology
      REAL SCHL  (IMNS),        SCHLI       , RCHL  (IMNS)
      REAL SFRC  (IMNS),        SFRCI       , RFRC  (IMNS)
      REAL SHRD  (IMNS),        SHRDI       , RHRD  (IMNS)
      REAL TMPSUM(IMNS),        TMPSMI      , RTMPSM(IMNS)

*---- Auxilary variables

*     weights
      REAL WTT   (IMNS), WSH   (IMNS), WRT   (IMNS), WFLT  (IMNS)
      REAL WSWT  (IMNS), WST   (IMNS), WRSMN (IMNS), WRSMX (IMNS)
*     photosynthesis
      REAL AMAX  (IMNS), EFF   (IMNS), DRESP (IMNS)
      REAL RM    (IMNS), RS    (IMNS)
      REAL GTDM  (IMNS), DTGA  (IMNS)
      REAL GPHOT (IMNS), GPHOTT
      REAL FGRSHD(IMNS), FGRSUN(IMNS), FGRL  (IMNS), FGRCN (IMNS)
*     light interception
      REAL KDRDR (IMNS), KDRT  (IMNS)
      REAL EXDF        , EXDRDR      , EXDRT
      REAL ARDF  (IMNS), ARDRDR(IMNS), ARDRT (IMNS)
      REAL ARSHD (IMNS), ARSUN (IMNS), ARCN  (IMNS), ARL   (IMNS)
      REAL DARCN (IMNS), FARCN (IMNS)
      REAL LAIT  (IMNS), LAI   (IMNS , IMNFLC)     , LAIC  (IMNS)
      REAL LD    (IMNS)
*     maintenance
      REAL MRT   (IMNS), MRFL  (IMNS), MRBR  (IMNS), MRSW  (IMNS)
      REAL MRHW  (IMNS), MRFR  (IMNS), MRCR  (IMNS)
*     allocation fractions
      REAL FSH   (IMNS), FST   (IMNS), FCR   (IMNS)
*     growth rates
      REAL GFL   (IMNS), GBR   (IMNS), GSW   (IMNS), GHW   (IMNS)
```

```
      REAL GSH   (IMNS), GCR   (IMNS), GFR   (IMNS), GST   (IMNS)
      REAL GRT   (IMNS), GRS   (IMNS), GLT   (IMNS)

*     death rates
      REAL DFLT  (IMNS), DSWT  (IMNS)
      REAL DFL   (IMNS , IMNFLC), DSW (IMNS, IMNSWC)
      REAL DBR   (IMNS), DHW   (IMNS), DCR   (IMNS)
      REAL DFR   (IMNS), DRS   (IMNS), DST   (IMNS), DSH   (IMNS)
      REAL DRT   (IMNS), DLT   (IMNS)
*     thinning
      REAL FTHIN (IMNS), TFLT  (IMNS), TSWT  (IMNS)
      REAL TFL   (IMNS , IMNFLC), TSW (IMNS, IMNSWC)
      REAL TBR   (IMNS), THW   (IMNS), TCR   (IMNS)
      REAL TFR   (IMNS), TRS   (IMNS), TLT   (IMNS)
*     phenology
      REAL DVS   (IMNS), JF    (IMNS)

*     stationairy state of frost hardiness, SSHRD, and
*     change of SSHRD with temperature and photoperiod
      REAL SSHRD (IMNS), DHRDDT(IMNS), DHRDDP(IMNS)
*     stand characteristics
      REAL STVOL (IMNS), TRVOL (IMNS), DBH   (IMNS), BAREA (IMNS)
      REAL CANCLO(IMNS), CP    (IMNS), CNLENG(IMNS), CNBASE(IMNS)
      REAL NTRT        , DBHT
*     annual totals: A...
      REAL AGPHOT(IMNS), AMRT  (IMNS), AGTDM (IMNS)
      REAL AARCN (IMNS)
*     average of annual totals: AA...
      REAL AAGPCN(IMNS), AAMRT (IMNS), AAGTDM(IMNS)
      REAL AAARCN(IMNS)

*---- Model parameters

*     photosynthesis
      REAL AMAXM (IMNS), EFF20 (IMNS), GAMM20 (IMNS), IECO2 (IMNS)
      REAL DRSP20(IMNS), RSMIN (IMNS), RB     (IMNS), RC    (IMNS)
*     light interception
      REAL KDF   (IMNS), SCV   (IMNS), SLA   (IMNS), LAIMAX(IMNS)
*     maintenance, and mineral content (N, P, K, Ca, Mg, S)
      REAL ASRQ  (IMNS), REFTMP(IMNS), Q10   (IMNS)
      REAL CMRFL (IMNS), CMRBR (IMNS), CMRSW (IMNS), CMRHW (IMNS)
      REAL CMRFR (IMNS), CMRCR (IMNS)
*     mineral content of organs
      REAL NFL(IMNS),NBR(IMNS),NSW(IMNS),NHW(IMNS),NCR(IMNS),NFR(IMNS)
      REAL PFL(IMNS),PBR(IMNS),PSW(IMNS),PHW(IMNS),PCR(IMNS),PFR(IMNS)
      REAL KFL(IMNS),KBR(IMNS),KSW(IMNS),KHW(IMNS),KCR(IMNS),KFR(IMNS)
      REAL CFL(IMNS),CBR(IMNS),CSW(IMNS),CHW(IMNS),CCR(IMNS),CFR(IMNS)
      REAL MFL(IMNS),MBR(IMNS),MSW(IMNS),MHW(IMNS),MCR(IMNS),MFR(IMNS)
*     coefficients for reserves
      REAL CRSFL (IMNS), CRSBR (IMNS), CRSSW (IMNS), CRSHW (IMNS)
      REAL CRSCR (IMNS), CRSFR (IMNS), CRSNX (IMNS)
*     coefficients for death rates
      REAL CDFL  (IMNS , IMNFLC)     , CDFL2 (IMNFLC),CDBR (IMNS)
      REAL CDSW  (IMNS), CDHW  (IMNS), CDCR  (IMNS), CDFR  (IMNS)
      REAL CDLT  (IMNS)
      REAL CFLUSH(IMNS), CLFFL (IMNS), CLSW  (IMNS)
*     phenology
      REAL SCHLBB(IMNS), SFRCBB(IMNS), SFRCLF(IMNS)
      REAL TMINCH(IMNS), TOPTCH(IMNS), TMAXCH(IMNS)
      REAL C1FRC (IMNS), C2FRC (IMNS), C3FRC (IMNS)
      REAL DAYLLF(IMNS), BATMP (IMNS)
      REAL RPMIN (IMNS), RPMAX (IMNS), RTMIN (IMNS), RTMAX (IMNS)
      REAL P1    (IMNS), P2    (IMNS), AP    (IMNS), BP    (IMNS)
      REAL T1    (IMNS), T2    (IMNS), AT    (IMNS), BT    (IMNS)
      REAL NLCF  (IMNS), NLCH  (IMNS), TAU   (IMNS), RMIN  (IMNS)
      REAL CR    (IMNS)
      REAL MNBB  (IMNS), MNLF  (IMNS), DBBDT (IMNS), DLFDT (IMNS)
      INTEGER BDBRST(IMNS,IMNOBS),FORGRN(IMNS,IMNOBS)
      INTEGER FOLFLL(IMNS,IMNOBS)
      INTEGER BDBST2(IMNOBS), FRGRN2(IMNOBS), FOLFL2(IMNOBS)

*     stand characteristics
```

```
      REAL BADEN (IMNS), MCNRAD(IMNS)
*     Richard-Chapman coefficients for height growth
      REAL HGHMAX(IMNS), C1HGHT(IMNS), C2HGHT(IMNS)
*     ratio DBH to LAIMAX
      REAL DBHLAI(IMNS)
*     Shumacher-Hall coefficients for volume increment, and their reverse
      REAL CSH1  (IMNS), CSH2  (IMNS), CSH3  (IMNS)
      REAL CSH1R (IMNS), CSH2R (IMNS), CSH3R (IMNS)
*     Thinning
      REAL THAGE (IMNS,IMNTH), FTHVOL(IMNS,IMNTH), FTHTRE(IMNS,IMNTH)
      REAL THAGE2(IMNTH),      FTHVL2(IMNTH),      FTHTR2(IMNTH)

*---- AFGEN FUNCTIONS
*     photosynthesis
      INTEGER ILADVS(IMNS), ILATMP(IMNS), ILAAGE(IMNS)
      INTEGER ILGTMP(IMNS), ILGVPD(IMNS)
      REAL AMDVS (IMNS), AMDVST(IMNP,IMNS)
      REAL AMTMP (IMNS), AMTMPT(IMNP,IMNS)
      REAL AMAGE (IMNS), AMAGET(IMNP,IMNS)
      REAL GMTMP (IMNS), GMTMPT(IMNP,IMNS)
      REAL GSVPD (IMNS), GSVPDT(IMNP,IMNS)
*     allocation
      INTEGER ILFFL (IMNS), ILFBR (IMNS), ILFRT(IMNS), ILFFR(IMNS)
      INTEGER ILFRS (IMNS)
      REAL FFL   (IMNS), FFLTB (IMNP,IMNS)
      REAL FBR   (IMNS), FBRTB (IMNP,IMNS)
      REAL FRT   (IMNS), FRTTB (IMNP,IMNS)
      REAL FFR   (IMNS), FFRTB (IMNP,IMNS)
      REAL FRS   (IMNS), FRSTB (IMNP,IMNS)
*     phenology
      INTEGER      ILDVS (IMNS)
      REAL         DVSTB (IMNP,IMNS)

      COMMON /PLANT /
     &          INS   , IPSPEC, IPLTYP, IFLCL , ISWCL , INTH  , INOBS ,
     &          SPNAME,
     &          WFL   , WFLI  , RWFL  , WSW   , WSWI  , RWSW  ,
     &          WBR   , WBRI  , RWBR  , WHW   , WHWI  , RWHW  ,
     &          WCR   , WCRI  , RWCR  , WFR   , WFRI  , RWFR  ,
     &          WRS   , WRSI  , RWRS  , WLT   , WLTI  , RWLT  ,
     &          NTR   , NTRI  , RNTR  , STAGE , STAGEI, RSTAGE,
     &          HGHT  , HGHTI , RHGHT , CNRAD , CNRADI, RCNRAD,
     &          SCHL  , RCHL  , SFRC  , RFRC  , SHRD  , RHRD  ,
     &          TMPSUM, RTMPSM,
     &          WTT   , WSH   , WRT   , WFLT  , WSWT  , WST   ,
     &          WRSMN , WRSMX ,
     &          AMAX  , EFF   , DRESP , RM    , RS    ,
     &          GTDM  , DTGA  , GPHOT , GPHOTT,
     &          FGRSHD, FGRSUN, FGRL  , FGRCN ,
     &          KDRDR , KDRT  ,
     &          EXDF  , EXDRDR, EXDRT , ARDF  , ARDRDR, ARDRT ,
     &          ARSHD , ARSUN , ARCN  , ARL   , DARCN , FARCN ,
     &          LAIT  , LAI   , LAIC  , LD    ,
     &          MRT   , MRFL  , MRBR  , MRSW  , MRHW  , MRFR  , MRCR  ,
     &          FSH   , FST   , FCR   ,
     &          GFL   , GBR   , GSW   , GHW   , GSH   , GCR   ,
     &          GFR   , GST   , GRT   , GRS   , GLT   ,
     &          DFLT  , DSWT  , DFL   , DSW   , DBR   , DHW   , DCR   ,
     &          DFR   , DRS   , DST   , DSH   , DRT   , DLT   ,
     &          FTHIN , TFLT  , TSWT  , TFL   , TSW   , TBR   , THW   ,
     &          TCR   , TFR   , TRS   , TLT   ,
     &          DVS   , JF    ,
     &          SSHRD , DHRDDT, DHRDDP,
     &          H     , STVOL , TRVOL , DBH   , BAREA ,
     &          CANCLO, CP    , CNLENG, CNBASE,
     &          NTRT  , DBHT  ,
     &          AGPHOT, AMRT  , AGTDM , AARCN ,
     &          AAGPCN, AAMRT , AAGTDM, AAARCN,
     &          AMAXM , EFF20 , GAMM20, IECO2 , DRSP20, RSMIN ,
     &          RB    , RC    ,
     &          KDF   , SCV   , SLA   , LAIMAX,
     &          ASRQ  , REFTMP, Q10   ,
```

```
     &          CMRFL , CMRBR , CMRSW , CMRHW , CMRFR , CMRCR ,
     &          NFL   , NBR   , NSW   , NHW   , NCR   , NFR,
     &          PFL   , PBR   , PSW   , PHW   , PCR   , PFR,
     &          KFL   , KBR   , KSW   , KHW   , KCR   , KFR,
     &          CFL   , CBR   , CSW   , CHW   , CCR   , CFR,
     &          MFL   , MBR   , MSW   , MHW   , MCR   , MFR,
     &          CRSFL , CRSBR , CRSSW , CRSHW , CRSCR , CRSFR , CRSNX ,
     &          CDFL  , CDFL2 , CDBR  , CDSW  , CDHW  , CDCR  , CDFR  ,
     &          CDLT  , CFLUSH, CLFFL , CLSW  ,
     &          SCHLBB, SFRCBB, SFRCLF, TMINCH, TOPTCH, TMAXCH,
     &          C1FRC , C2FRC , C3FRC , DAYLLF, BATMP ,
     &          RPMIN , RPMAX , RTMIN , RTMAX ,
     &          P1    , P2    , AP    , BP    ,
     &          T1    , T2    , AT    , BT    ,
     &          NLCF  , NLCH  , TAU   , RMIN  ,
     &          CR    , MNBB  , MNLF  , DBBDT , DLFDT ,
     &          BDBRST, FORGRN, FOLFLL, BDBST2, FRGRN2, FOLFL2,
     &          BADEN , MCNRAD, HGHMAX, C1HGHT, C2HGHT, DBHLAI,
     &          CSH1  , CSH2  , CSH3  , CSH1R , CSH2R , CSH3R ,
     &          THAGE , FTHVOL, FTHTRE, THAGE2, FTHVL2, FTHTR2,
     &          ILADVS, ILATMP, ILAAGE, ILGTMP, ILGVPD,
     &          AMDVS , AMDVST, AMTMP , AMTMPT, AMAGE , AMAGET,
     &          GMTMP , GMTMPT, GSVPD , GSVPDT,
     &          ILFFL , ILFBR , ILFRT , ILFFR , ILFRS ,
     &          FFL   , FFLTB , FBR   , FBRTB , FRT   , FRTTB ,
     &          FFR   , FFRTB , FRS   , FRSTB ,
     &          ILDVS , DVSTB
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Acronyms used in FORGRO 3.5

AAARCN	annually averaged absorbed radiation by the crown	MJ m^{-2} ground yr^{-1}
AAGPCN	annually averaged gross photosynthesis by the crown	t CH$_2$O ha^{-1} yr^{-1}
AAGTDM	annually averaged gross total dry matter	t DM ha^{-1} yr^{-1}
AAMRT	annually averaged total maintenance requirements	t CH$_2$O ha^{-1} yr^{-1}
AARCN	annually averaged absorbed radiation by the crown	MJ m^{-2} ground yr^{-1}
AGPHOT	annual gross photosynthesis	t CH$_2$O ha^{-1} yr^{-1}
AGTDM	annual averaged gross total dry matter	t DM ha^{-1} yr^{-1}
AMAGE	reduction factor accounting for effect of foliage age on AMAXM	-
AMAGET	table of AMAXM reduction factor accounting for effect of foliage age on AMAXM	-
AMAX	actual maximum CO$_2$ assimilation rate at light saturation for individual leaves	kg CO$_2$ ha^{-1} leaf h^{-1}
AMAXM	potential maximum CO$_2$ assimilation rate at light saturation for individual leaves	kg CO$_2$ ha^{-1} leaf h^{-1}
AMDVS	reduction factor accounting for effect of development stage on AMAXM	-
AMDVST	table of AMAXM reduction factor accounting for effect of development stage on AMAXM	-
AMRT	annual total maintenance respiration	t CH$_2$O ha^{-1} yr^{-1}
AMTMP	reduction factor accounting for effect of temperature stage on AMAXM	-
AMTMPT	table of AMAXM reduction factor accounting for effect of temperature stage on AMAXM	-
ANGOT	daily extra-terrestrial radiation	J m^{-2} ground d^{-1}
AOB	intermediate variable in calculating daylength and solar sine	-
AP	constant for effect of photoperiod on hardening	-
ARCN	absorbed radiation by the crown	J m^{-2} ground s^{-1}
ARDF	absorbed radiation (PAR) at the selected canopy height, diffuse flux	J m^{-2} leaf s^{-1}
ARDRDR	absorbed radiation (PAR) at the selected canopy height, direct component of direct flux	J m^{-2} leaf s^{-1}
ARDRT	absorbed radiation (PAR) at the selected canopy height, total direct flux	J m^{-2} leaf s^{-1}
ARL	absorbed radiation (PAR) by a foliage layer at the selected canopy height	J m^{-2} ground s^{-1}
ARPP	absorbed radiation (PAR) by sunlit foliage area perpendicular to the direct beam	J m^{-2} leaf s^{-1}
ARSHD	absorbed radiation (PAR) by shaded foliage area	J m^{-2} leaf s^{-1}
ARSUN	absorbed radiation (PAR) by sunlit foliage area	J m^{-2} leaf s^{-1}
ASRQ	assimilate requirements for plant dry matter production	kg CH$_2$O (kg living DM)$^{-1}$
AT	constant for effect of temperature on hardening	-
ATMTR	atmospheric transmission coefficient	-
AVRAD	daily incoming total global radiation	J m^{-2} ground d^{-1}
BADEN	basic density of wood	kg m-3
BAREA	basal area	m2 ha^{-1}
BATMP	base temperature for temperature sum	°C
BDBRST	date of budburst	daynumber
BDBST2	help variable to read BDBRST	daynumber
BP	constant for effect of photoperiod on hardening	-
BT	constant for effect of temperature on hardening	-
C1FRC	coefficient for rate of forcing	-
C1HGHT	coefficient for Chapman-Richards equation for height growth	-
C2FRC	coefficient for rate of forcing	-
C2HGHT	coefficient for Chapman-Richards equation for height growth	-
C3FRC	coefficient for rate of forcing	-
CANCLO	canopy closure	-
CBR	Calcium concentrations in branches	kg kg^{-1}
CCR	Calcium concentrations in coarse roots	kg kg^{-1}
CDBR	coefficient for death rate of branches	yr^{-1}
CDCR	coefficient for death rate of coarse roots	yr^{-1}
CDFL	coefficient for death rate of foliage	yr^{-1}
CDFL2	help variable to read CDFL	yr^{-1}
CDFR	coefficient for death rate of fine roots	yr^{-1}
CDHW	coefficient for death rate of heartwood	yr^{-1}
CDLT	coefficient for decomposition of litter	yr^{-1}
CDSW	coefficient for death rate of sapwood	yr^{-1}
CFL	Calcium concentrations in foliage	kg kg^{-1}
CFLUSH	coefficient for leaf flush in spring	d^{-1}
CFR	Calcium concentrations in fine roots	kg kg^{-1}
CHW	Calcium concentrations in branches	kg kg^{-1}
CLFFL	coefficient for leaf fall in autumn	d^{-1}
CLSW	coeficient for longevity of last sapwood ring	yr^{-1}
CMRBR	coefficient for maintenance respiration of branches	kg CH$_2$O (kg DM)$^{-1}$
CMRCR	coefficient for maintenance respiration of coarse roots	kg CH$_2$O (kg DM)$^{-1}$

CMRFL	coefficient for maintenance respiration of foliage	kg CH_2O (kg DM)$^{-1}$
CMRFR	coefficient for maintenance respiration of fine roots	kg CH_2O (kg DM)$^{-1}$
CMRHW	coefficient for maintenance respiration of heartwood	kg CH_2O (kg DM)$^{-1}$
CMRSW	coefficient for maintenance respiration of sapwood	kg CH_2O (kg DM)$^{-1}$
CNBASE	height of crown base	m
CNLENG	crown length	m
CNRAD	crown radius	m
CNRADI	initial crown radius	m
CNTR	county name for weather data	-
CO2E	external CO_2 concentration	µmol mol^{-1}
COSLD	intermediate variable in calculation of daylength	-
CP	projected crown area	m^{-2} ha^{-1}
CR	competence for hardening	-
CRSBR	coefficient for reserves in branches	-
CRSCR	coefficient for reserves in branches	-
CRSFL	coefficient for reserves in foliage	-
CRSFR	coefficient for reserves in fine roots	-
CRSHW	coefficient for reserves in heartwood	-
CRSNX	ratio maX to miN of reserve level	-
CRSSW	coefficient for reserves in sapwood	-
CSH1	coefficient of Shumacher-Hall equation for volume increment	-
CSH1R	coefficient of reversed Shumacher-Hall equation for volume increment	-
CSH2	coefficient of Shumacher-Hall equation for volume increment	-
CSH2R	coefficient of reversed Shumacher-Hall equation for volume increment	-
CSH3	coefficient of Shumacher-Hall equation for volume increment	-
CSH3R	coefficient of reversed Shumacher-Hall equation for volume increment	-
CSW	Calcium concentrations in sapwood	kg kg^{-1}
DARCN	daily absorbed radiation (PAR) by the crown	J m^{-2} ground d^{-1}
DATMP	daily temperature, average of minimum and maximum temperature	°C
DAY	daynumber since 1 Januari	-
DAYL	*daylength*	*h d*$^{-1}$
DAYLLF	day length at average date of leaf fall	h d^{-1}
DBBDT	shift of budburst with temperature	d °C^{-1}
DBH	mean diameter at breast height	cm tree^{-1}
DBHLAI	ratio DBH to maximal LAI	-
DBHT	total DBH, over all species	cm tree^{-1}
DBR	death rate of branches	kg DM yr^{-1}
DCR	death rate of coarse roots	kg DM yr^{-1}
DDTMP	daily daytime temperature	°C
DEC	declination of the sun	radians
DELT	time interval of integration	d
DFL	death rate of each foliage class	kg DM yr^{-1}
DFLT	death rate of total foliage	kg DM yr^{-1}
DFR	death rate of fine roots	kg DM yr^{-1}
DHRDDP	change of stationary state of frost hardiness as function of photoperiod	°C
DHRDDT	change of stationary state of frost hardiness as function of temperature	°C
DHW	death rate of heartwood	kg DM yr^{-1}
DLFDT	shift of leaf fall with temperature	d °C^{-1}
DLT	decomposition rate of litter	kg DM yr^{-1}
DRAD	daily incoming total radiation	J m^{-2} ground d^{-1}
DRESP	rate of dark respiration	kg CH_2O ha^{-1} d^{-1}
DRS	death rate of reserves	kg DM yr^{-1}
DRSP20	rate of dark respiration at 20°C	kg CO_2 ha^{-1} leaf h^{-1}
DRT	death rate of roots (fine + coarse roots)	kg DM yr^{-1}
DSINB	integral if SINB over the day	d^{-1}
DSINBE	as DSINB, but with correction for lower atmospheric transmission at low solar elevations	d^{-1}
DSH	death rate of shoot (foliage + branches + stem)	kg DM yr^{-1}
DST	death rate of stem (sapwood + heartwood)	kg DM yr^{-1}
DSW	death rate of for each sapwood class	kg DM yr^{-1}
DSWT	death rate of total sapwood	kg DM yr^{-1}
DTGA	daily total gross CO_2 assimilation rate	kg CO_2 ha^{-1} ground d^{-1}
DUMMY	variable to continue the program after a warning	-
DVS	development state	-
DVSTB	table DVS as function of state of forcing of temperature sum	-
DVSTB	temperature sum vs. development state coniferous trees	-
EFF	initial light use efficiency for individual leaves	kg CO_2 ha^{-1} leaf h^{-1} (J m^{-2} leaf s^{-1})$^{-1}$
EFF20	value of EFF at 20°C	kg CO_2 ha^{-1} leaf h^{-1} (J m^{-2} leaf s^{-1})$^{-1}$
ELV	elevation above sealevel of meteorological station	m
EXDF	exponent for light intensity calculation (PAR), diffuse flux	-
EXDRDR	exponent for light intensity calculation (PAR), direct component of direct flux	-
EXDRT	exponent for light intensity calculation (PAR), total direct flux	-

FARCN	fraction absorbed radiation by the crown	-
FBR	allocation to branches	-
FBRTB	table of allocation to branches as function of DVS	-
FCR	allocation to coarse roots	-
FFL	allocation to foliage	-
FFLTB	table of allocation to foliage as function of DVS	-
FFR	allocation to fine roots	-
FFRTB	table of allocation to fine roots as function of DVS	-
FGRCN	assimilation rate of the crown	kg CO_2 ha^{-1} ground h^{-1}
FGRL	assimilation rate of leaf layer at selected canopy height	kg CO_2 ha^{-1} leaf h^{-1}
FGRSHD	assimilation rate of shaded foliage	kg CO_2 ha^{-1} leaf h^{-1}
FGRSUN	assimilation rate of sunlit foliage	kg CO_2 ha^{-1} leaf h^{-1}
FILEO	file name for output variables	-
FILEP	file name for plant variables	-
FILER	file name for rerun variables	-
FILES	file name for soil variables	-
FILET	file name for time variables	-
FINTIM	period of simulation	d
FOLFL2	help variable to read FOLFLL	-
FOLFLL	observed date of fall of foliage	-
FORGRN	observed date for stage 'forest green'	-
FRGR	switch to use photosynthesis model of FORGRO	-
FRGRN2	help variable to read FOLGRN	-
FRS	allocation to reserves	-
FRSTB	table of allocation to reserves as function of DVS	-
FRT	allocation to roots	-
FRTTB	table of allocation to roots as function of DVS	-
FSH	allocation to shoot (foliage + branches + stem)	-
FST	allocation to stem	-
FTHIN	fraction of either volume or number of trees removed by thinning	-
FTHTR2	help variable to read FTHTRE	-
FTHTRE	fraction of number of trees removed by thinning	-
FTHVL2	help variable to read FTHTRE	-
FTHVOL	fraction of stemvolume removed by thinning	-
GAMMA	CO_2 compensation point	µmol mol^{-1}
GAMM20	value of GAMMA at 20°C	µmol mol^{-1}
GASCON	gas constant	J mol^{-1} K^{-1}
GBR	growth rate of branches	kg DM d^{-1}
GCR	growth rate of coarse roots	kg DM d^{-1}
GFL	growth rate of foliage	kg DM d^{-1}
GFR	growth rate of fine roots	kg DM d^{-1}
GHW	growth rate of heartwood	kg DM d^{-1}
GLT	rate of litter accumulation	kg DM d^{-1}
GMTMP	temperature factor for mesophyl conductance	-
GMTMPT	table of tempeerature factor for mesophyl conductance	-
GPHOT	daily total gross CH_2O assimilation rate	kg CH_2O ha^{-1} ground d^{-1}
GPHOTT	total value of GPHOT over all species	kg CH_2O ha^{-1} ground d^{-1}
GRS	growth rate of reserves	kg DM d^{-1}
GRT	growth rate of roots (fine + coarse roots)	kg DM d^{-1}
GSH	growth rate of shoot (foliage + branches + stem)	kg DM d^{-1}
GST	growth rate of stem	kg DM d^{-1}
GSVPD	stomatal conductance as function of vapour pressure deficit	m s^{-1}
GSVPDT	table of stomatal conductance as function of vapour pressure deficit	m s^{-1}
GSW	growth rate of sapwood	kg DM d^{-1}
GTDM	daily total dry matter production	kg DM ha^{-1} ground d^{-1}
H	height in integration loop	m
HGHMAX	maximal height at this site	m
HGHT	height of the top of the canopy	m
HGHTI	initial value of HGHT	m
HOUR	selected hour during the day at which instantaneous CO_2 assimilation rate is calculated	h
I	counter	-
I1	counter for reruns	-
I2	counter for length of a string	-
IDAY	integer variable for daynumber since 1 Januari	d
IDTMP	switch for temporary output file	-
IECO2	ratio internal to external CO_2 concentration	-
IFLCL	counter for number of foliage classes	-
IG	counter for 3-point Gaussian integration	-
IG1	counter for 5-point Gaussian integration	-
IL	counter for number of foliage layers	-
ILAAGE	length of AMAGET	-

ILADVS	length of AMDVST	-
ILATMP	length of AMTMPT	-
ILDVS	length of AMDVST	-
ILFBR	length of FBRT	-
ILFFL	length of FFLT	-
ILFFR	length of FFRT	-
ILFRS	length of FRST	-
ILFRT	length of FRTT	-
ILGTMP	length of GMTMPT	-
ILGVPD	length of GSVPDT	-
IMNFLC	maximum number of foliage classes	-
IMNL	maximum number of foliage layers	-
IMNOBS	maximum number of observations	-
IMNP	maximum number of parameters	-
IMNS	maximum number of species	-
IMNSWC	maximum number of sapwood classes	-
IMNTH	maximum number of thinnings	-
INGP	number of points of 3-point Gaussian integration	-
INGP1	number of points of 5-point Gaussian integration	-
INITP	control variable for FILEP	-
INOBS	actual number of observations	-
INS	actual number of species	-
INS2	check for number of species	-
INSETS	actual number of rerun sets	-
INTH	actual number of thinnings	-
IPLTYP	plant type (1 = deciduous, 2 = coniferous)	-
IPSPEC	species number	-
IRUN	actual number of reruns	-
IRUNLA	switch for using measured (1) of simulated (2) LAI	-
IS	counter for actual species number	-
ISTAT1	help variable	-
ISTAT2	help variable	-
ISTN	reference number of meteorological station	-
ISWCL	actual number of sapwood classes	-
ITABLE	format for output file	-
ITASK	control variable for which task a subroutine should do (1=inialization, 2=rate calculation, 3=integration,4=terminal calculations)	-
ITOLD	last value of ITASK	-
IUNITO	unit number of output file	-
IUNITP	unit number of plant file	-
IUNITR	unit number of rerun file	-
IUNITS	unit number of soil file	-
IUNITT	unit number of timer file	-
IYEAR	year for which weather data are requested	-
IYR	counter for actual year	-
JF	joint factor (temperature + photoperiod) for determining date of leaf fall	-
KBR	Potassium concentration in branches	kg kg^{-1}
KCR	Potassium concentration in coarse roots	kg kg^{-1}
KDF	extinction coefficient for diffuse light	-
KDRDR	extinction coefficient for direct component of direct light	-
KDRT	extinction coefficient for total direct light	-
KFL	Potassium concentration in foliage	kg kg^{-1}
KFR	Potassium concentration in fine roots	kg kg^{-1}
KHW	Potassium concentration in heartwood	kg kg^{-1}
KSW	Potassium concentration in sapwood	kg kg^{-1}
LAI	leaf area index	ha leaf ha^{-1} ground
LAIC	leaf area index above seleved height in the canopy	ha leaf ha^{-1} ground
LAIMAX	maximum leaf area index	ha leaf ha^{-1} ground
LAIT	total LAI of a species	ha leaf ha^{-1} ground
LAITOT	total LAI over all species	ha leaf ha^{-1} ground
LAT	latitude of the meteorological station	degrees
LD	leaf density at selected height in the canopy	m2 leaf m-3 canopy
LONG	longitude of the meteorological station	degrees
MBR	Magnesium concentrations in foliage	kg kg^{-1}
MCNRAD	maximum crown radius	m
MCR	Magnesium concentrations in coarse roots	kg kg^{-1}
MFL	Magnesium concentrations in foliage	kg kg^{-1}
MFR	Magnesium concentrations in fine roots	kg kg^{-1}
MHW	Magnesium concentrations in heartwood	kg kg^{-1}
MNBB	mean date of budburst	daynumber
MNLF	mean data of leaf fall	daynumber
MRBR	maintenance respiration by branches	kg CH$_2$O ha^{-1} d^{-1}

MRCR	maintenance respiration by coarse roots	kg CH_2O ha^{-1} d^{-1}
MRFL	maintenance respiration by foliage	kg CH_2O ha^{-1} d^{-1}
MRFR	maintenance respiration by fine roots	kg CH_2O ha^{-1} d^{-1}
MRHW	maintenance respiration by heartwood	kg CH_2O ha^{-1} d^{-1}
MRSW	maintenance respiration by sapwood	kg CH_2O ha^{-1} d^{-1}
MRT	total maintenance respiration	kg CH_2O ha^{-1} d^{-1}
MSW	Magnesium concentrations in sapwood	kg kg^{-1}
NBR	Nitrogen content in branches	kg kg^{-1}
NCR	Nitrogen content in coarse roots	kg kg^{-1}
NFL	Nitrogen content in foliage	kg kg^{-1}
NFR	Nitrogen content in fine roots	kg kg^{-1}
NHW	Nitrogen content in heartwood	kg kg^{-1}
NLCF	critical nightlength to start forcing for hardiness model	h d^{-1}
NLCH	critical nightlength for full hardening	h d^{-1}
NSW	Nitrogen content in sapwood	kg kg^{-1}
NTR	number of trees	ha^{-1}
NTRI	initial number of trees	ha^{-1}
NTRT	total number of trees over all species	ha^{-1}
NYRS	number of years for simulation	-
OUTPUT	*logical for call to OUTDAT subroutine*	-
P1	lower limit of effective range of photoperiod to change frost hardiness	h d^{-1}
P2	upper limit of effective range of photoperiod to change frost hardiness	h d^{-1}
PAR	instantaneous flux of photosynthetic active radiation	J m^{-2} ground s^{-1}
PARDIF	*instantaneous flux of diffuse PAR*	*J m^{-2} ground s^{-1}*
PARDIR	instantaneous flux of direct PAR	J m^{-2} ground s^{-1}
PATM	atmospheric pressure	Pa
PBR	Phosphorus content in branches	kg kg^{-1}
PCR	Phosphorus content in foliage	kg kg^{-1}
PFL	Phosphorus content in foliage	kg kg^{-1}
PFR	Phosphorus content in fine roots	kg kg^{-1}
PGN	switch to use photosynthesis model of PGEN	-
PHW	Phosphorus content in heartwood	kg kg^{-1}
PI	ratio of circumference to diameter of a circle	-
PRDEL	time of interval for output	d
PSW	Phosphorus content in sapwood	kg kg^{-1}
Q10	factor accounting for increase of maintenance respiration with a 10°C rise in temperature	-
RAD	factor to convert degrees to radians	-
RADDIF	incoming global diffuse radiation	J m^{-2} ground s^{-1}
RADDIR	incoming global direct radiation	J m^{-2} ground s^{-1}
RAIN	water input through rainfall	mm d^{-1}
RB	leaf boundary layer resistance	s m^{-1}
RC	cuticulair resistance	s m^{-1}
RCHL	rate of chilling	CU d^{-1}
RCNRAD	rate of expansion crown radius	m d^{-1}
REFTMP	reference temperature for maintenance respiration	°C
RELHUM	relative humidity	-
RFRC	rate of forcing FU	d^{-1}
RHGHT	rate of heigth increase	m d^{-1}
RHRD	rate of hardening	°C d^{-1}
RM	mesophyll resistance	s m^{-1}
RMIN	minimum level of frost hardiness	°C
RNTR	rate of change in number of trees	d^{-1}
RPMAX	maximal change of SSHRD with photoperiod	°C
RPMIN	minimal change of SSHRD with photoperiod	°C
RS	stomatal resistance	s m^{-1}
RSMIN	*min. stomatal resistance at light saturation*	*s m^{-1}*
RSTAGE	rate of change of stand age	yr^{-1}
RTMAX	maximal change of SSHRD with temperature	°C
RTMIN	minimal change of SSHRD with temperature	°C
RTMPSM	rate of change of temperature sum	°Cd d^{-1}
RWBR	rate of change of weight of branches	kg DM ha^{-1} d^{-1}
RWCR	rate of change of weight of coarse roots	kg DM ha^{-1} d^{-1}
RWFL	rate of change of weight of foliage	kg DM ha^{-1} d^{-1}
RWFR	rate of change of weight of fine roots	kg DM ha^{-1} d^{-1}
RWHW	rate of change of weight of heartwood	kg DM ha^{-1} d^{-1}
RWLT	rate of change of weight of litter	kg DM ha^{-1} d^{-1}
RWRS	rate of change of weight of reserves	kg DM ha^{-1} d^{-1}
RWSW	rate of change of weight of sapwood	kg DM ha^{-1} d^{-1}
SC	solar constant	J m^{-1} d^{-1}
SCHL	state of chilling	CU
SCHLBB	state of chilling required for budburst	CU

SCHLI	initial state of chilling	CU
SCV	scattering coefficient	-
SFRC	initial state of forcing	CU
SFRCBB	state of forcing required for budburst	FU
SFRCI	initial state of forcing	FU
SFRCLF	state of forcing required for leaf fall	FU
SHRD	state of frost hardiness	°C
SHRDI	initial state of frost hardiness	°C
SINB	sine of solar elevation	-
SINLD	intermediate varaible for calculating daylength	-
SLA	specific leaf area	m2 leaf kg^{-1} leaf DM
SPNAME	species name	-
SSHRD	stationary state of frost hardiness	°C
STAGE	stand age	yr
STAGEI	initial stand age	yr
STTIME	start time of simulation	-
STVOL	stem volume	m3 ha^{-1}
SVP	saturated vapour pressure of the air	mbar
T1	lower limit of effective range of temperature to change frost hardiness	°C
T2	upper limit of effective range of temperature to change frost hardiness	°C
TAU	time constant for hardening	d^{-1}
TBR	biomass of branches removed by thinning	kg DM ha^{-1} d^{-1}
TCR	biomass of coarse roots removed by thinning	kg DM ha^{-1} d^{-1}
TERMNL	logical indicating whether the simulation should stop	-
TFL	biomass of each foliage class removed by thinning	kg DM ha^{-1} d^{-1}
TFLT	total biomass of foliage removed by thinning	kg DM ha^{-1} d^{-1}
TFR	biomass of branches removed by thinning	kg DM ha^{-1} d^{-1}
THAGE	age at which thinning occurs	yr
THAGE2	help variable to read THAGE	yr
THW	biomass of heartwood removed by thinning	kg DM ha^{-1} d^{-1}
TIME	day since start of simulation	d
TLT	change in litter because of thinning	kg DM ha^{-1} d^{-1}
TMAXCH	maximum temperature for chilling	°C
TMINCH	minimum temperature for chilling	°C
TMN	daily minimum air temperature	°C
TMPSCN	temperature scenario	°C
TMPSMI	initial value of temperature sum	°C d
TMPSUM	temperature sum	°C d
TMX	daily maximum air temperature	°C
TOPTCH	optimum temperature for chilling	°C
TRS	biomass of reserves removed by thinning	kg DM ha^{-1} d^{-1}
TRVOL	tree volume	m3 tree^{-1}
TSOIL	soil temperature	°C
TSW	biomass of each sapwood class removed by thinning	kg DM ha^{-1} d^{-1}
TSWT	total biomass sapwood removed by thinning	kg DM ha^{-1} d^{-1}
VAPOUR	vapour pressure of the air	mbar
VPD	vapour pressure deficit of the air	mbar
WBR	weight of branches	kg DM ha^{-1}
WBRI	initial weight of branches	kg DM ha^{-1}
WCR	weight of coarse roots	kg DM ha^{-1}
WCRI	initial weight of coarse roots	kg DM ha^{-1}
WFL	weight of each foliage class	kg DM ha^{-1}
WFLI	initial weight of each foliage class	kg DM ha^{-1}
WFLT	total weight of foliage	kg DM ha^{-1}
WFR	weight of fine roots	kg DM ha^{-1}
WFRI	initial weight of fine roots	kg DM ha^{-1}
WGAUS	weights of point for 3-point Gaussian integration	-
WGAUS1	weights of point for 5-piont Gaussian integration	-
WHW	weight of heartwood	kg DM ha^{-1}
WHWI	initial weight of heart wood	kg DM ha^{-1}
WIND	windspeed	m s^{-1}
WLT	weight of litter	kg DM ha^{-1}
WLTI	initial weight of litter	kg DM ha^{-1}
WRS	weight of reserves	kg DM ha^{-1}
WRSI	initial weight of reserves	kg DM ha^{-1}
WRSMN	minimum weight of reserves	kg DM ha^{-1}
WRSMX	maximum weight of reserves	kg DM ha^{-1}
WRT	weight of roots (fine + coarse roots)	kg DM ha^{-1}
WSH	weight of shoot (foliage + branches + stem)	kg DM ha^{-1}
WST	weight of stem	kg DM ha^{-1}
WSW	weight of each sapwood class	kg DM ha^{-1}
WSWI	initial weight of each sapwood class	kg DM ha^{-1}

WSWT	total weight of sapwood	kg DM ha^{-1}
WTRDIR	directory and path of weather files	-
WTRMES	flag for messages from the weather system	-
WTROK	help variable	-
WTT	total tree weight	kg DM ha^{-1}
XGAUS	points for 3-point Gaussian integration	-
XGAUS1	points for 5-point Gaussian integration	-

Example of TIMER.DAT

```
**********************************************************************
* Defining the simulation run                                        *
**********************************************************************
*
* Weather control variables
*
WTRDIR = 'C:\METEO\NL\'
CNTR   = 'NL'      ! Country code
ISTN   = 12        ! Station code
IYEAR  = 1940      ! Year
*
* Time variables and output file options
*
STTIME = 1.        ! Start day of simulation
FINTIM = 18263.    ! Finish time of simulation
PRDEL  = 365.      ! Time between consecutive outputs to file
ITABLE = 4         ! Format of output file
                   ! (0 = no output table, 4 = normal table,
                   !  5 = Tab-delimited (for Excel), 6=TTPLOT format)
IDTMP  = 0         ! Switch variable what should be done with the
                   ! temporary output files (0 = do not delete,
                   ! 1 = delete)
IRUNLA = 0         ! 1 = LAI measured, 0 = LAI simulated
*
* Method of photosynthesis
*
FRGR   = 1.        ! FORGRO
PGN    = 0.        ! PGEN
*
* Environmental control
*
CO2E   = 350.      ! External CO2 concentration
TMPSCN = 0.        ! temperature scenario
*
* Definition competing species:
*
IPSPEC = 1,3,4     ! 1=Beech, 2=Douglas Fir, 3=Oak, 4=Birch, 5=P.pinaster, 6=P. sylvestris
IPLTYP = 1,1,1     ! 1=deciduous,  2=coniferous
```

Example of SPEC<nr>.DAT

```
****************************************************************************
* Plant data set for Fagus sylvatica                                       *
****************************************************************************

SPNAME = 'Fagus'

* Initial states

WFLI   = 0.            ! foliage classes (age)                  [kg DM ha-1]
WBRI   = 7500.         ! branches                               [kg DM ha-1]
WSWI   = 2705., 2705., 2705.,2705., 2705.! sapwood classes (rings)  [kg DM ha-1]
WHWI   = 156444.       ! heart wood                             [kg DM ha-1]
WCRI   = 7500.         ! coarse roots                           [kg DM ha-1]
WFRI   = 750.          ! fine roots                             [kg DM ha-1]
WLTI   = 50000.        ! litter                                 [kg DM ha-1]
SCHLI  = 72.51         ! chilling                               [CU]
SFRCI  = 0.            ! forcing                                [FU]
SHRDI  = -23.          ! frost hardiness                        [°C]
TMPSMI = 0.            ! temperature sum                        [°C d]
NTRI   = 1000.         ! number of trees                        [ha-1]
STAGEI = 40.           ! stand age                              [yr]
HGHTI  = 20.0          ! height                                 [m]
CNRADI = 1.9           ! crown radius                           [m]

* Parameters

* Phenology

SCHLBB = 117.6191      ! state of chilling required for budburst   [CU]
SFRCBB = 3.5824        ! state of forcing required for budburst    [FU]
SFRCLF = 68.59         ! state of forcing required for leaf fall    [FU]
TMINCH = -19.4188      ! minimum temperature for chilling           [°C]
TOPTCH = -0.2442       ! optimum temperature for chilling           [°C]
TMAXCH = 76.9514       ! maximum temperature for chilling           [°C]
C1FRC  = 1.            ! coefficients for rate of forcing
C2FRC  = -0.1017       !
C3FRC  = -33.0535      !
DAYLLF = 10.40         ! daylength at date of leaf fall             [h d-1]
CFLUSH = 0.5           ! coefficient for leaf flush in spring       [d-1]
CLFFL  = 50.           ! coefficient for leaf fall in autumn        [d-1]
BATMP  = 4.4           ! base temperature for temperature sum       [°C]
MNBB   = 121.          ! mean date of budburst for regression model
MNLF   = 288.          ! mean data of leaf fall for regression model
DBBDT  = -2.           ! shift of budburst with temperature for regression model
DLFDT  =  0.           ! shift of leaf fall with temperature for regression model
*      Observed dates of budburst, 'forest green' and foliage fall, in The Netherlands
*      1940 1941 1942 1943 1944 1945 1946 1947 1948 1949 1950 1951 1952 1953:
BDBST2 = 121, 130, 121, 115, 119, 120, 113, 123, 114, 114, 125, 123, 118, 115
FRGRN2 = 129, 141, 133, 123, 132, 128, 122, 128, 120, 123, 131, 128, 126, 124
FOLFL2 = 282, 284, 281, 289, 293, 289, 282, 286, 290, 298, 294, 299, 283, 287

* Frost hardiness

RPMIN  = 0.            ! minimal change of SSHRD with photoperiod
RPMAX  = -18.5         ! maximal change of SSHRD with photoperiod
RTMIN  = 0.            ! minimal change of SSHRD with  temperature
RTMAX  = -47.          ! maximal change of SSHRD with  temperature
P1     = 8.            ! lower and upper limit of effective range   [h d-1]
P2     = 16.           ! of photoperiod to change frost hardiness
AP     = -2.31         ! constants, to describe to effect of night-
BP     = 18.5          ! length on frost hardiness
T1     = 10.           ! lower and upper limit of effective range
T2     = -16.          ! of temperature to change frost hardiness
AT     = 1.81          ! constants, to describe to effect of tempe-
BT     = -18.1         ! rature on frost hardiness
NLCF   = 14.08         ! critical nightlength to start forcing
NLCH   = 8.            ! critical nightlength for full hardening
TAU    = 12.           ! time constant
RMIN   = -2.3          ! minimum level of frost hardiness           [°C]
```

```
* Photosynthesis and respiration

AMAXM  = 20.           ! maximal value of AMAX                  [kg CO2 ha-1 leaf h-1]
EFF20  = 0.45          ! photosynthetic light use efficiency    [kg CO2 ha-1 leaf h-1
                       !                                         (J m-2 leaf s-1)-1]
GAMM20 = 50.           ! CO2 compensation point                 [µmol mol-1]
IECO2  = 0.70          ! ratio internal to external CO2 concentration [-]
DRSP20 = 1.4           ! dark respiration                       [kg CO2 ha-1 leaf h-1]
RSMIN  = 250.          ! min. stomatal resistance at light saturation [s m-1]
RB     = 30.           ! leaf boundary layer resistance         [s m-1]
RC     = 5000.         ! cuticulair resistance                  [s m-1]
ASRQ   = 1.5           ! assimilate requirements                [kg CH2O kg-1 DM]
Q10    = 2.0           ! temperature effect on respiration      [-]
REFTMP = 25.           ! reference temperature                  [°C]

* Light interception

KDF    = 0.65          ! extinction coefficient for diffuse light   [-]
SLA    = 20.           ! specific leaf area                     [m2 leaf kg-1 leaf DM]
LAIMAX = 6.0           ! maximum leaf area index
SCV    = 0.20          ! scattering coefficient

* Death rates

CLSW   = 1.0           ! coeficient for longevity of last sapwood ring [yr-1]
                       ! coeficients for death rates:           [yr-1]
CDFL2  = 0.0           ! 0.0, 0.1, 0.5, 5.0, 10.0: for foliage classes of coniferous trees
CDBR   = 0.03          !
CDSW   = 0.0           !
CDHW   = 0.0           !
CDCR   = 0.03          !
CDFR   = 1.0           !
CDLT   = 0.01          !

* Reserve level

CRSFL  = 0.05          ! coefficients for reserve level         [-]
CRSBR  = 0.05          !
CRSSW  = 0.03          !
CRSHW  = 0.00          !
CRSCR  = 0.03          !
CRSFR  = 0.05          !
CRSNX  = 4.            ! ratio maX to miN of reserve level

* Stand characteristics

CNBASE = 4.0           ! height of crown base                   [m]
DBH    = 20.           ! mean diameter at breast height         [cm tree-1]
DBHLAI = 3.33          ! ration DBH to maximal LAI
BADEN  = 550.          ! basic density                          [kg m-3]
HGHMAX = 40.0          ! maximal height at this site            [m]
C1HGHT = -0.0337       ! coefficients for Chapman-Richards eq. for
C2HGHT = 1.4214        ! height growth
MCNRAD = 3.3           ! maximum crown radius                   [m]
CSH1   = 0.087905      ! coefficients of Shumacher-Hall equation for
CSH2   = 1.9005        ! volume increment
CSH3   = 0.8073        !
THAGE2 =               ! age at which thinning occurs
       0. ,  0. ,  0. ,  0. ,  0.,
      45. , 50. , 55. , 60. , 65.,
      70. , 75. , 80. , 85. , 90.
FTHVL2 =               ! fraction of stemvolume removed by thinning
      0.18, 0.17, 0.15, 0.13, 0.11,
      0.10, 0.08, 0.07, 0.06, 0.05,
      0.05, 0.04, 0.04, 0.03, 0.03
FTHTR2 =               ! fraction of total number of trees or real number of
                       ! trees removed by thinning
      0.30, 0.27, 0.24, 0.21, 0.18,
      0.16, 0.14, 0.12, 0.10, 0.09,
      0.07, 0.06, 0.05, 0.04, 0.03
```

```
* Mineral content

NFL     = 0.0180          ! Nitrogen content in biomass components      [kg kg-1]
NBR     = 0.0035
NSW     = 0.0030
NHW     = 0.0005
NCR     = 0.0030
NFR     = 0.0100
PFL     = 0.0011          ! Phosphorus content in biomass components   [kg kg-1]
PBR     = 0.0004
PSW     = 0.0003
PHW     = 0.0001
PCR     = 0.0003
PFR     = 0.0010
KFL     = 0.0060          ! Potassium concentrations in biomass components [kg kg-1]
KBR     = 0.0008
KSW     = 0.0008
KHW     = 0.00015
KCR     = 0.0008
KFR     = 0.0040
CFL     = 0.0024          ! Calcium concentrations in biomass components [kg kg-1]
CBR     = 0.0007
CSW     = 0.0005
CHW     = 0.0006
CCR     = 0.0008
CFR     = 0.0020
MFL     = 0.0010          ! Magnesium concentrations in biomass components [kg kg-1]
MBR     = 0.0002
MSW     = 0.0001
MHW     = 0.00005
MCR     = 0.0001
MFR     = 0.0005

* AFGEN functions

AMDVST =                  ! development state vs. AMAX
      0., 0.,
      1., 1.,
      2., 1.,
      3., 0.
AMTMPT =                  ! temperature vs. AMAX
   -30.0, 0.0,
    -5.0, 0.0,
     0.0, 0.1,
    13.0, 1.0,
    25.0, 1.0,
    35.0, 0.1,
    50.0, 0.0
AMAGET =                  ! age vs. AMAX
      0., 1.00,
    100., 1.00,
    366., 0.90,
    730., 0.75,
   1095., 0.65,
   1460., 0.55,
   1825., 0.45,
   3650., 0.33,
   5475., 0.10,
   9999., 0.10
GMTMPT  =                 ! temperature vs. mesophyl conductance
   -50.0, 0.0,
     5.0, 0.0,
    10.0, 1.0,
    25.0, 1.0,
    30.0, 1.0,
    35.0, 0.0,
    50.0, 0.0
GSVPDT  =                 ! vapour pressure deficit vs. stomatal conductance
     0.0, 5.0,
     5.0, 3.5,
    10.0, 2.6,
    15.0, 1.9,
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```
     20.0, 1.3,
     25.0, 0.7,
     30.0, 0.5,
    100.0, 0.01
DVSTB  =                ! forcing vs. development state upto DVS=1 (leaf unfolding
      0., 0.,           ! temperature sum for the rest of the growing season
  3.5824, 1.,
   2000., 2.,
   5000., 3.
FFLTB  =                ! allocation to foliage
    0.00, 1.00,         ! table only used for coniferous trees
    0.95, 1.00,
    1.00, 1.00,
    1.25, 1.00,
    1.50, 1.00,
    1.75, 1.00,
    2.00, 1.00,
    3.00, 1.00
FBRTB  =                ! allocation to branches
    0.00, 0.20,
    0.95, 0.20,
    1.00, 0.20,
    1.25, 0.20,
    1.50, 0.20,
    1.75, 0.20,
    2.00, 0.20,
    3.00, 0.20
FRTTB  =                ! allocation to roots
    0.00, 0.20,
    0.95, 0.20,
    1.00, 0.20,
    1.25, 0.20,
    1.50, 0.20,
    1.75, 0.20,
    2.00, 0.20,
    3.00, 0.20
FFRTB  =                ! allocation to fine roots
    0.00, 0.80,
    0.95, 0.80,
    1.00, 0.80,
    1.25, 0.80,
    1.50, 0.80,
    1.75, 0.80,
    2.00, 0.80,
    3.00, 0.80
FRSTB  =                ! allocation to reserves
    0.00, 1.00,         ! table only used for coniferous trees
    0.95, 1.00,
    1.00, 1.00,
    1.25, 1.00,
    1.50, 1.00,
    1.75, 1.00,
    2.00, 1.00,
    3.00, 1.00
```