Quantification of forage supply to ungulates in forests

Part 1: dynamic simulation of the herb layer

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SUMMARY

Within the Dutch Research Programme on Forest Grazing, a dynamic forest development model is being developed. The model can take into account varying degrees of grazing by ungulates and their interaction with the developing forest. One of the modules (Forage Supply Module) simulates the dynamic development of the herb layer biomass and species composition under the developing forest. The module for the herb layer starts with an initial biomass of the seven relevant herb layer species. It then simulates the growth rate per month using growth rates in relation to light levels and maximum attainable standing crops under the given circumstances of site and forest type.

The present study assesses the functions and relations required to parametrize this Forage Supply Module. These consisted of:
- initial biomass for the relevant species under varying circumstances;
- growth rate per month in relation to light level;
- peak standing crop of the relevant herb layer species for various sites and forest types;
- functions to translate total aboveground dry matter into height, cover and edible biomass.

This report gives the results for these assessments. An overview of existing herb layer simulation models is included as well.

1 INTRODUCTION

1.1   Introduction to the Research Programme on Forest Grazing

Large areas of Dutch forests consist of rather monotonous, monospecious and evenaged forests on poor dry sandy soils. Almost 40% of the standing forest area consists of Scots pine with an average age of approximately 60 years. Vast areas of this forest type are characterised by excessive growth of wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.) in the herb layer. The weighted average cover of this species in the Potential Natural Vegetation forest type Betulo-Quercetum, amounts to 25 to 50% (Dirkse 1993). Since the publication of the Dutch Forestry Policy Plan in 1986 (revised in 1993), policy is aiming at a steady transformation of this heritage from the past. In the near future 20% of the forest will have nature conservation as its main objective. To increase the nature value of the forest, management regimes have to be changed to develop small scale, mixed forests, rich in species and stucture, situated in a differentiated forest-open-land landscape.

To investigate whether large herbivores (roe deer, red deer, ponies and Highland cattle) and the omnivore wild boar can be used to develop and maintain open forest landscapes on poor sandy soils in The Netherlands in a highly self-regulating way, the Research Programme on Forest Grazing was started in 1990. Its results will indicate whether forest grazing is a useful management tool in developing and maintaining natural forests.

The programme includes study of the most important processes of the herbivore - forest ecosystem interactions. The subprojects regarding these processes are:
- food selection and diet composition;
- quantification of food resources;
- habitat use of red deer, roe deer and wild boar;
- performance of herbivores under Dutch forest conditions;
- effects of grazing and trampling on the litter layer;
- interspecific relations of red deer, roe deer and wild boar;
- forest development in relation to forest grazing.
An overall forest development simulation model will be used to study the long-term forest development under various grazing pressures.

As part of the subproject "quantification of food resources", the present study was carried out to parametrize a dynamic module that simulates the dynamic development of the seven most important herb layer species under forest development. The basic principle of this module is that herb layer species growth and biomass are simulated based on relative growth rates in relation to relative light levels under the forest canopy. This report comprises those parametrizations of the forage supply module in the forest development model. Sub-report no 2 in this series, gives the parametrization of the forage supply of the shrubs and young trees (Van Hees in prep) and sub-report no 3 describes the forest development model documentation and the scenario results (Jorritsma in prep). Because the overall model is not

completed yet, small modifications in the parameters and functions as presented here, may occur in report no 3. Those modifications will be accounted for in report no 3.

In the following paragraphs of this chapter, the aim of this study is defined, the module principles are outlined and a characterisation of the relevant herb layer species is given. In chapter two, the methods are described, followed by the results in chapter three and a discussion in chapter four.

1.2   Objectives of the herb layer forage supply study

Main aim of the present study as presented in this report was to parametrize the functions and relationships necessary for the dynamic module which simulates the forage supply of the grasses and herbs of the herb layer under forest and in open land. To do so, the following main objectives for this sub-project were determined:
1) assess the initial herb layer species composition, ground coverage and biomass for two relevant sites, varying tree species and forest densities;
2) quantify the relative growth rate per month of the relevant species in relation to the relative light level;
3) quantify the peak standing crop of the relevant species in relation to site, forest tree species and light level.
4) assess translation functions to calculate total aboveground biomass from height and cover data and asses functions to calculate the edible part from the total aboveground biomass.

1.3   Principles of the herb layer forage supply module

This paragraph gives an overview of the herb layer forage supply module that is part of the forest development model. For more details concerning this module and the overall forest development model, see Jorritsma (in prep). Forage supply to ungulates consists of a wide variety of menu components. These can be grouped as: non-woody herb layer species, woody herb layer species, shrubs and trees in the shrub layer, overhanging branches, mast and roots. The herb layer forage supply module as presented in the present study, considers only the forage supply of the non-woody and dwarf shrub herb layer species. The forest development model includes through other modules, tree saplings in the herb layer and shrubs and trees in the shrub layer (Van Hees in prep).

The forest development model is parametrized for two site types of the higher sandy soils of The Netherlands: the poor, dry, sandy soils with the Betulo-Quercetum roboris as Potentially Natural Vegetation (PNV) and the moderately rich, dry, loamy soils with the Fago-Quercetum petraeae as PNV representing the two most common forest associations of The Netherlands (Dirkse 1993).

The Betulo-Quercetum roboris site can either be a strongly podsolized soil (Haarpodzolgrond = Humic podsol) or an inland sand-dune soil i.e. deposited drift sand with the original podsol profile still existing underneath (Duinvaaggrond = Albic Arenosol). A forest development scenario (with a certain number of ungulates) is parametrized starting from four initial forest types: Scots pine, pedunculate oak, a forest consisting of a mixture of Scots pine, pedunculate oak and birch or an open land situation with heather as dominant species.

The Fago-Quercetum petraeae site is usually a brown forest soil (Holt-podzolgrond = Leptic podsol). A forest development scenario (with a certain number of ungulates) is parametrized starting from five initial forest types: a forest dominated by Scots pine, pedunculate oak or beech or a mixture of species consisting of Scots pine, pedunculate oak, birch and beech or an open land situation with heather as dominant species.

The model calculations are carried out for a patch covering 400 m^2 and calculations are carried out in time steps of one month. Seven herb layer species are considered in terms of height, cover, total aboveground biomass, relative growth rate and edible biomass. Plant organs are not distinguished. Herb layer species composition and cover are only imposed in the initial situation. Initial species composition, initial total aboveground biomass and peak standing crop for the relevant circumstances are laid upon the module from input tables. Vegetation cover including the woody species in the herb layer is assumed not to exceed 100%.

The degree to which the overstorey canopy reduces the light intensity on the forest floor is commonly regarded as the most important site factor for the herb layer species in forests (Chazdon 1988, Simmons & Buckley 1992, Mitchell & Bartling 1991, Qarro & De Montard 1992, Bojorquez Tapia et al. 1990). Second most important (Röhrig 1991) are the soil conditions, both physical and chemical. Basic principle of the forage supply module therefore is that herb layer species growth (in terms of net dry matter increase per unit of total aboveground dry matter) can be dynamically simulated in relation to the relative light level that reaches the forest floor. In the present study, it is assumed that stand basal area is an indirect measure of this relative light level (Bredemeier & Dohrenbusch 1984). The net growth rate is further adjusted for the peak standing crop i.e. the maximum achievable total aboveground dry matter that the herb layer species can reach on the specific site and forest type.

The curve representing the development of the total aboveground biomass of the herb layer species, is assumed to be logistic (see also Figure 3.5). Growth is regarded in terms of net aboveground growth, i.e. being the result of Net Primary Production minus litterfall. Growth is simulated in terms of Relative Growth Rate (RGR) i.e. growth in terms of grams net increase/decrease per kilogram aboveground biomass per month. Growth can as such be negative. Net increase in total aboveground biomass is divided over increase in height and increase in cover. When approaching its maximum height, relatively more growth is allocated towards increase in

cover. It is assumed that the total edible biomass of the herb layer vegetation is available to the ungulates, as if it were in a manger.

The seven most important herb layer species of the Veluwe forests are regarded. These species are: common bent-grass (*Agrostis capillaris* L.), heather(*Calluna vulgaris* (L.) Hull.), wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.), purple moor-grass (*Molinia caerulea* (L.) Moench), bracken (*Pteridium aquilinum* (L.) Kuhn.), blueberry (*Vaccinium myrtillus* L.) and cowberry (*Vaccinium vitis-idaea* L.). Of these species, bracken and cowberry are not considered as direct forage suppliers, but merely as species which indirectly influence the forage supply by competing for space with forage supplying species. Furthermore, common bent-grass is assumed to be the representative for Carex, Holcus and Festuca spp.

The module simulates growth from functions which describe the relative growth rate for each of the seven species per month under optimal field circumstances in combination with light response curves. These light response curves give the relative decrease of growth under decreasing light level. The light level reaching the forest floor is determined by the forest canopy in the forest development model. For the present study, it is assumed that basal area of the forest can be used as an indirect measure of the light level reaching the forest floor. Growth can furthermore be limited when the total aboveground biomass reaches its peak standing crop under the given circumstances.

When grazing does not occur, resulting total aboveground biomass is taken to the next time step. When grazing occurs, a reduction factor as a function of age, season and height of the herb layer species can be introduced to determine the edible part of the herb layer (kg d.m. mth^{-1}). Then a certain degree of grazing is imposed from the diet choice module on the forage supply module. The grazing rate per ground vegetation species per month, determines the amount which is left for the regrowth and thus forage supply in the next time step.

Milchunas & Lauenroth (1993) state that Net Primary Production is certainly affected by grazing, but it remains uncertain to what degree. They state in their review of effects of grazing that Net Primary Production may be slightly enhanced after light grazing on fertile sites. Under all other circumstances they report a significant decrease of Net Primary Production due to grazing. In the module it is assumed that the Relative Growth Rate is not affected by grazing. This results in a linear decrease of the net growth under a certain degree of grazing (e.g. when the total aboveground biomass is reduced by 10% due to grazing, the net growth is also reduced by 10%). Monthly and annual output consists of species composition, cover percentage and herb layer species total aboveground dry matter and forage supply per patch.
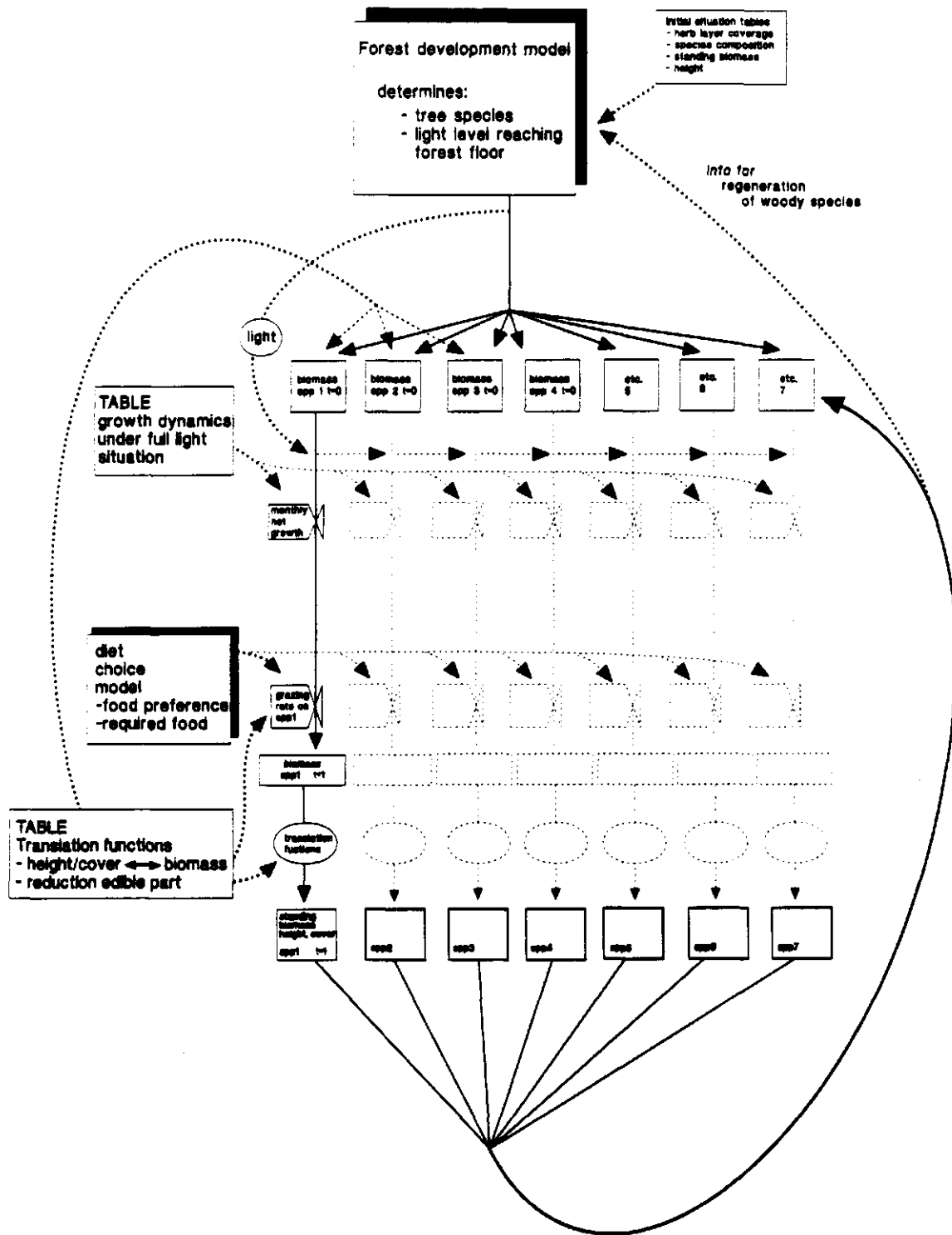
Figure 1.1   Outline of the Forage Supply Module that simulates the forage supply of one patch with a size of 400 m², through the dynamic development of the herb layer under developing forest.

1.4   Ecological accounts of the relevant species

Agrostis capillaris L.

A wintergreen, polycarpic perennial. Leaf expansion occurs in late spring followed by flowering from June to August. Foliage usually less than 15 cm in height; flowering shoots to 50 cm (Grime et al. 1988). It has an exceptionally wide ecological range, but relevant here is that abundant occurence is characteristic on soils which contain a certain amount of raw humus due to slow litter decomposition (Weeda et al. 1994). It is abundant on road sides and open spots, where it is encouraged by light. Common bent-grass can occur massively on clear cut areas on nutrient poor sandy and loamy soils. It languishes in deep shade. According to Ellenberg (1991) it is a plant of half light (7) which grows usually in full light, but that can grow in shade to approximately 30% of relative light intensity. The species' leaf canopy is rapidly renewed after grazing in spring or summer (Grime et al. 1988).

Calluna vulgaris (L.) Hull

An evergreen dwarf shrub, flowering from August to September. The leaves on short lateral shoots may survive up to 3 years. It is a relatively short lived shrub that can attain ages up to 30 years and a height of up to 80 cm. Heather occurs on acidic pastures, heathland and moorland and is characteristic for the Pleistocene area of The Netherlands. It is characteristic for nitrogen- and phosphorus-poor soils (Grime et al. 1988). It germinates the best on somewhat moist open sites and dominates only on dry to moist sunny spots or spots with only very light shading. It can form monospecious dense stands, under which no other plants grow. The Ellenberg (1991) light figure is 8. It is a light plant, only rarely occuring on spots with less than 40% relative light intensity. It languishes under a woody overstorey. The plant can endure heavy grazing by sheep very well, but vanishes already at moderate grazing by cattle and horses (Weeda et al. 1988). It can recover from all kinds of damages as long as the plant is not too old and the stem basis is not damaged. It can resprout from the stem basis after fire and grazing.

Deschampsia flexuosa (L.) Trin

Wavy hair-grass is a tufted or rhizomatous and mat-forming winter green perennial. It flowers in June and July. The foliage reaches heights of up to 20 cm and the flowering shoots heights up to 60 cm. It is capable of forming large clonal patches as a result of rhizome growth. In The Netherlands it is very common in the pleistocene areas as an indicator of very acid, nutrient poor and dry, well drained soils where raw humus accumulates. Wavy hair-grass occurs the most massively on clear cut areas, storm- and fire-damaged spots. It occurs both under coniferous and deciduous forests in which trees with an open crown dominate. The species is rather vulnerable to submergence under deciduous litter. The succession stages characteristic for the heathland and inland-dune afforestations of moss phase, wavy hair-grass phase and bilberry phase follow one another much faster under deciduous forest on loamy soils than under pine forest. The light figure is 6 (Ellenberg 1991); in between a half light and half shadow plant. It rarely occurs on spots with less than 20% relative light intensity.

Wavy hair-grass grows best in full sun, but can tolerate quite some shade according to Weeda et al. (1994). It languishes in deep shade. According to Grime et al. (1988), the species is particularly shade-tolerant. Wavy hair-grass is eaten by sheep and rabbits (Grime et al. 1988), but in heathland habitats, new shoots of heather are preferred and grazing here can lead to an increase in D. flexuosa.

Molinia caerulea (L.) Moench

Purple moor-grass is a tufted or turf forming deciduous grass reaching heights up to 70 cm. It has a bimodal pH distribution. At both high and low pH, M. caerulea tends to be associated either with moist grassland or with soligenous mire. New growth, fuelled by belowground carbohydrate reserves, begins in April or May. M. caerulea often occupies the transition zone between wetland and dryland. In The Netherlands, it usually occurs on moderate to very acid, nutrient poor soils. It endures fluctuations in the groundwater table very well. In forests it usually occurs in rather open forest stands of the Betulo-Quercetum. Dominance can usually be traced back to a strong influence by man who has diminished shade in the forest, applied a clear-cut or lowered the water table. The species persists in moderate shade (Grime et al. 1989), but tends to produce few flowers under these conditions. The light figure is according to Ellenberg (1991) 7: a half light plant usually in full light, but also in shade to 30% of full light level.

Pteridium aquilinum (L.) Kuhn

A polycarpic perennial fern, with fronds arising directly from deep underground rhizome from late spring onwards, persisting until autumn. It can reach heights of up to 180 cm. Typically found in woodland on acidic soils in most undisturbed vegetation types. It shows maximum vigour on productive brown forest soils. The species germinates on open spots on soils poor in humus, but rich in minerals. Full maturity of bracken is however reached on completely other sites: on calcium and nutrient-poor sites with large amounts of raw humus. In full light, the plant fully dominates, but under oak-beech forest it does not expand any further. The litter is thought to be toxic for many plant species and prevents germination of them (Grime et al. 1988). In The Netherlands, bracken is regarded an indicator of an old forest site. The Ellenberg (1991) light figure is 6; in between a half light and half shade plant. It rarely occurs on spots with less than 20% relative light intensity, and it is found in a wide range of shaded and unshaded habitats.

Vaccinium myrtillus L.

A deciduous dwarf shrub. Bilberry's green shoot growth commences in spring. It reaches a height of up to 60 cm. Bilberry forms extensive patches as a result of rhizome growth. It occurs on acidic, dry to moist soils as a local dominant in the field layer of open woodlands. The height of the ungrazed bilberry shrubs indicates which Potential Natural Vegetation will develop on the site. On sandy soils, poor in loam, bilberry will only reach a height of 20 to 30 cm indicating the Betulo-Quercetum forest vegetation type. When the shrubs reach a height of 50 cm or more, this indicates a loamy soil on which a Fago-Quercetum may develop (Pers. comm. Koop, IBN-DLO). On former heathland sites with a well developed podzol profile, it

can dominate almost the total vegetation. It usually occurs in moderate shade. The Ellenberg (1991) figure is 5; a plant of half shadow. Onely rarely occuring in full light, bust mostly on spots with more than 10% relative light intensity.

Vaccinium vitis-idaea L.
A dwarf evergreen shrub with numerous rhizomes. It occurs on acidic, calcium- and nutrient-poor both sandy or dry peat soils. On the sandy soils it occurs in the Betulo-Quercetum and in pine forests on former heathland. Sometimes it occurs on afforested inland sand dune sites together with Empetrum nigrum (Weeda et al. 1988). Where cowberry dominates, no other species germinate. In The Netherlands, it sometimes occurs also outside the forest, but only in regions with more than average precipitation. V. vitis-idaea is regarded as more drought tolerant than V. myrtillus. The plants are little grazed. The Ellenberg (1991) figure is 5; a plant of half shadow, rarely occuring in full light, bust mostly on spots with more than 10% relative light intensity.

2 METHODS

2.1 Concerning initial species composition and biomass

To parametrize the initial situation, species composition, cover and biomass were required for the herb layer species in the relevant forest types. Species composition of the herb layer on varying sites and under varying forest types were assessed based on vegetation recordings that were carried out in the National Forest Inventory (Dirkse & De Molenaar 1994). Vegetation was recorded in 9 cover classes in plots of 300 m² in 1984/1985. Because the Potentially .Natural Vegetation (PNV) of the site and the forest type according to the National Forest Inventory (i.e "Dorschkamp" forest type) (CBS 1985) were also available in the data base, it was possible to make selections according to these parameters. The stand basal area per tree species of those same 234 plots of the Veluwe, was recorded within the Wood Harvesting Statistic and Prognosis Harvestable Wood (HOSP). By coupling these two data bases it was possible to assess the herb layer species composition and cover for relevant forest types, and to correlate the herb layer cover to stand basal area.

A multivariate analysis of the herb layer species abundancies in relation to the site factors was carried out using CANOCO 3.11 (Ter Braak 1988). In this analysis, the explanatory value of the site factors total basal area, basal area per tree species, PNV and forest type were tested using Canonical Correspondence Analysis (CCA). Forward selection of the site factors was used to assess relative importance of these site factors. This multivariate analysis was carried out using untransformed abundancy codes of all vascular herb layer species in the data base.

To calculate total cover percentages for the herb layer, average absolute covers for each class were used as given in the right-hand column of Table 2.1. The average absolute cover was usually chosen at the lower end of the distribution of cover within the class, in order not to exceed the 100% total cover.

The statistical programme GENSTAT (Payne et al. 1987) was used to correlate herb layer cover to stand basal area of selected forest types. These relations are used in the module to assess initial situations and as a framework to evaluate scenario results. A tree species was seen as dominant when its basal area comprised more than 60% of the total basal area. Selections were also carried out on combinations of functional tree species groups e.g. Douglas-fir and Norway spruce. A once-only biomass sampling experiment was carried out to translate the above mentioned cover percentages into total aboveground biomass. See for details on this biomass sampling experiment, paragraph 2.3.

Table 2.1   Cover classes used in the vegetation recordings of the available data-base.

cover class	distribution of actual cover	average of the class used for the correlations
1	<0.1	0
2	0.1-1	1
3	1-5	3
4	5-10	8
5	10-25	15
6	25-50	30
7	50-75	50
8	75-90	75
9	90-100	95

2.2   Concerning growth rate assessment

Scientific literature was sufficiently available to assess the annual net aboveground growth figures. Most available data were assessed for 100% cover and full light circumstances. Reduction of relative growth rate in relation to decreasing light intensity was assessed from indications available in various ecological studies concerning growth and light intensity and on peak standing crop figures in relation to basal area obtained from the biomass sampling experiment (see paragraph 2.3).

2.3   Concerning peak standing crop assessment

A biomass sampling experiment of the herb layer species was carried out once-only in the course of June and July 1994 with the aim to assess both the aboveground peak standing crop and the stand level total aboveground biomass in relation to forest density (basal area), tree species and site type. The assessment of peak standing crop was necessary to determine the asymptotic values of total aboveground biomass for various sites and tree species. The assessment of stand level total aboveground biomass was required as a framework to test scenario results and to translate the herb layer cover percentages that were available for the Veluwe area (see § 2.1), into biomass figures. The time of clipping was chosen in such a way that the summer maximum of standing crop would be covered. For each group of stands selected according to site and tree species, three to four stands were selected that covered the range in basal area's and herb layer diversity. 58 stands were selected and sampled.

In each stand, the original plot that was recorded in 1984/1985 was located. The sub-plots, where the vegetation would be clipped, were located stratified according to the height of the vegetation. One sample was taken at a spot where the vegetation seemed to have reached (based on height and cover) its peak standing crop under those site factors, and three samples were taken on spots where (based on height and cover) the vegetation could be characterised as the average for the patch. The patch average aboveground biomass was used in combination with the cover percentage of the species in that stand to achieve an area (stand) averaged total aboveground biomass.

Clipping was carried out using steel circles with varying surfaces. In case of A. capillaris, C. vulgaris, D. flexuosa, M. caerulea, V. myrtillus and V. vitis-idaea, a surface of 0.1 m^2 was sampled. In case of P. aquilinum an area of 0.5 m^2 was sampled. Before sampling, the top height of the vegetation was recorded three times and an average top height calculated and the cover percentage within the steel circle was recorded too. Herb layer biomass was clipped at the ground level i.e. at the top of the litter layer.

Samples were taken to the lab and in case of V. myrtillus divided in an edible and unedible part (see § 2.4). Samples were then dried at a temperature of 70 °C for 24 hours and weighed.

2.4   Concerning the assessment of translation functions

The relation between height and biomass was assessed from literature data obtained in the open field for A. capillaris, D. flexuosa and P. aquilinum. For these species and the other four, the biomass sampling experiment provided additional data too. The determination of the edible part was assessed from literature data for the species A. capillaris, C. vulgaris and D. flexuosa. Those literature data were assessed in biomass sampling experiments in which green and non-green material was distinguished. For Calluna, current year shoots and leaves had been distinguished in available data. This factor was not required for the two species that are not grazed, P. aquilinum and V. vitis-idaea. The edible part of V. myrtillus was determined in the biomass sampling experiment carried out in the present study, dividing the sample into current year shoots and leaves and rest of the plant in accordance with Van der Grift & Huijser (1991) who mention an edible length of the shoots of 4 cm. An extra reduction factor will be laid upon the module to account for the edible part for roe deer.

3 RESULTS

3.1 Explanatory value of various site factors

Table 3.1 gives the result of the Canonical Correspondence Analysis of the explanatory value of the site factors for herb layer species abundancies. The total variance explained by the available site factors amounted to 13.5%. The percentages explained by each of the axes are 3.6, 2.5, 1.6 and 1.1% respectively (see Appendix C).

Table 3.1 Explanatory value of the site factors by forward selection in CCA. Cumulative fit = percentage explained variance of a model that includes the present and other above standing site factors. Significance has been tested using 99 permutations (Ter Braak 1988). ** = p ≤ 0.01; *: siginifant 0.01 < p ≤ 0.05; n.s.: not siginificant; p > 0.05.

Site factor	Cumulative fit (%)
Basal area of other deciduous trees (sic)#	24**
Forest type (Dorschkamp type)	39**
Basal area of Pseudotsuga mensiezii	48*
Basal area of Picea spp.	57*
Basal area of Quercus robur	65*
Potential Natural Vegetation	72**
Thickness of the litter layer	78**
Basal area of Fagus sylvatica	84*
Basal area of Scots pine	88 n.s.
Basal area of dead trees	92 n.s.
Basal area of Larix kaempferi	95 n.s.
Basal area of Quercus rubra	98 n.s.
Basal area of Pinus nigra spp.	100*

#: as in HOSP data base, usually birch.

The cumulative percentage variance of species-environment relation that were found are 26.6, 44.8, 56.8 and 64.8. The total variance explained can be characterised as reasonable. Other factors (and coincidence) that were not regarded in this analysis will probably explain the rest of the variance.

These results indicate that the available site factors were a reasonably good set to explain and correlate the vegetation abundancies. It indicated that it was realistic to split the data bases according to PNV, forest type and tree species and to establish correlations between herb layer cover and stand basal area.

3.2 Initial conditions

3.2.1 Herb layer species composition in relation to the forest

The following tables present both the weighed frequencies of occurence of the relevant herb layer species under varying tree species as the average cover for each species under varying stand densities. The weighed frequency tables (3.2. and 3.3.) include those herb layer species that occured under at least one of the tree species with a presence of 40% or more. The percentages that are presented in Tables 3.2 and 3.3 are a chance of a certain herb layer species occuring in the specific forest type. The figures are no indication of the cover of the herb layer species in the specific forest type. The figures can be used as a chance of germination of the herb layer species in the specific forest type. Table 3.4 that presents average cover data, was assessed based on the vegetation recordings that were carried on the Veluwe (Dirkse 1993). The results show the significance of the various herb layer species in terms of cover. For each combination of site, tree species and basal area (usually 3 to 5 recordings), a standard vegetation species composition was assessed (Table 3.5). The results presented in Table 3.5, are used as initial situation conditions.

Table 3.2 Weighed frequencies* (%) of the most important herb layer species (including tree seedlings) under tree species in the Betulo-Quercetum of The Netherlands (modified after Dirkse & De Molenaar 1994).

Tree species	Douglas-fir	Norway spruce	Scots pine	oak	birch
Agrostis capillaris	*	*	*	*	*
Betula pendula	33	52	44	33	15
Calluna vulgaris	22	64	54	39	65
Carex pilulifera	58	2	19	32	31
Deschampsia flexuosa	89	79	84	82	63
Dryopteris carthusiana	41	40	19	19	14
Frangula alnus	11	45	41	49	14
Molinia caerulea	37	57	43	25	67
Prunus serotina	12	24	49	57	9
Pteridium aquilinum	*	*	*	*	*
Quercus robur	31	33	69	77	50
Rubus fruticosus	41	64	28	51	32
Rumex acetosella	59	55	23	26	21
Sorbus aucuparia	69	39	53	70	13
Vaccinium myrtillus	9	15	40	50	31
Vaccinium vitis-idaea	*	*	*	*	*

*: a weighed frequency takes into account a weighing factor for the area that is represented by the recorded plot; it represents the number of times that a certain species may occur in this type of stand. It says nothing about the cover.

*: the weighed frequency of occurence of this herb layer species is less than 10% under any of the tree species, but the species is still mentioned here, because it is one of the main forage supplying plant species.

Table 3.3 Weighed frequencies* (%) of the most important herb layer species under tree species in the Fago-Quercetum of The Netherlands (modified after Dirkse & De Molenaar 1994).

Tree species	Dou-glas-fir	Norway spruce	Scots pine	larch	beech	oak	birch
Agrostis capillaris	9	17	2	18	6	13	19
Betula pubescens	7	18	7	47	0	8	24
Calluna vulgaris	15	24	6	21	0	2	2
Chamerion angustifolium	16	45	8	28	3	6	22
Ceratocapnos claviculata	31	42	32	26	33	20	17
Deschampsia flexuosa	55	33	55	63	21	34	53
Dryopteris dilatata	41	63	49	25	17	37	22
Dryopteris carthusiana	29	44	37	50	9	18	31
Lonicera periclymenum	7	18	25	15	1	43	31
Molinia caerulea	20	42	42	50	6	23	45
Prunus serotina	31	57	50	49	17	42	47
Pteridium aquilinum	*	*	*	*	*	@	*
Quercus robur	22	53	40	46	19	42	34
Rubus fruticosus	36	46	57	35	21	69	76
Rumex acetosella	27	42	15	34	1	9	8
Sorbus aucuparia	50	51	68	79	33	2	79
Vaccinium myrtillus	20	27	29	29	6	14	22
Vaccinium vitis-idaea	*	*	*	*	*	*	*

#: a weighed frequency takes into account a weighing factor for the area that is represented by the recorded plot; it represents the number of times that a certain species may occur in this type of stand. It says nothing about the cover.
*: the weighed frequency of occurence of this herb layer species is less than 10% under any of the tree species, but the species is still mentioned here, because it is one of the main forage supplying plant species.
@: the authors noted that bracken occurs almost exclusively in this forest type, although it did not reach the 10% weighed frequency

However, the importance of these herb layer species for the forage supply is expressed in a better way by their cover. Both table 3.4. and 3.5. give this abundance of the species in cover. Both tables were assessed based on the data base of the National Forest Inventory (Dirkse IBN-DLO, pers. comm.). Table 3.5.

Table 3.4 Number of plots out of a total of 224 plots of the Veluwe in which the cover of the specified herb layer species exceeds 25% (Dirkse IBN-DLO, pers. comm.). The species that are included in the module, are underlined. A. capillaris is seen as representative for Carex, Holcus and Festuca spp.

	No of plots		
Agrostis capillaris	0	Lonicera periclyme-num	0
Betula pendula	0	Molinia caerulea	7
Betula pubescens	0	Prunus serotina	0
Calluna vulgaris	9	Pteridium aquilinum	4
Chamerion angustifolium	0	Quercus robur	0
Corydalis claviculata	0	Rubus fruticosus	2
Deschampsia flexuosa	69	Rumex acetosella	0
Dryopteris dilatata	1	Sorbus aucuparia	0
Dryopteris carthusiana	0	Vaccinium myrtillus	15
Frangula alnus	0	Vaccinium vitis-idaea	2

Overall, the weighed frequencies in Tables 3.2 and 3.3. are higher in the Betulo-Quercetum than in the Fago-Quercetum, with D. flexuosa reaching the highest frequencies. Furthermore, the Betulo-Quercetum is characterised by occurence of C. vulgaris and M. caerulea. V. myrtillus is more rare under Douglas-fir than under all other stand types whereas it is more common under oak. C. vulgaris and M. caerulea seem to be favoured under birch stands of the Betulo-Quercetum.

In the Fago-Quercetum, D. flexuosa seems to be favoured under Douglas-fir and beech and it is the most commonly recorded species under 6 out of seven stand types. A. capillaris is generally more common in the Fago-Quercetum than in the Betulo-Quercetum. V. myrtillus is favoured under Scots pine, larch and Norway spruce.

Table 3.5 Dominant herb layer species composition in cover classes* for each combination of site, tree species and basal area as obtained from the combined data bases National Forest Inventory (pers. comm. Dirkse IBN-DLO) and the Wood Harvesting Statistic and Prognosis Harvestable Wood.

Betulo-Quercetum

Tree species	Scots pine				Douglas-fir			oak		birch
Basal area	5	10	20	25	5	15	25	10	20	-
common bent-grass		1	2	1						
heather	2	2	1	1	2	1		3	2	6
wavy hair-grass	8	9	7	6	6	3	3	8	7	5
purple moor-grass								3	3	6
bracken										
blueberry			3	3		2		3	5	5
cowberry				1						
bare forest floor	6	3	7	8	8	9	9	5	6	4

*: See for explanation of the classes Table 2.1.

Table 3.4 shows that the set of herb layer species as chosen in the module, represents the most important herb layer species very well. It also shows the absolute importance of wavy hair-grass as a forage supplier. Only Rubus fruticosus that is not included in the module, can achieve high coverage in some stands. A. capillaris seems to be overrated by including it in the module, but this species is treated in the module as a representative for Carex, Holcus and Festuca spp. and is as such of more importance than might appear from Table 3.4.

The standard herb layer species cover as presented in table 3.5, shows the importance of D. flexuosa in the Betulo-Quercetum forests. This species is also the most important in the Fago-Quercetum, but less pronounced. In the Fago-Quercetum forests, C. vulgaris is less important, but V. myrtillus and V. vitis-idaea are of greater importance. P. aquilinum occurs only under some tree species of the F-Quercetum. M. caerulea is of significant importance under birch stands of both the forest associations. Total coverage is usually less in the Fago-Quercetum than in the Betulo-Quercetum. Tables 3.5 and 3.6 are used in the module as initialisation tables.

Table 3.5 continued

Fago-Quercetum

Tree species	Scots pine					Douglas-fir		
Basal area	5	15	20	25	35	15	30	40
common bent-grass		1	1					
heather	5	4	2					
wavy hair-grass	4	5	5	4	3	4	5	3
purple moor-grass	1	4	4					
bracken		2	2					
blueberry	5	5	6	5	5	1	2	1
cowberry	3	3	3	5	5			
bare forest floor	7	7	7	8	7	9	8	9

Tree species	oak			beech			mixture of deciduous tree spp.			birch
Basal area	15	20	25	5	15	20	15	25	35	-
common bent-grass	1	1								5
heather							4			1
wavy hair-grass	8	6	6	5	4	1	5	5	3	6
purple moor-grass										6
bracken		6	5						2	
blueberry	5	6	5	2	2	1	5	5	3	5
cowberry		2		2				5		
bare forest floor	4	4	6	8	9	9	7	7	9	4

Table 3.6 Dominant herb layer species composition in cover classes* for two types of heathland.

Open terrain: dry heathland			
	no grass	moderate grass growth	severe grass growth
heather	7	6	4
wavy hair-grass	3	6	7
bare soil	7	6	6
Open terrain: wet heathland			
	no grass	moderate grass growth	severe grass growth
heather	7	6	4
purple moor-grass	3	6	7
bare soil	7	6	6

*: See for explanation of the classes Table 2.1.

3.2.2 Relation between stand basal area and herb layer cover

The following figures present the best relations that were found between understorey cover and stand basal area. The presented functions are used in the module to initialise the herb layer cover and as a framework to test module output. Restrictions were made according to site, forest type, dominant tree species and herb layer species.
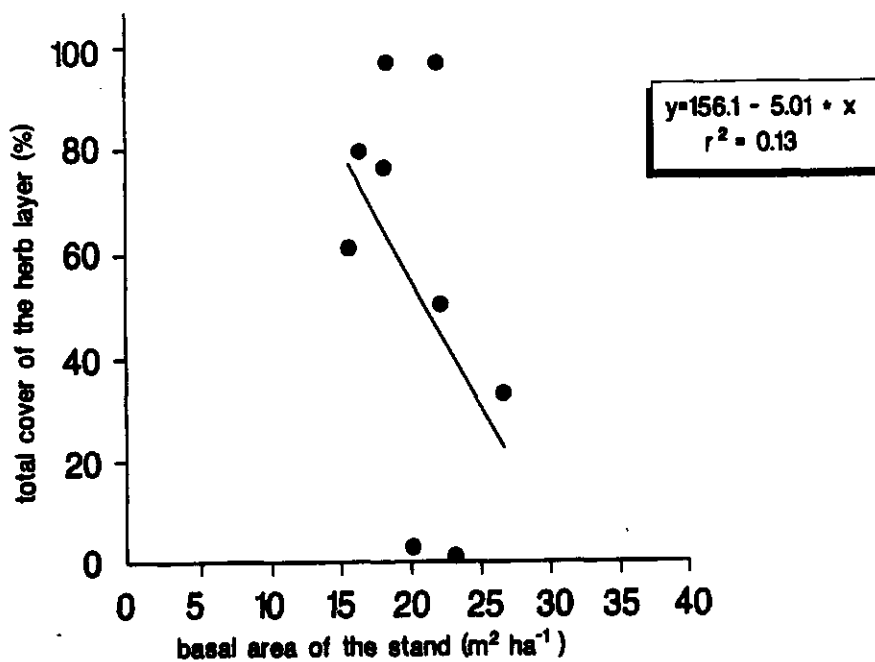
Figure 3.1   Linear regression model between forest stand basal area and total herb layer cover for Scots pine stands on inland sand dune soils on the Veluwe, The Netherlands (light coniferous forest). Y is the herb layer cover (%) and X is the basal area of the stand (m² ha⁻¹).
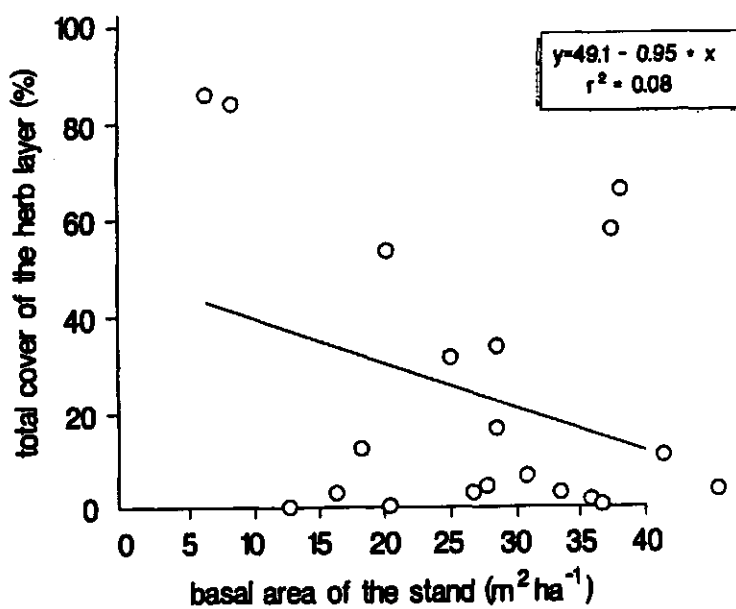

Figure 3.2   Linear regression model between forest stand basal area and total herb layer cover for Douglas-fir and Norway spruce stands on the Veluwe, The Netherlands (dark coniferous forest).
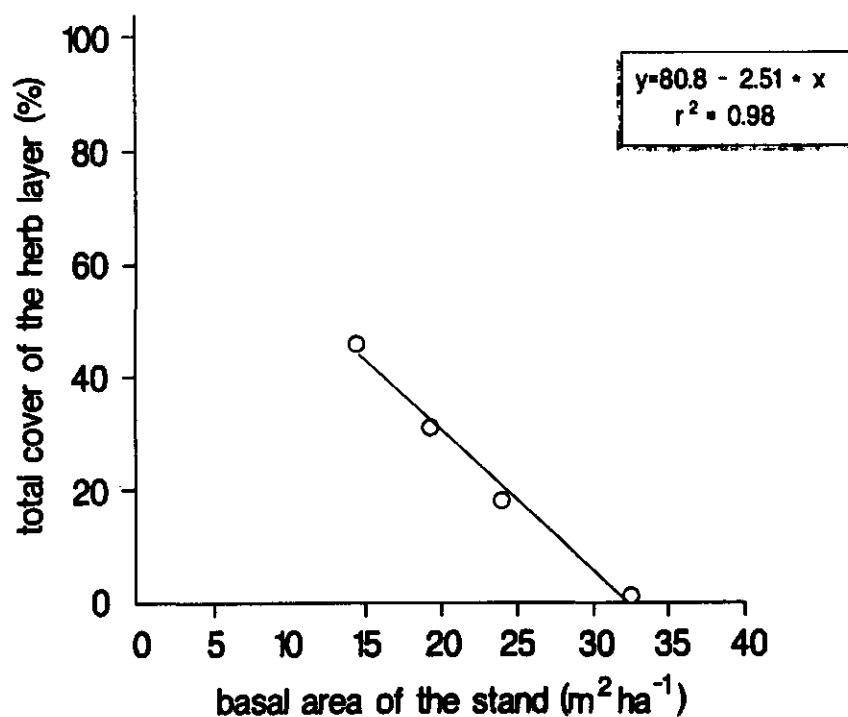
Figure 3.3   Linear regression model between forest stand basal area and total herb layer cover for oak stands on the Veluwe, The Netherlands (light deciduous forest).
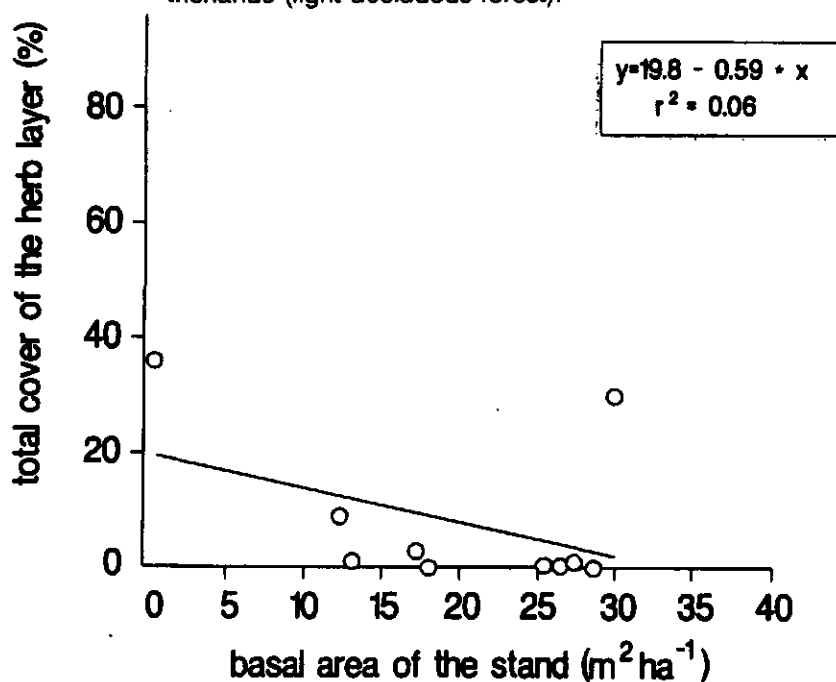

Figure 3.4   Linear regression model between forest stand basal area and total herb layer cover for beech stands on the Veluwe, The Netherlands (dark deciduous forest).

The results of Figure 3.1 to 3.4. are assumed to be representative for respectively light coniferous forest, dark coniferous forest, light deciduous forest and dark deciduous forest. A higher level restriction of the data according to either Fago-Quercetum or Betulo-Quercetum did not result in a significant difference. Other restrictions according to tree species, combination of tree species or forest type (according to the National Forest Inventory) did not result in any relation. Generally, the above presented relations are weak except for the light deciduous forests. In the module, they are therefore only used as a framework to test module results.

3.3 Growth rates

Growth is calculated in the module in terms of net growth rate i.e. the resultant of Net Primary Production (NPP) minus litterfall and other losses. This net growth rate can therefore be negative also, e.g. in autumn when litterfall rates are higher than Net Primary Production. It is named net relative growth rate (NRGR) when this net growth is expressed in terms of biomass increase (or decrease) per unit of total aboveground biomass; usually $g \ kg^{-1} \ mth^{-1}$ or $g \ kg^{-1} d^{-1}$. This NRGR can also be negative.

3.3.1 Annual course of Relative Growth Rate

For the herb layer species A. capillaris, D. flexuosa and M. caerulea, sufficient repeated biomass measurements were available for Dutch circumstances, to assess the annual course of production. For C. vulgaris, Dutch data in combination with data from the UK were used. For P. aquilinum, data from the UK were used and for V. vitis-idaea and V. myrtillus, Finnish data were used. Based on the total aboveground biomass curves, net growth rates were calculated. This net growth rate was then converted into a growth rate per unit of total aboveground biomass. The curves that are presented here and used in the module are valid for full light conditions. The simulation module corrects (based on the curves presented in paragraph 3.3.2) for the relative light level that penetrates through the forest canopy.

The vegetation development of the dwarf shrub species C. vulgaris, V. myrtillus and V. vitis-idaea is imposed also in stages as juvenile, building, mature and degenerating. These stages are important to determine the total annual growth rate that is distributed to assess an annual course of the net growth rate. To set a framework for Relative Growth Rates, literature data valid for optimal circumstances and seedling RGR, are presented in Table 3.7.

Main information source for A. capillaris was found in Wallis de Vries (1989). Of the two sites in The Netherlands with A. capillaris that he studied, the site Baronie Cranendonck is the best applicable because of the sandy soil type. Most relevant data on annual course of total aboveground of D. flexuosa were found in Oeffelt & Oostveen (1985) with comparisons in Wallis de Vries (1989), Aerts (1994), Al-Mufti et al. (1977) and Lehtonen et al. (1977). Oeffelt

& Oostveen (1985) found a clear double peak in the total aboveground biomass of D. flexuosa although this is not always supported by other authors. Wallis de Vries (1989), Van Eerden et al. (1991) and Aerts (1994) report a gradual increase of the total aboveground from April till October. Given the physiological stages of D. flexuosa during the seasons, the module also imposes a course of net growth rate which depicts two peaks in the total aboveground biomass.

For the dwarf shrub species C. vulgaris, not only the course of the relative growth rate over the year is imposed in the module, but because of the steady build-up of biomass in a period of 40 years, also a growth rate for each age-class of Calluna is imposed (see Figure 3.5).

Table 3.7 Seedling Relative Growth Rates of the relevant species under optimal conditions (Grime et al. 1988) and RGR maximum values according to Grime & Hunt (1975).

Species	seedling RGR (wk^{-1})	RGRmax (wk^{-1})
Agrostis capillaris	1.0-1.4	no data
Calluna vulgaris	<0.5	0.35
Deschampsia flexuo-sa	0.5-0.9	0.81
Molinia caerulea	no data	no data
Pteridium aquilinum	no data	no data
Vaccinium myrtillus	0.5-0.9	0.52
Vaccinium vitis-idaea	<0.5	0.23

Satisfying curves, describing the build-up of total aboveground and the annual net growth rate for heather in The Netherlands are given in Figure 3.5. This curve was chosen based on the wide variety of data available. A maximum total aboveground of 12500 kg ha^{-1} is reasonable for heathlands that are not affected by excessive grass growth.

Table 3.8 Build-up of biomass and relative net annual growth rate of C. vulgaris in the open field on a podzolic soil in The Netherlands (after Chapman et al. 1975 and Diemont & Oude Voshaar 1994)

age (yr)	Total above-ground biomass (kg ha^{-1})	Net annual growth rate (kg ha^{-1} yr^{-1})	Relative net annual growth rate (kg kg^{-1} yr^{-1})
5	1400	450	0.32
10	4300	676	0.16
15	7400	572	0.08
20	9600	376	0.04
25	11000	211	0.02
30	11800	104	0.01
35	12200	48	0.00

$$\ln B = 7.13 - 4.46 \cdot (0.863^{X})$$
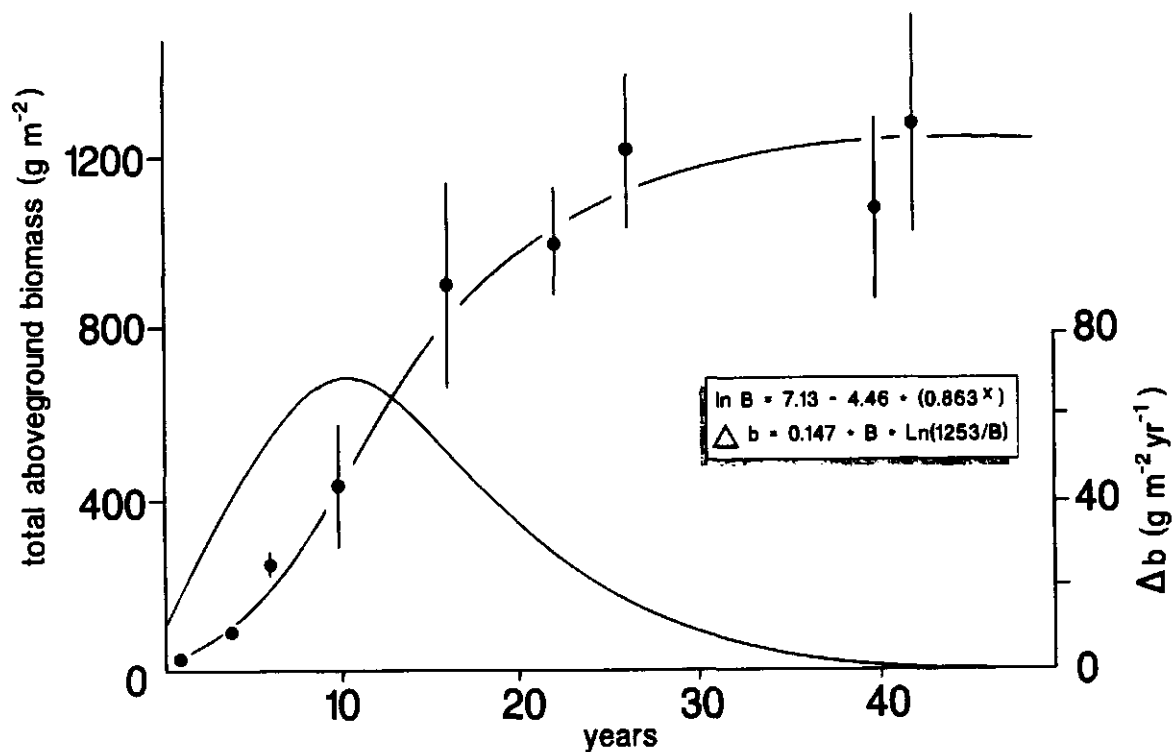$$\Delta b = 0.147 \cdot B \cdot \text{Ln}(1253/B)$$

Figure 3.5 Total aboveground dry matter of Calluna vulgaris (continuous line) and net annual growth rate (dashed line) in relation to the age of heathland (modified after Chapman et al. 1975 and Diemont & Oude Voshaar 1994). B is aboveground dry matter (g m^{-2}) and X is age (years). Δb is annual increment (g m^{-2} yr^{-1}).

The best available data concerning the annual course of the net growth rate of heather are given by Miller (1979) and Aerts (1994). The forage supply module imposes an annual growth rate based on Figure 3.5. which is then divided over the year according to the data given by Miller (1979). The annual production of 1780 kg ha^{-1} which he found is distributed as follows:

Table 3.9 Distribution of the total annual net growth of C. vulgaris over the months (Miller 1979).

Month	Monthly growth as percentage of total annual growth
April	0
May	12
June	23
July	25
August	25
September	11
October	4
November	0

Annual course of total aboveground biomass of M. caerulea was based on data obtained by Wallis de Vries (1989) and Aerts 1994). Annual course of total aboveground biomass of P. aquilinum was based on data obtained by Al-Mufti et al. (1977). Although the growth starts from the underground rhizomes of bracken, the module assumes that growth starts from a small amount of aboveground biomass (10 kg ha^{-1}).

The best data on annual production of V. myrtillus in The Netherlands are available from Jongman & Ruyter (1976) in combination with data of boreal circumstances from Kellomäki et al. (1977a), Vuokko et al. (1977) and Flower-Ellis (1971). According to Jongman & Ruyter (1976), V. myrtillus can reach an age of up to 14 years in The Netherlands although only 10% of the individuals reaches an age of over 7 years. In the pioneer phase the growth is slow, followed by the building phase with a strong increase of biomass which remains rather stable till the 14th year after which the degeneration starts.

Highest total aboveground biomass recorded in early autumn by Jongman and Ruyter in an ungrazed plot under scots pine with some indigenous oaks, was 680 g m^{-2}, this is equivalent to 6800 kg ha^{-1} when it is assumed that this can be reached over a whole hectare. They described the dwarf shrub understorey as consisting of very high V. myrtillus sometimes up to 1 meter high. In practice this physiological stage will almost never be reached

over a whole hectare at the same time. From the biomass sampling experiment, a maximum biomass at the hectare level was 2700 kg ha^{-1}. The forage supply module assumes that the assymptotic value which can be reached by V. myrtillus (under rather open forest on brown forest soil) is 3000 kg ha^{-1}. The build-up of biomass can be described as is given in Table 3.10.

Table 3.10   Build-up of biomass and relative annual growth rate of V. myrtillus on a Fago-Quercetum site in The Netherlands (Modified after Flower-Ellis 1971).

age (yr)	Total above-ground biomass (kg ha^{-1})	Net annual growth rate (kg ha^{-1} yr^{-1})	Relative net annual growth rate (kg kg^{-1} yr^{-1})
3	200	100	0.5
5	700	250	0.36
7	1300	300	0.23
10	2100	270	0.13
12	2550	225	0.09
14	2900	175	0.06
15	3000	100	0.03

Annual course recordings of the growth of V. myrtillus were found in Vuokko et al. (1977) and Kellomäki et al. (1977b). The first present the annual course of height increment of V. myrtillus in Finland. Height increment starts May 20st, reaches its highest value by the end of May and height increment ends mid June. Kellomäki et al. (1977b) present results of the annual production of V. myrtillus in Finland from which it appears that the gross part of the annual production occurs in between May 10th and June 10th. Jongman & Ruyter (1976) state that in The Netherlands the gross part of the production occurs in April and May. Based on that statement, the following distribution of production over the months is imposed in the module.

Repeated total aboveground measurements for V. vitis-idaea are very scarce. The same growth pattern and build-up of biomass as used for V. myrtillus was assumed in the module (Vukko et al. 1977). This was corrected for growth rates using the peak standing crop data from the biomass sampling experiment. The peak standing crop of V. vitis-idaea amounted on average 36% of the peak standing crop of V. myrtillus in the same stand. This ratio was used to assess the course of the relative growth rate.

Table 3.11   Distribution of annual growth of V. myrtillus over the months (after Jongman & Ruyter 1976, Vuokko et al. 1977).

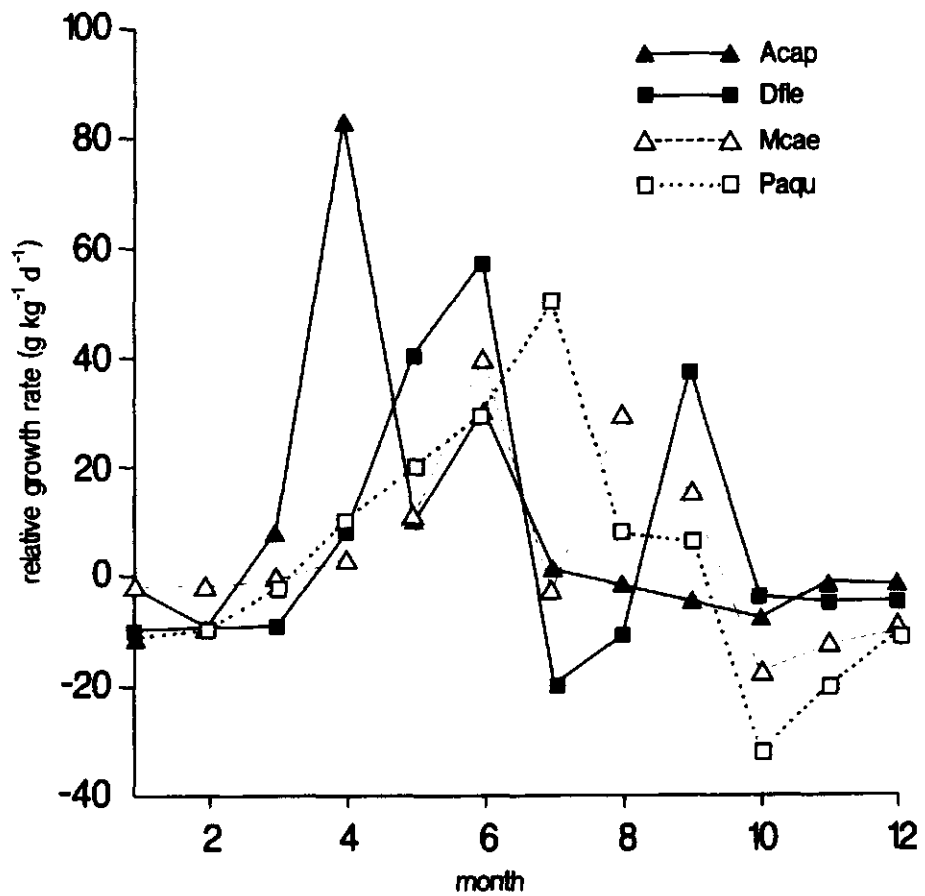| Month	Monthly growth as percentage of total annual growth
April	60
May	30
June	10

Figure 3.6   Annual course of the net relative growth rate of the herb layer species A. capillaris, D. flexuosa, M. caerulea and P. aquilinum for optimal circumstances in full light (Aerts 1994, Al-Mufti et al. 1977, Van Eerden et al. 1990, Lehtonen et al. 1977, Oeffelt & Oostveen 1985, Wallis de Vries 1989).
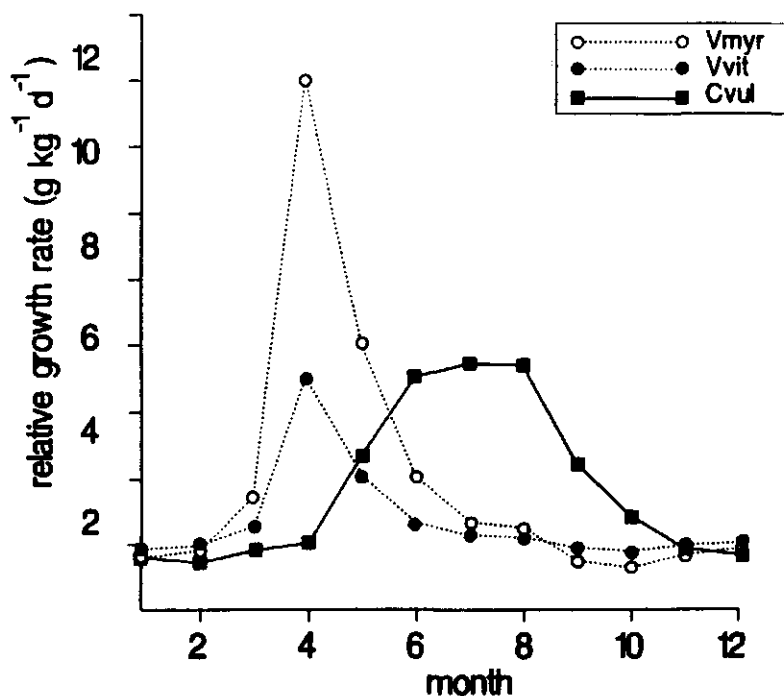
Figure 3.7   Annual course of the net relative net growth rate of the herb layer species C. vulgaris, V. myrtillus and V. vitis-idaea for optimal circumstances in full light (Chapman et al. 1975, Diemont & Oude Voshaar 1994, Flower-Ellis 1971, Jongman & Ruyter 1976, Kellomäki et al. 1977b, Vukko et al. 1977).

3.3.2 Reduction factor for relative growth in relation to relative light level

The module simulates the net relative growth rate based on the annual growth rhythm in full light (par 3.3.1.) and curves which depict the inherent growth in relation to the relative light level (Figure 3.8). These light response curves were assessed based on divergent sources (Levine et al. 1993, Ellenberg 1991, Grime et al. 1988, Vaïsänen et al. 1977, pers. comm. Bijlsma, IBN-DLO). The presented curves were corrected based on the peak standing crop data that were assessed in relation to the stand basal area (depicting light level).

Väisänen et al. (1977) studied the role of available light as a limiting factor to the annual growth level of V. myrtillus, V. vitis-idaea and D. flexuosa. The productivity of D. flexuosa was linearily correlated with the photosynthetic light ratio. The productivity of the two Vaccinium species reaches its maximum at a relatively low photosynthetic light ratio (ratio between the total amount of CO_2 fixed in an actual environment divided by the total amount of CO_2 fixed in the reference environment).

Kellomäki et al. (1977a) use the effect of the increase of basal area of a stand to determine the herb layer production during the time course of the forest development. It appears that D. flexuosa is very productive during the first 20 years of the forest development with a peak annual production of

over 500 kg ha^{-1}. The adaption of the two Vaccinium species to low light intensities results in an increase in the abundance of these two species at the expense of D. flexuosa.
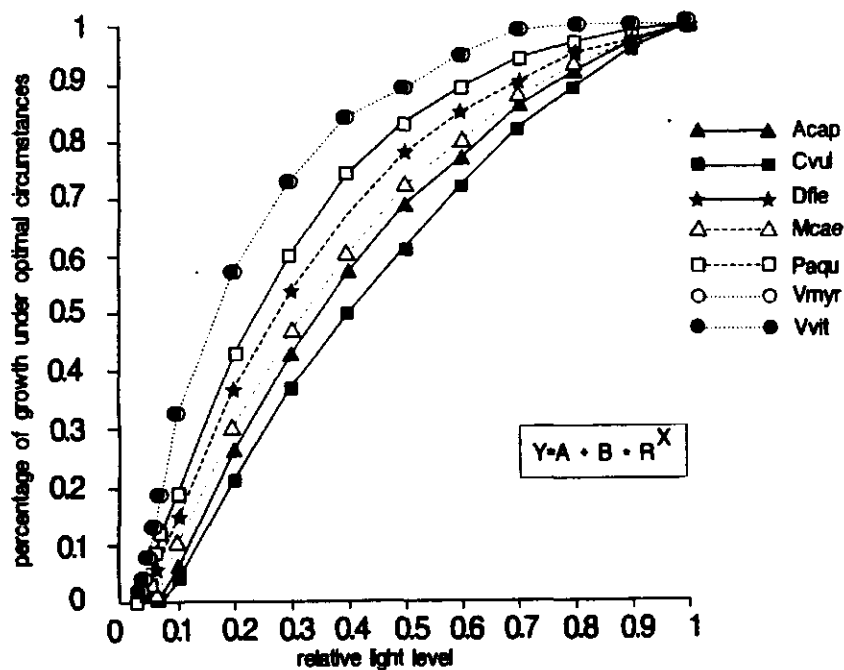

Figure 3.8   Light response curves of the seven herb layer species as implemented in the forage supply module. X = the fraction of available light relative to full light, Y = fraction of the Relative Growth Rate at full light (reduction factor), R, B and X are coëfficient values. The coëfficient values are given in table 3.12.

Table 3.12   Coëfficient values for the light response curves of the six herb layer species.

	R	B	A
A. capillaris	0.1534	-1.3881	1.2248
C. vulgaris	0.2655	-1.5859	1.4345
D. flexuosa	0.06385	-1.22068	1.0795
M. caerulea	0.10850	-1.31798	1.1480
P. aquilinum	0.03996	-1.18311	1.05808
V. myrtillus	0.00827	-1.1646	1.01527
V. vitis-idaea	0.00827	-1.1646	1.01527

3.4 Peak standing crop of the herb layer species in relation to tree species and stand basal area

The module uses an asymptotic value (peak standing crop) for the maximum total aboveground biomass that a species can reach under certain site circumstances. This peak standing crop is used to curve the growth when this ceiling is being approached. These data were assessed in the biomass sampling experiment in which the selected stands covered the variety of sites, tree species and stand densities currently present on the Veluwe. The following figures present the results. In table 3.13, data are presented for combinations of sites and tree species for which only a few data were available.
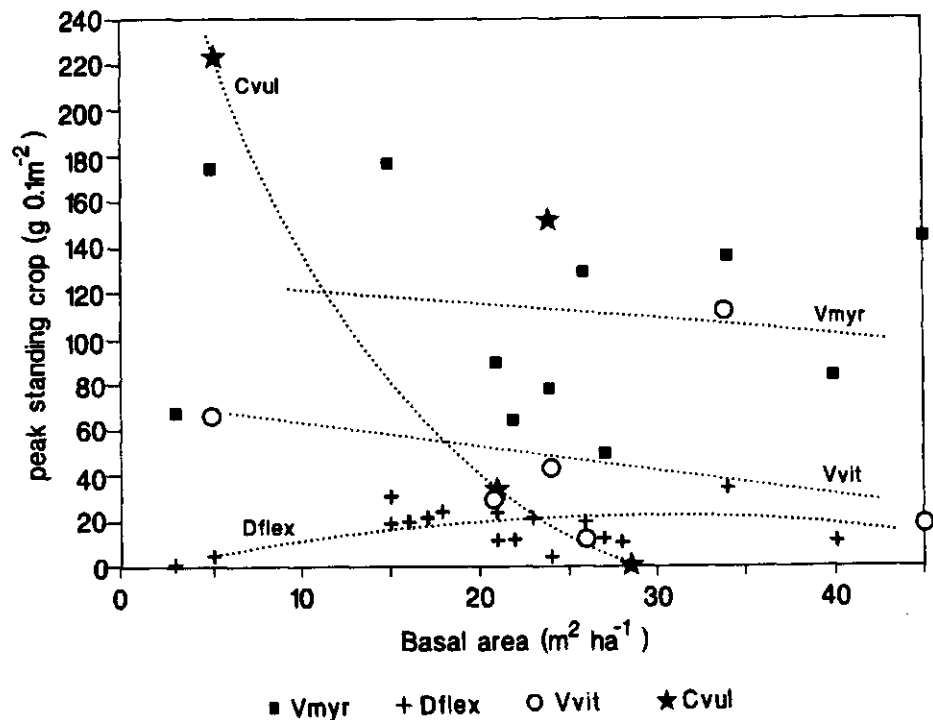

■ Vmyr   + Dflex   O Vvit   ★ Cvul

Figure 3.9   Peak standing crop of herb layer species in relation to basal area of Scots pine stands on Betulo-Quercetum sites.
Acap = Agrostis capillaris; Cvul = Calluna vulgaris; Dflex = Deschampsia flexuosa; Mcae = Molinia caerulea; Paqu = Pteridium aquilinum; Vmyr = Vaccinium myrtillus; Vvit = Vaccinium myrtillus
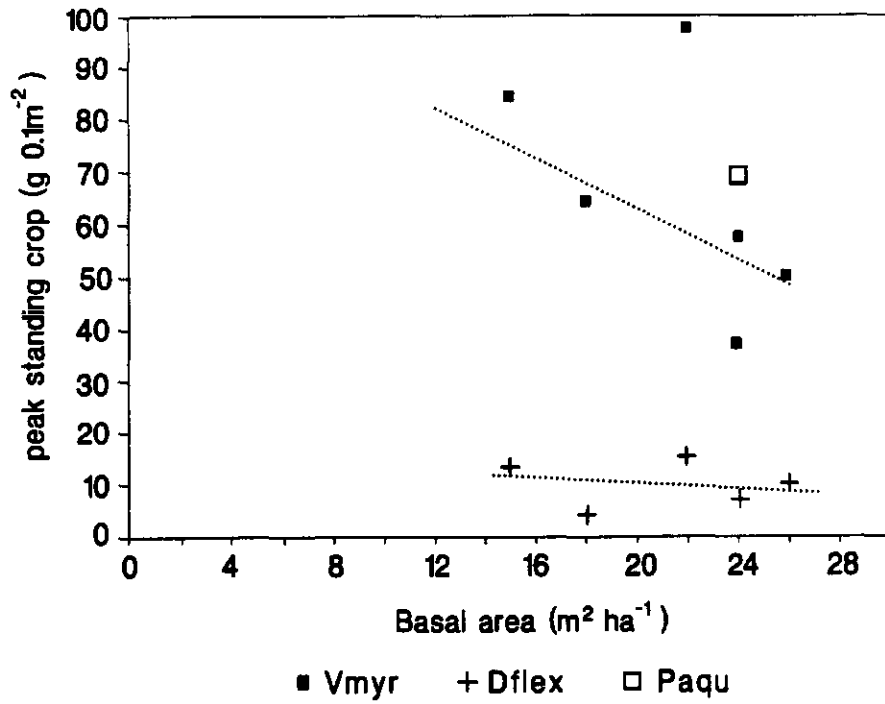
Figure 3.10   Peak standing crop of herb layer species in relation to basal area of pedunculate oak stands on Betulo-Quercetum sites.
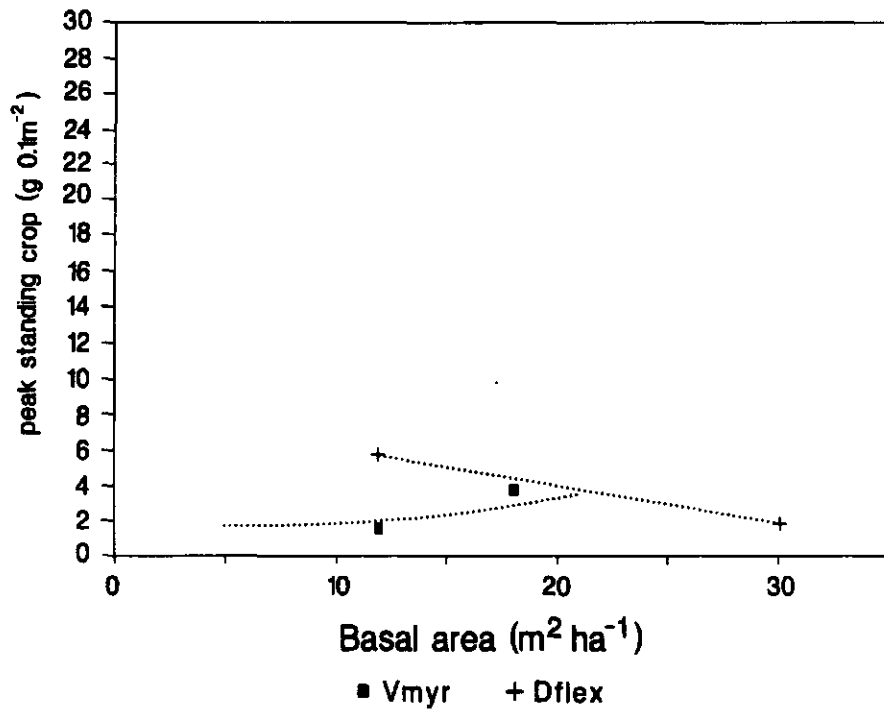

Figure 3.11   Peak standing crop of herb layer species in relation to basal area of beech stands on Betulo-Quercetum sites.
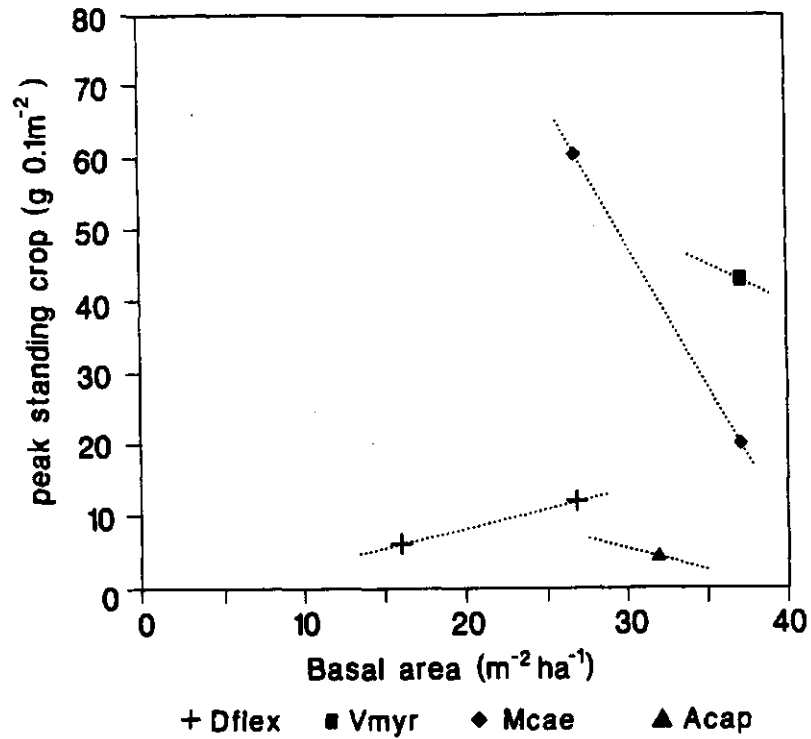
Figure 3.12   Peak standing crop of herb layer species in relation to basal
area of pedunculate oak stands on Fago-Quercetum sites.
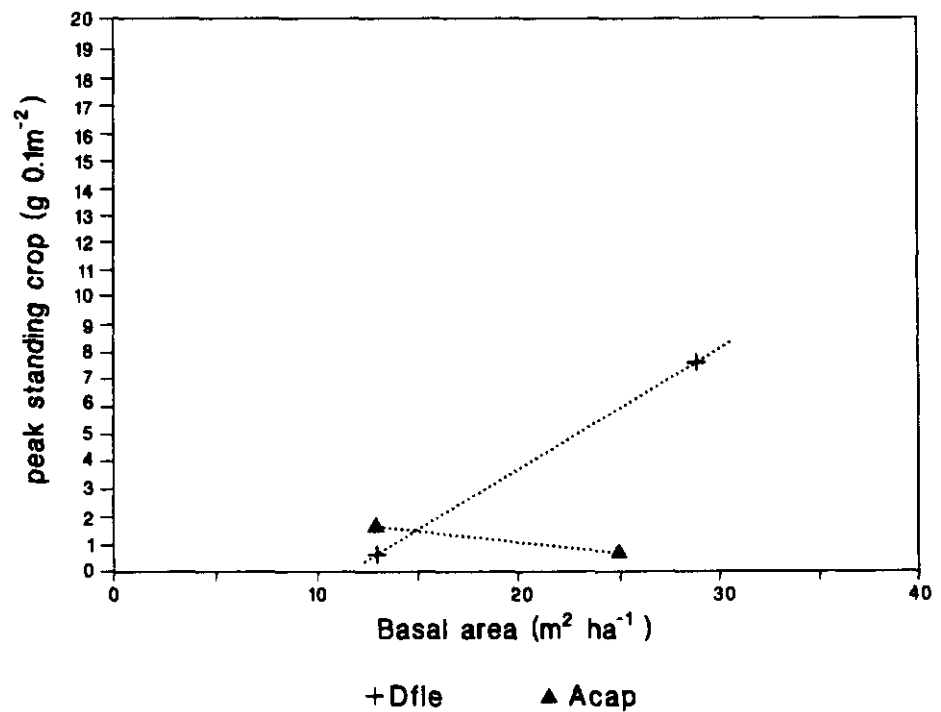

Figure 3.13   Peak standing crop of herb layer species in relation to basal
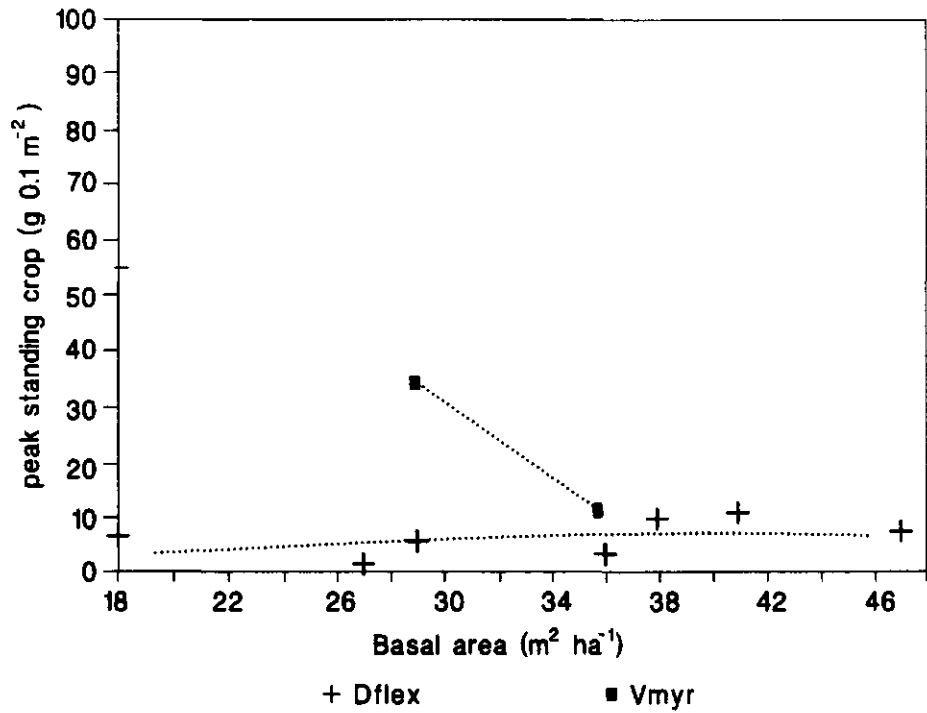area of beech stands on Fago-Quercetum sites.

Figure 3.14 Peak standing crop of herb layer species in relation to basal area of Douglas-fir stands on Fago-Quercetum sites.
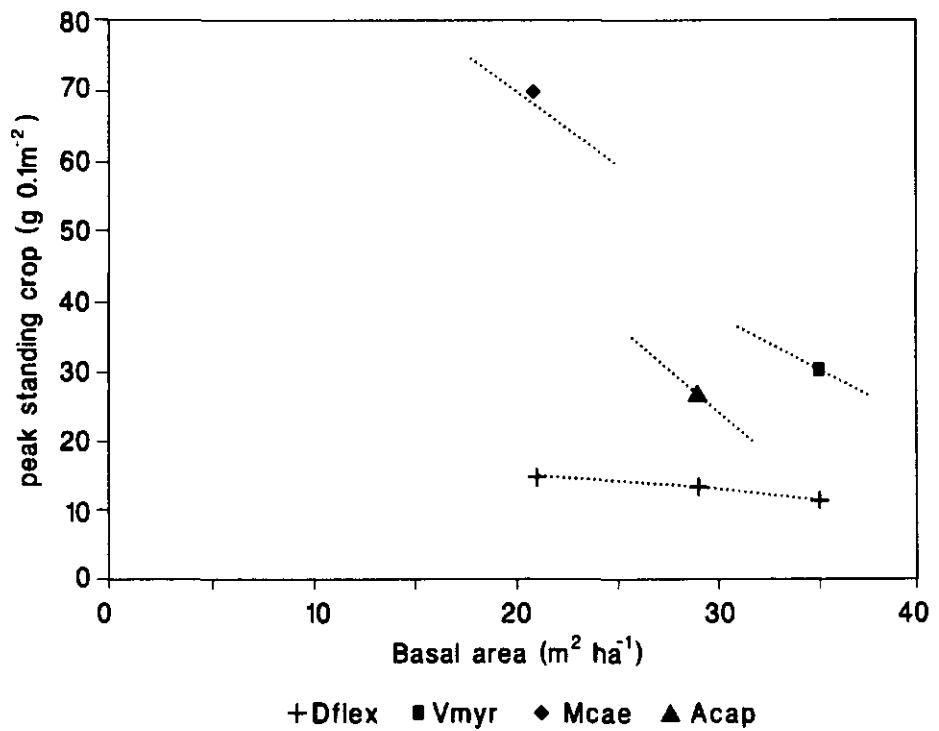

Figure 3.15 Peak standing crop of herb layer species in relation to basal area of Japanese larch stands on Fago-Quercetum sites.

The above given dashed lines can sometimes only be seen as best guesses based on the gathered data. When only one recording was available, an angle of the relation was indicated by a short dashed line. This angle was based on relations found in other figures.

On Betulo-Quercetum sites, wavy hair-grass seems to be insensible to the stand basal area. The peak standing crop is limited to approximately 5 g $0.1m^{-2}$ under beech. With increasing basal area of Scots pine and oak, the peak standing crop of both blueberry and cowberry are reduced. Under beech, this seems to be the opposite, but this may have been caused by the limited range of basal area that is covered. Heather is heavily suppressed with increasing basal area of Scots pine.

On Fago-Quercetum sites, wavy hair-grass seems to be slightly favoured by an increasing basal area of the stand. Purple moor-grass seems to be very sensible to the basal area of oak, and the direction of the line given in figure 3.15 was based on this. Blueberry is reduced with increasing basal area of Douglas-fir. The direction of the dashed lines for blueberry under oak and Japanese larch was based on this. The same goes for common bent-grass.

Table 3.13   Peak standing crop values for herb layer species (g $0.1m^{-2}$) on combinations of site and tree species for which only a few data were available. The data for open heathland are from Aerts 1994, Diemont & Oude Voshaar 1994, Oeffelt & Oost-veen 1985, Wallis de Vries 1989, and Van Wieren 1988)

	Basal area (m^2 ha^{-1})	Cvul	Dfle	Mcae	Paqu	Vmyr
Douglas-fir on Betulo-Querce-tum	7		3.3	29.0		42.9
Scots pine on Fago-Querce-tum	17		14.0			70.3
birch on Fago-Quercetum	19			34.8	215.3	143.6
open heathland	0	250	50	70		

The absolute peak standing crop that was recorded for blueberry on Fago-Quercetum sites was 143.6 g $0.1m^{-2}$ and was found under birch. It remains somewhat strange that the highest values for blueberry were found under Scots pine on Betulo-Quercetum sites (up to 177 g $0.1m^{-2}$), because it is generally believed that blueberry reaches the greatest heights on Fago-Quercetum sites (pers. comm. Koop, IBN-DLO). Anyway, it is likely that the

absolute peak standing crop of blueberry for the Veluwe area is covered by the data.

Differences in peak standing crops on different site types are vague, also because of the limited number of data for each herb layer species, site and tree species. From table 3.14. it appears that the peak standing crop of A capillaris, D. flexuosa and P. aquilinum on F-Quercetum sites is more than twice the peak standing crop on B-Quercetum sites. The peak standing crop of M. caerulea and V. myrtillus on F-Quercetum sites is smaller than the peak standing crop on B-Quercetum sites. For V. myrtillus this was unexpected and somewhat in contradiction with the results in table 3.5. Heather and bilberry were not sampled on F-Quercetum sites. The effect of the tree species is more clear. High peak standing crop crop values are reached under Scots pine, oak and birch and low values under Douglas-fir and beech.

Table 3.14   Absolute peak standing crop (g $0.1m^{-2}$) regardless of the tree species present on the two site types.

	Betulo-Quercetum	Fago-Quercetum
A. capillaris	10.0	26.5
C. vulgaris	228.5	*
D. flexuosa	34.4	70.3
M. caerulea	111.9	70.0
P. aquilinum	69.3	215.3
V. myrtillus	176.7	143.6
V. vitis-idaea	112.9	*

*: no recordings of this species on this site type.

3.5 Translation functions

To translate net growth into an increase in height or to translate cover data into total aboveground biomass, functions between cover and biomass and height and biomass were required. For all species except bracken, these functions were assessed based on the data of the biomass sampling experiment.

3.5.1 Correlation between height and biomass of the herb layer species

The following figures present the relation between height of the species at the sample plot level (0.1 m^2) and its total aboveground biomass at the sample plot level. The functions were assessed under summer maximum biomass circumstances.
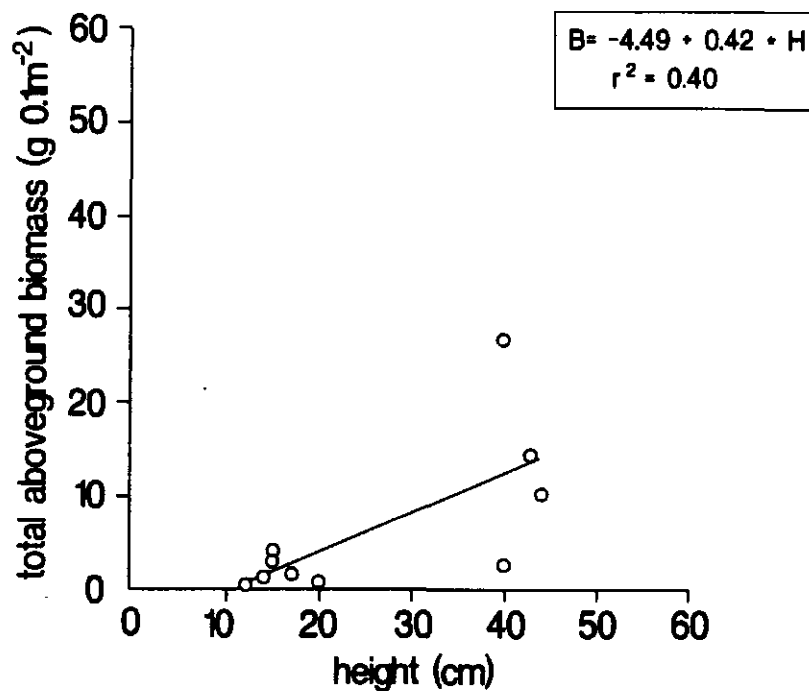
Figure 3.16   Relation between height of A. capillaris (cm) and total
aboveground biomass (g 0.1m⁻²) under forest on the Veluwe. B
= total aboveground biomass (g 0.1m⁻²) and H is height (cm).

Figure 3.17   Relation between height of C. vulgaris (cm) and total above-
ground biomass (g 0.1m⁻²) under forest on the Veluwe. B =
total aboveground biomass (g 0.1m⁻²) and H is height (cm).

Figure 3.18   Relation between height of D. flexuosa (cm) and total above
ground biomass (g 0.1m⁻²) under forest on the Veluwe. B =
total aboveground biomass (g 0.1m⁻²) and H is height (cm).

Figure 3.19   Relation between height of M. caerulea (cm) and total above-
ground biomass (g 0.1m⁻²) under forest on the Veluwe. B =
total aboveground biomass (g 0.1m⁻²) and H is height (cm).

$$B = 6649 - 97423 \cdot 0.0305^H$$
$$r^2 = 0.77$$

Figure 3.20 Relation between height of P. aquilinum (m) and total above-
ground biomass (kg ha⁻¹). Data from the UK, after Lowday &
Marrs (1992). B = total aboveground biomass (kg ha⁻¹) and H
is height (m). The function for bracken is only valid for heights
over 0.7 m.

$$B = -16.6 + 1.88 \cdot H$$
$$r^2 = 0.58$$

Figure 3.21 Relation between height of V. myrtillus (cm) and total above-
ground biomass (g 0.1m⁻²) under forest on the Veluwe. B =
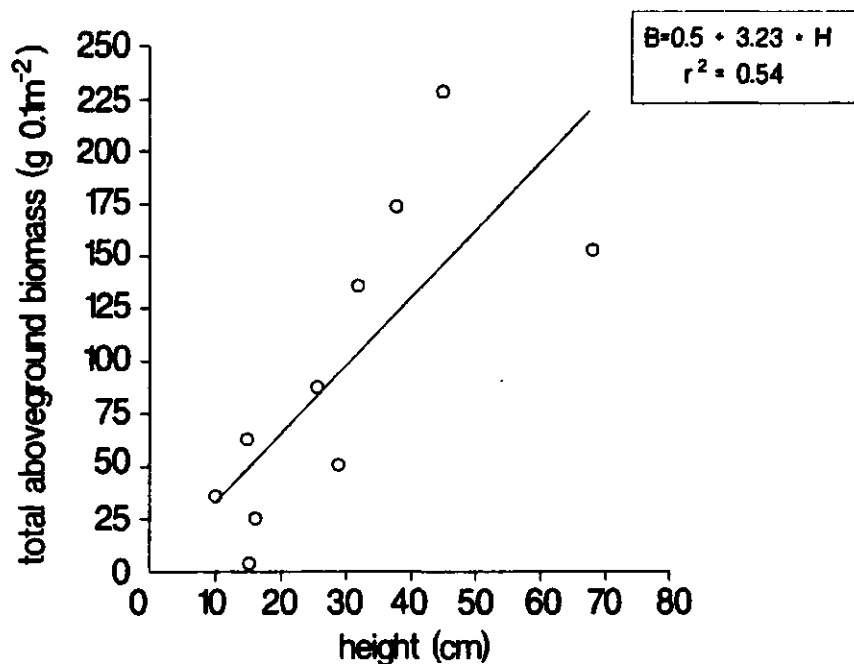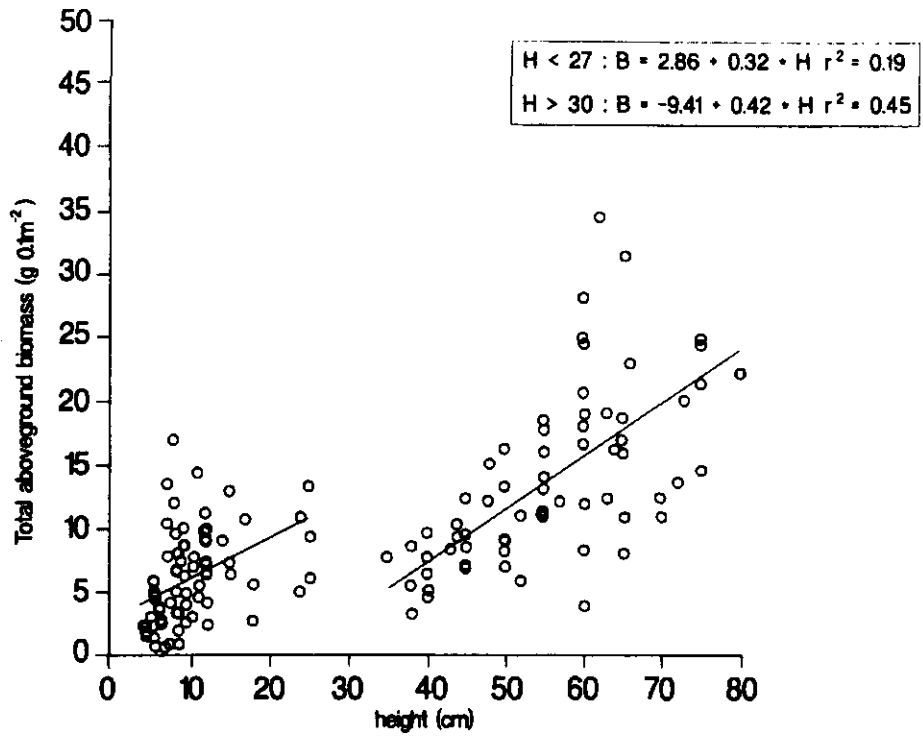total aboveground biomass (g 0.1m⁻²) and H is height (cm).

Figure 3.22   Relation between height of V. vitis-idaea (cm) and total
              aboveground biomass (g $0.1m^{-2}$) under forest on the Veluwe. B
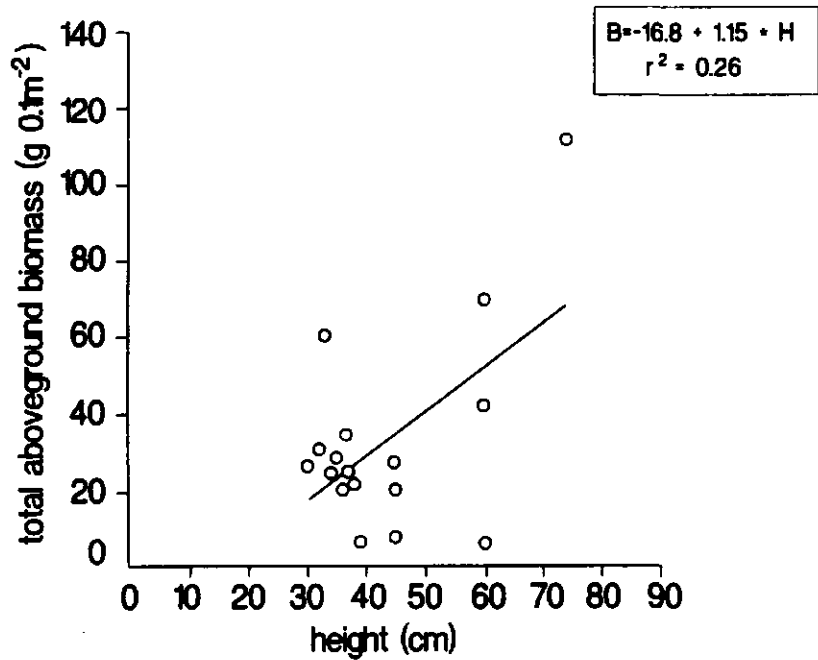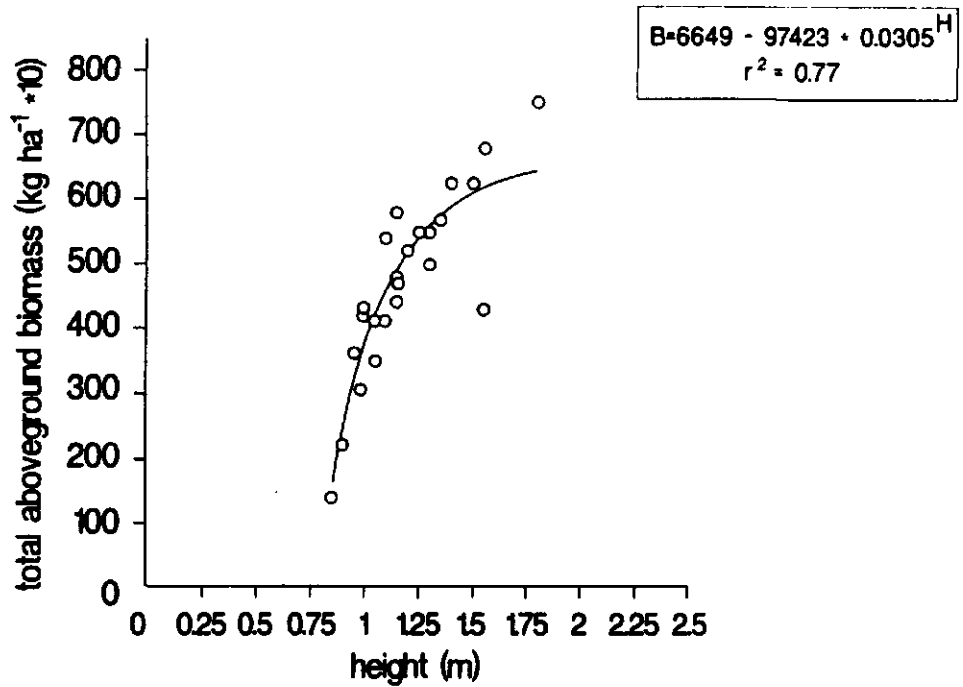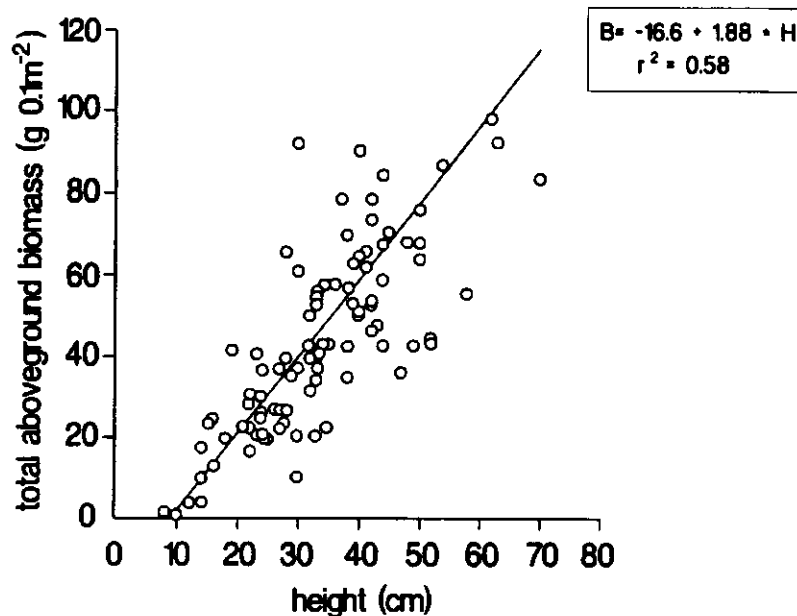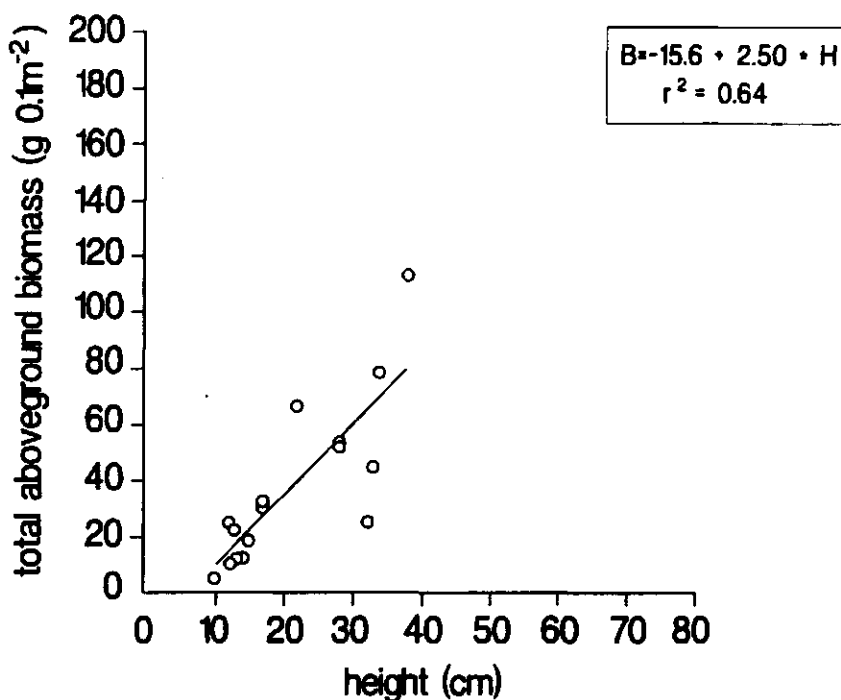   = total aboveground biomass (g $0.1m^{-2}$) and H is height (cm).

Although these usually linear functions do not always give a high ex-
planatory value, they represent the best fit for the available range in data.
Others (like Wallis de Vries 1989) who have used a light disc to measure the
height of the vegetation, usually present curves that gradually approach
asymptotic values for the total aboveground biomass. This is also the case
for bracken in Fig 3.20 (Lowday & Marrs 1992). The fact that others someti-
mes present asymptotic curves, is probably due to the technique that they
used to measure height. They measured the height with a light disc that
was lowered on top of the vegtation, whereas in the present study the top
height was recorded with a measuring tape. In case of wavy hair-grass it
was decided to fit two seperate lines for two ranges in height. This resulted
in a better fit. This seperation is obvious in the two groups of data. These
groups represent the two types in which wavy hair-grass occurs under
forests: infertile (left function in Fig 3.18) and fertile (right function in Fig
3.18).

3.5.2 Correlation between cover and biomass of the herb layer species

Based on data obtained in the biomass sampling experiment, relations at
the sample plot level (Fig 3.23-3.28) and at the stand level (Fig. 3.29-3.32)
were assessed. At the sample plot level too few data were available to fit a
model for bracken. At the stand level, too few data were available to fit a
model for common bent-grass, heather and bracken. The functions at the
sample plot level are used in the module to carry out the translation calcul-

ations. The functions at the hectare level are used as a framework to verify module output.

$$B = -0.28 + 1.39 \cdot 1.03^C$$
$$r^2 = 0.82$$

Figure 3.23   Relation between cover of A. capillaris at the sample plot level and its total aboveground biomass (g 0.1m^{-2}) in the plot. B = aboveground dry matter (g 0.1 m^{-2}), C = percentage cover of the herb layer species in the plot (0-100).

$$B = 7.6 + 1.50 \cdot 1.05^C$$
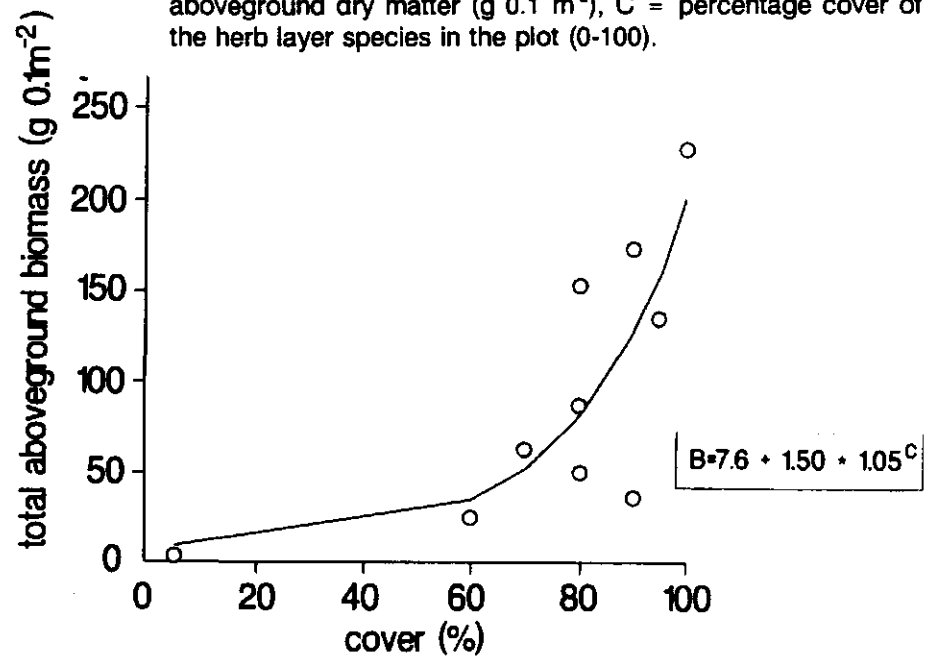
Figure 3.24   Relation between cover of C. vulgaris at the sample plot level and its total aboveground biomass (g 0.1m^{-2}) in the plot. B = aboveground dry matter (g 0.1 m^{-2}), C = percentage cover of the herb layer species in the plot (0-100).
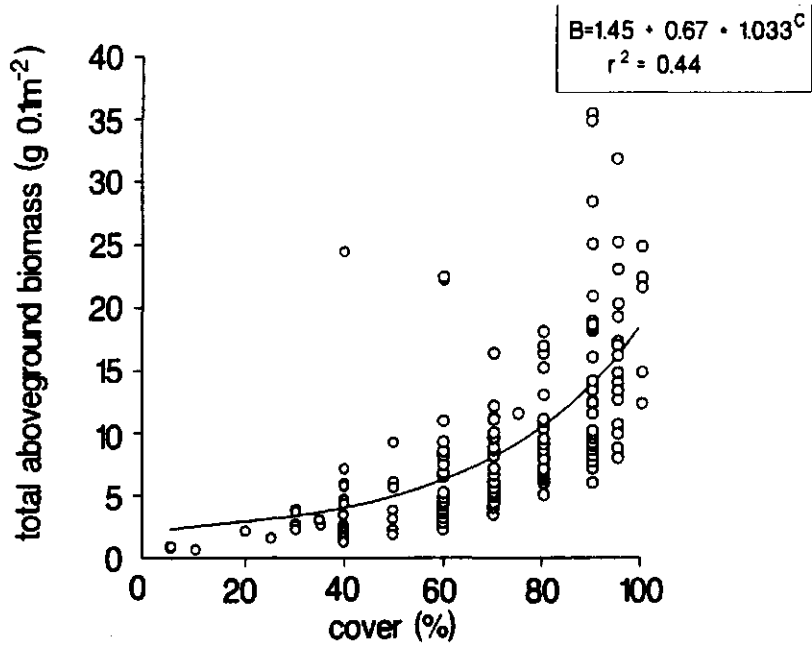
Figure 3.25 Relation between cover of D. flexuosa at the sample plot level and its total aboveground biomass (g $0.1m^{-2}$) in the plot. B = aboveground dry matter (g 0.1 m^{-2}), C = percentage cover of the herb layer species in the plot (0-100).
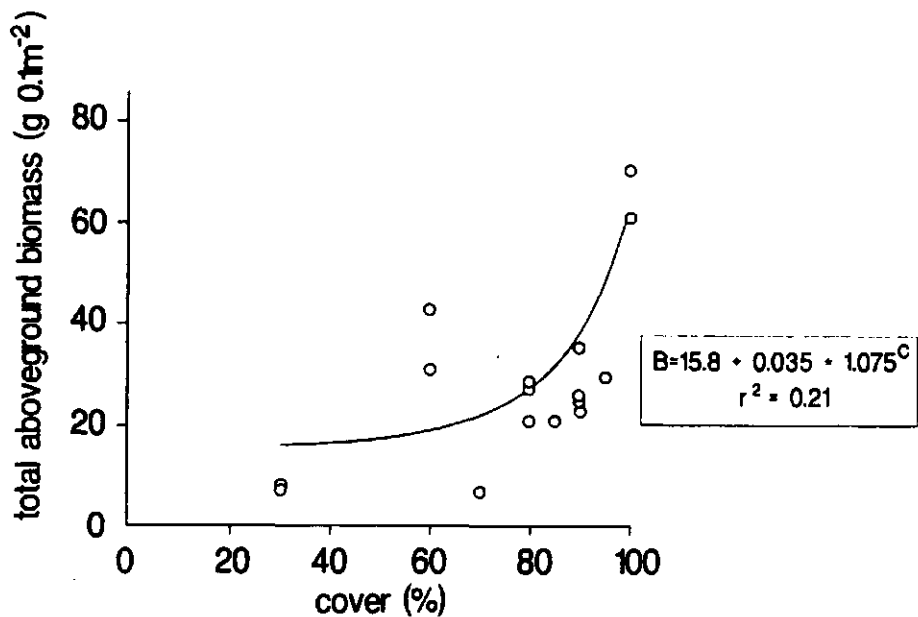
Figure 3.26 Relation between cover of M. caerulea at the sample plot level and its total aboveground biomass (g $0.1m^{-2}$) in the plot. B = aboveground dry matter (g 0.1 m^{-2}), C = percentage cover of the herb layer species in the plot (0-100).
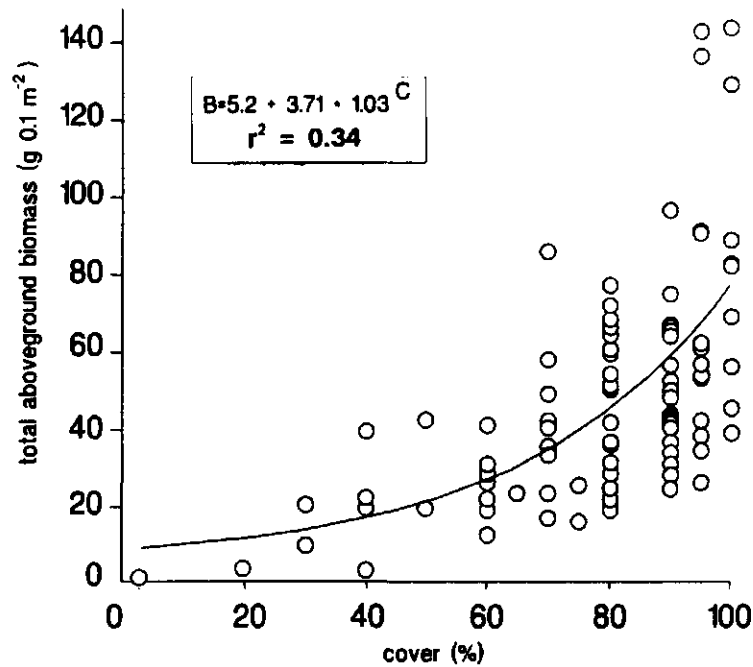
Figure 3.27 Relation between cover of V. myrtillus at the sample plot level
and its total aboveground biomass (g 0.1m⁻²) in the plot. B =
aboveground dry matter (g 0.1 m⁻²), C = percentage cover of
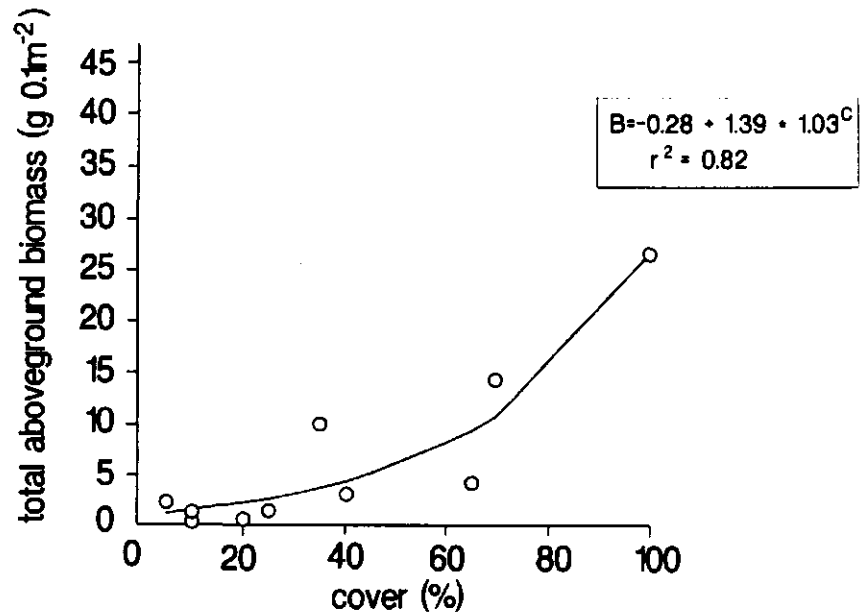the herb layer species in the plot (0-100).
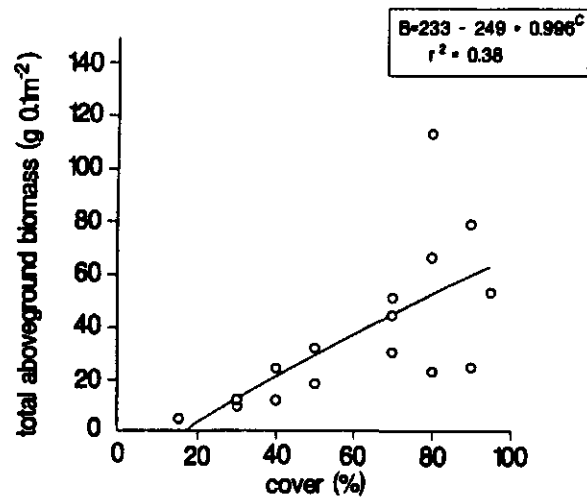
Figure 3.28 Relation between cover of V. vitis-idaea at the sample plot level
and its total aboveground biomass (g 0.1m⁻²) in the plot. B =
aboveground dry matter (g 0.1 m⁻²), C = percentage cover of
the herb layer species in the plot (0-100).

The above given relations should not be extrapolated outside the range of
the presented data, because the maximum is covered in the data set
already.
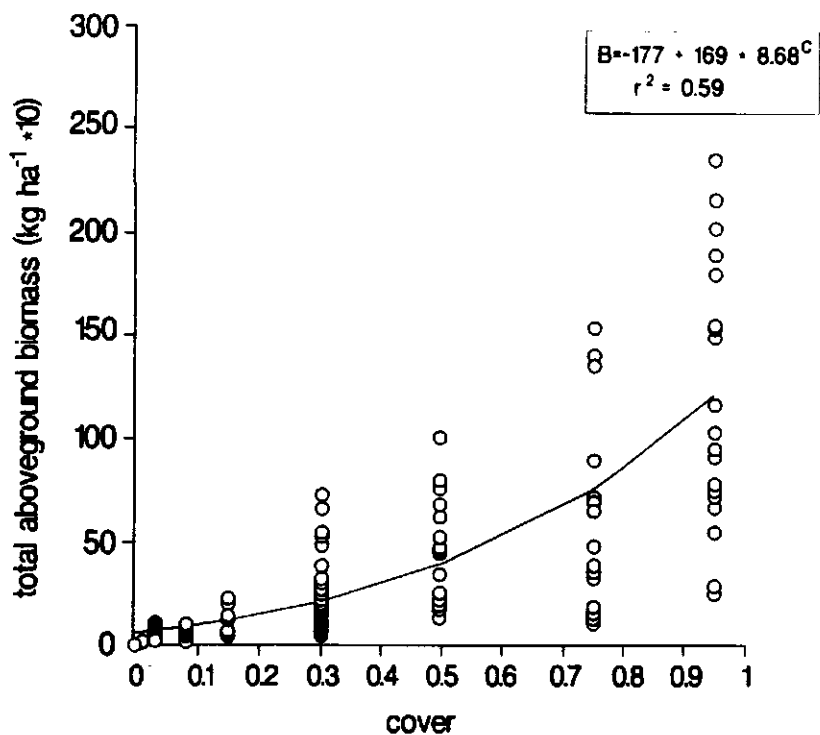
Figure 3.29 Relation between cover of D. flexuosa at the stand level and its total aboveground biomass in the stand (kg ha⁻¹).
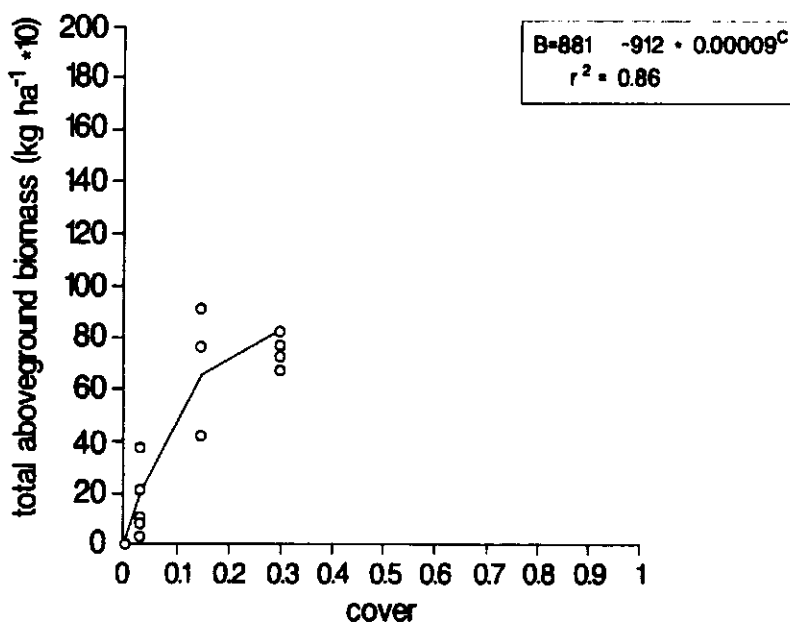
Figure 3.30 Relation between cover of M. caerulea at the stand level and its total aboveground biomass in the stand (kg ha⁻¹).
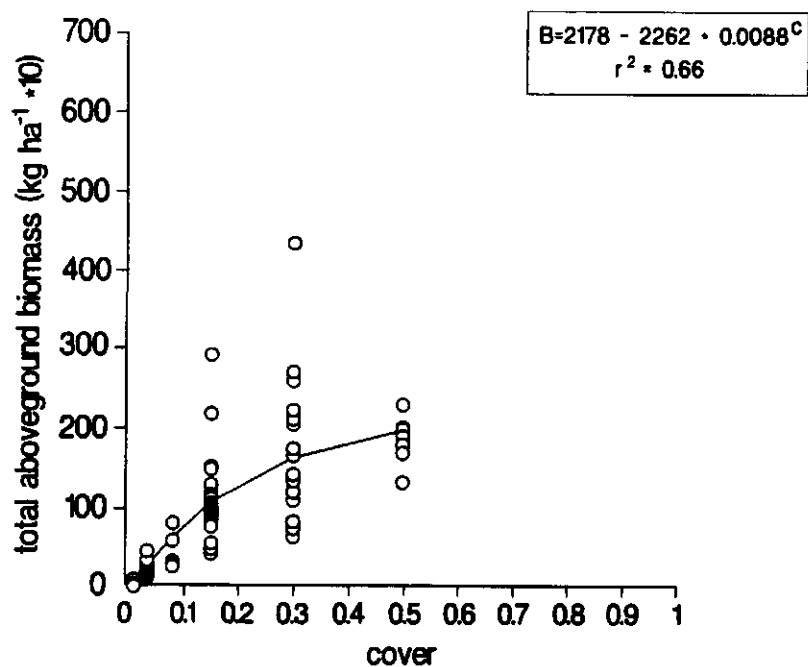
Figure 3.31   Relation between cover of V. myrtillus at the stand level and its
total aboveground biomass in the stand (kg ha⁻¹).
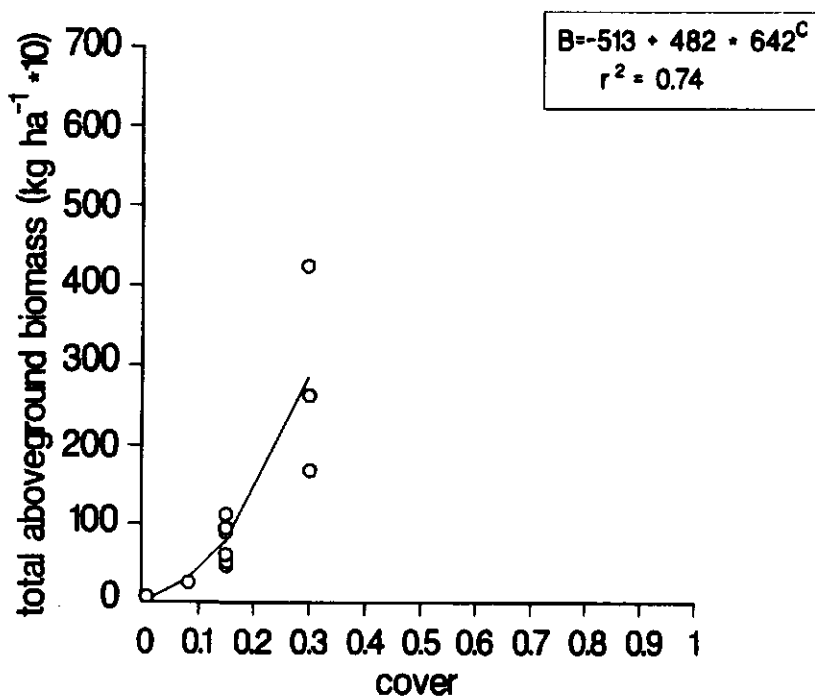
Figure 3.32   Relation between cover of V. vitis-idaea at the stand level and
its total aboveground biomass in the stand (kg ha⁻¹).

Although the distribution in biomass at a specific cover class can be quite large, any sub-division of some of the larger data sets into sub-sets according to height-classes did not result in clear differences.

3.5.3. Edible part of the total aboveground biomass

Starting point to calculate the edible part of the total aboveground per month is that all current year's growth is considered edible. For the dwarf shrub species, an edible fraction is also calculated in relation to age (i.e. height). Cowberry and bracken are assumed to have an edible fraction of 0% throughout the year. The percentages living material that are presented in this paragraph are used in the module as a framewerk to verify module output.

For D. flexuosa, A. capillaris and M. caerulea percentages living material of total aboveground were derived from literature (see Table 3.15, Oeffelt & Van Oostveen 1985, Wallis de Vries 1989).

An additional reduction factor for grasses is incorporated to account for a percentage of biomass that cannot be grazed by the ungulates because it is too close to the ground. The height at which a grass sward cannot be grazed anymore is set at 0.5 cm (pers. comm. P. Slim IBN-DLO) although Wallis De Vries (1989) according to Van Dyne et al. (1980) mentions a height of 1 cm for horses and 2 cm for cattle. Above a height of 5 cm this factor is of very limited significance and not taken into account anymore (see Table 3.16).

For the dwarf shrub species V. myrtillus and C. vulgaris, not only an annual reduction factor is incorporated, but also a factor that takes into account the steady build-up of biomass that occurs in the course of e.g. 40 years. For C. vulgaris, the edible part is imposed for two groups of herbivores. For roe deer only the current year's green material is edible and for red deer, ponies and Highland cattle the total green material can be regarded as edible. This results in the edible fractions as given in Table 3.17.

Table 3.15   Percentage living material of the total aboveground through the seasons for D. flexuosa in the open field and under forest and for A. capillaris and M. caerulea (Oeffelt & Van Oostveen 1985, Wallis de Vries 1989).

	Percentage living material of the total above-ground biomass of wavy hair-grass			
month	under forest	open field	Percentage living material of the total aboveground biomass of common bent-grass	Percentage living material of the total aboveground biomass of purple moor-grass
January	25	35	8	0
February	20	30	6	0
March	20	35	5	10
April	35	40	6	40
May	80	80	40	60
June	90	90	90	90
July	85	85	90	92
August	80	80	85	90
September	70	70	65	85
October	55	60	50	60
November	45	50	25	0
December	35	40	15	0

Table 3.16   Edible fraction in relation to the height of the grass.

Height (cm)	edible fraction
< 0.5	0
0.5 - 1.0	0.5
1.0 - 2.0	0.65
2.0 - 5.0	0.85
> 5.0	1.0

Table 3.17   Edible fractions (%) of C. vulgaris for the relevant herbivores in relation to the total aboveground biomass in The Netherlands.

		Edible fraction for*	
age (yr)	total above-ground biomass (kg ha^{-1})	roe deer	red deer, pony, cattle
5	1400	26	50
10	4300	20	42
15	7400	16	31
20	9600	14	28
25	11000	13	26
30	11800	12	24
35	12200	11	23

*: edible fraction according to Chapman et al. (1975) roe deer: current year's green; red deer, pony and cattle: total green.

The division of this edible part over the seasons was made on the basis of the measurements reported by Prins et al. (1991), Woolhouse & Kwolek (1981) and Miller (1979). C. vulgaris is an evergreen and scenescence and litterfall, mainly of second- and third-year leaves and short shoots occurs in a rather long period from August till March (Chapman et al. 1975) with a peak in October. In total accounting for 85% of the annual litterfall. Based on Aerts (1994) it is assumed that the edible part of Calluna for roe deer gradually declines with 20% of the edible fraction during the period August - March (2.5% mth^{-1}), increasing again during the growth period May - August (Miller 1979) to the percentages given above in Table 3.17. For the other herbivores, it is reasonable to assume that the above given edible fraction is valid around August, gradually declining with in total 40% of this edible fraction in April (Aerts 1994) and then gradually rising again in the period

May till August according to the distribution of the annual production over the growing season (Miller 1979).

The assessment of the edible part of V. myrtillus is comparable with C. vulgaris although V. myrtillus is a deciduous dwarf shrub, shedding all leaves in a relatively short period. In contrast to Calluna, only very few biomass measurements of Vaccinium were available, especially for Dutch circumstances. Flower-Ellis (1971) gives biomass measurements distributed in leaves, current year shoots and older shoots. For the Swedish circumstances with total aboveground biomass up to 4480 kg ha^{-1}, the average part in leaves and current year shoots amounts to 25% with on average 10% in the leaves.

Because of a lack of Dutch data concerning the edible part of V. myrtillus, the biomass samples of V. myrtillus were divided into edible (current year shoots and leaves) and unedible (rest) in accordance with Van der Grift & Huijser (1991) who mention an edible length of the shoots of 4 cm. These data were correlated to the height of V. myrtillus in the plot to obtain a relation between height and edible part. The module that also considers height of the herb layer species, calculates an edible part, given the height of V. myrtillus.

$$ED\% = 3.2 + 109 / (1 + 0.053 \cdot H)$$
$$r^2 = 0.53$$
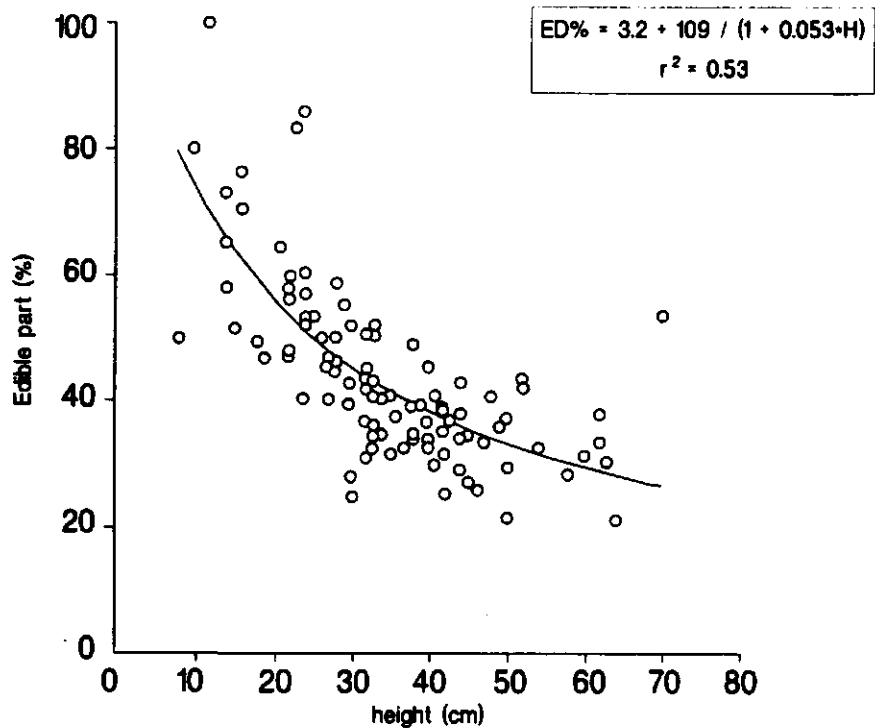
Figure 3.33 Edible part of blueberry in summer for red deer, cattle and pony as a percentage of total aboveground dry matter in relation to the height.
ED% is edible part as a percentage of total aboveground biomass and H is height (cm).

3.6 Inhibitory effect of herb layer coverage on woody species regeneration

In the forest development model, the herb layer cover has a feedback on the success of germination and establishment of tree seedlings. From various sources it is clear that a high coverage of a grass dominated herb layer has a restraining influence on the germination and establishment of tree seedlings (Jarvis 1964, Bredemeier & Dohrenbusch 1984, Kuper 1994).

Bredemeier & Dohrenbusch (1984) investigated the expansion of D. flexuosa under old stands of Norway spruce in Germany as to determine its role in counteracting natural regeneration. The ground vegetation cover relative to basal area decreased markedly in the shadier stands; the relative proportion of D. flexuosa increased. A crown density of more than 65% was advised in order to limit the competitiveness of D. flexuosa.
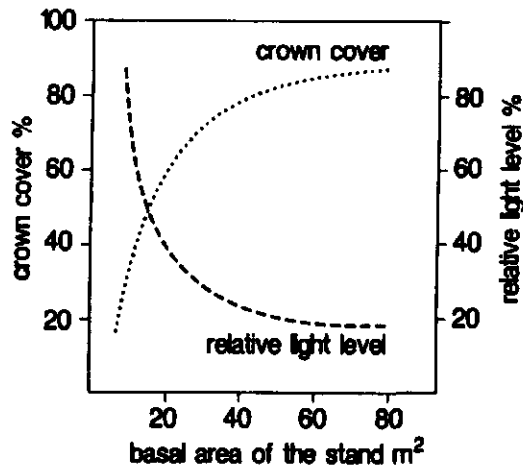
Figure 3.34 a: Crown cover (%) and relative light intensity (%) in relation to stand basal area of a Norway spruce stand in Germany (Bredemeier & Dohrenbusch 1984).
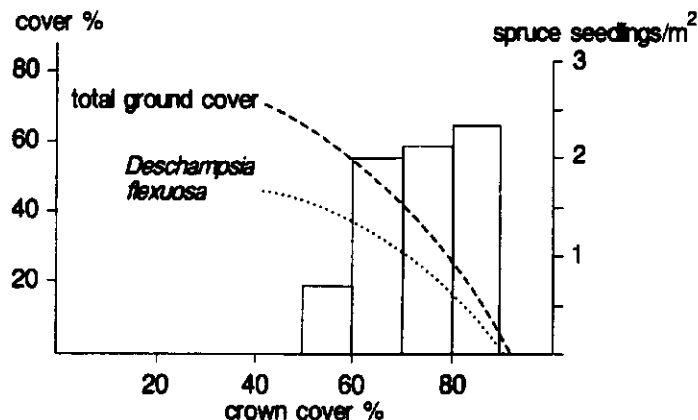
Figure 3.34 b: Degree of coverage of the entire ground vegetation (GVC), as well as D. flexuosa (DC) and concentration of young spruce seedlings in relation to crown cover (CC).

The curves for the ground vegetation and D. flexuosa plotted in Fig. 3.34b. are:

GVC = -0.015 * (CC)^2 + 0.7 * (CC) + 65.5   for 20<CC<90
DC = -0.013 * (CC)^2 + 0.9 * (CC) + 29.0   for 20<CC<90

Kuper (1994) found that Scots pine was unable to regenerate and survive in a dense vegetation of V. myrtillus, V. vitis-idaea and D. flexuosa. In a sowing experiment, 150 scots pine seeds weer sown in 18 untreated quadrats of 0.25m^2. After 6 months, 9 quadrats showed a total of 27 seedlings, of which only 3 seedlings had survived after 2 growing seasons. Those three were located on a spot with mosses and Galium saxatile. From an experiment in which the ground vegetation was clipped, Kuper concludes that Scots pine seedlings do not easily survive under blueberry and that there is a better chance for survival where there is no ground vegetation or where the ground vegetation consists of cowberry. Chances of success among grasses were low.

Out of 250 investigated Scots pine sapling established spontaneously, 21% established in a gap in the ground vegetation, the diameter of which exceeded half of the height of the surrounding dwarf shrubs, 48% on a spot that was dominated by cowberry only and 22% on a spot which was dominated by both bilberry and cowberry. Only 9% grew on a spot which was dominated by bilbery only (Kuper 1994).

Kuper (1994) reports that indigenous oak regeneration under Scots pine is successful as early as 40 to 50 years after germination of the Scots pine stand irrespectively of the ground cover, but only when the browsing by roe deer and red deer is limited or excluded. Beech can be brought in even earlier.

Lorimer et al (1994) found that tall understorey trees (Acer, Ostrya and Tilia higher than 1.5m) and vegetation shorter than 1.5m are a major obstacle to the development of both planted and natural seedlings of Quercus species. In undisturbed control plots, more than 70% of the planted oak seedlings died within five years, and survivors showed a net decrease in height. In plots with the tall understorey vegetation removed, 90% of the planted seedlings survived and average total height increased 50-96%.

The above presented infomation is used in the module to assess germination success response curves in relation to the cover of various herb layer species. See for details on those curves Jorritsma (in prep).

4 DISCUSSION

4.1 Discussion on reliability of results

This report presents functions and parameter values for a dynamic forage supply module of the herb layer of forests and heathland. The module has been parametrized for the Veluwe forest/heathland area in The Netherlands. At this time (Jan 1995), the relations and growth functions are not yet incorporated into the forest development model. Module output can therefore not be presented. At a later stage the complete module documentation (with possible adaptions in the functions as presented here) will be published (Jorritsma in prep). This paragraph discusses both the assumptions made in the forage supply module and the reliability of the results and functions as presented in this report.

The basic assumption underlying the forage supply module is that herb layer species net relative growth rate can be simulated from the light level penetrating through the forest canopy and reaching the forest floor. This major explanatory variable is further adjusted for two site types.
This assumption is supported by a large number of articles that show the significant relevance of the light level that reaches the forest floor (Davison & Forman 1982, Hester et al. 1991a & 1991b, Kellomäki & Väisänen 1991, Lieffers & Stadt 1993, McLaughlin 1978, Miyata 1983, Moore & Vankat 1986, Msika 1993, Qarro & De Montard 1992, Sakura et al. 1985, Väisänen et al. 1977, Whitney & Foster 1988).

However, most of these authors also recognise the importance of the wide variety of other site factors. Herb layer cover and biomass may be influenced by several factors that are determined by the overstorey canopy of a forest. Overstorey canopy reduces the light level that reaches the ground. Both total light and diffuse light will be reduced depending on the tree species, height and tree density in the forest (Verbraak 1991). But, overstorey canopy also reduces the amount of throughfall precipitation. Especcially evergreen tree species are known for the high amount of intercepted rainfall which evaporates directly from the needles. This reduction of the amount of available moisture can hamper the herb layer species. Anderson et al. (1969) found that understorey herb layer under pine forest in Wisconsin is more responsive to differences in throughfall precipitation determined by canopy openings than to difference in light. Soil moisture recharge exerts the major control of the herb layer cover on those sites. Correlations often found between light intensity and herb layer cover percentage may not be causal, especially on drought sensitive soils where moisture supply to herb layer species is expected to be critical.

More generally, overstorey canopy influences the total microclimate under the stand canopy (Msika 1993). Root competition with shrubs and trees is another factor which can reduce the growth of the herb layer species. Extensive tree root systems certainly reduce the amount of available moisture and/or nutrients. Van Dort et al. (1979) found that profound herb

layer cover differences under oak and beech forests in The Netherlands were not explained by differences in light reaching the forest floor. Intensive rooting of beech in the upper soil layers might be too competitive for understorey plants in contrast to the oak stands. Other site factors that determine the herb layer species composition and growth are: nitrogen availability, soil type (its texture, physical and chemical properties), moisture availability, throughfall and physical and chemical characteristics of the litter layer (Ellenberg 1988).

The module only considers the major forage suppliers. Those who are in terms of biomass only minor forage suppliers, were not included. It is recognised here that they may not be available in terms of large amounts of biomass, but that they are often highly preferred by the ungulate and are usually important nutrient suppliers (e.g. Festuca ovina and Galium saxatile).

The module also assumes that there is no effect of grazing on the relative growth rate. Any degree of grazing will as such result in the same reduction of the level of absolute regrowth (Tolvanen et al. 1992 & 1993a & 1993b).

Canoco results
The Canonical Correspondence Analysis showed that almost 14% of the variance in the data set could be expalined by the available site factors. This is a reasonable result that indicates that the investigated site factors can be used to explain the species adundancies. Somewhat remarkable was the high significance of the basal area of other deciduous tree species (mainly birch). Birch is apparantly associated with a very distinct forest and site type resulting in a separate group of species abundancies in comparison to the rest. The "Dorschkamp" forest type appeared to be a good explanatory site factor for the species abundancies, as can be expected. Spruce and Douglas-fir basal area apparantly also have a distinct effect on the vegetation.

Species composition
Based on the large data set of 234 vegetation recordings on the Veluwe area (appr. 100.000 ha), it was possible to assess satisfactory standard herb layer species compositions for the two site types and varying tree species. Especially table 3.5. will be used to assess the initial circumstances tables. This table was assessed based on usually 3 to 5 vegetation recordings for the given combinations. The results must be seen as standard species composition, since considerable differences could occur under comparable site and forest types. In such case, the most common composition was chosen. The weighed frequencies tables (3.2. and 3.3) will be used as input to calculate germination chances.

Basal area-herb layer cover
The stand basal area and herb layer cover relations that were assessed from the available data bases usually showed limited explanatory value. Although various stratifications according to tree species and forest types were made, the presented ones were found to be the best. Other stratifications gave no relation or resulted in too few data. The presented graphs

(Figures 3.1 to 3.4.) will be used as representative for a larger group of forest types. They indicate that the herb layer cover is to some extent determined by the stand basal area, which supports the choice to use basal area as an indirect measure for the light level. However, other site factors (e.g. soil type, nitrogen availability, management, soil moisture and coincidence) cause these relations to be weak. Since these relations are only used for the initial situation in combination with table 3.5, (net growth determines the expansion in cover), errors in these relations may not cause large errors in the long-term outcome.

Annual course of growth rates

The annual growth curves were assessed based on various sources in literature that presented annual course of total aboveground biomass of the species, usually in the open field. The curves (Fig 3.6 & 3.7) present the net growth of the species in grams per kilogram total aboveground biomass per day (Relative Growth Rate). The sources that were used preferably showed the annual course of total aboveground biomass under optimal field circumstances. Those site circumstances were not always reported, but usually the recordings were made in the open field i.e. full light. The maximum values within the curves were kept within the framework of seedling RGR data available for experimental conditions.

Light response curves

Light response curves were assessed based on various sources in literature concerning growth of the species in relation to available light (Kellomäki et al. 1977b, Väisänen et al. 1977, Kellomäki & Väisänen 1993). These indications and general ecological knowledge gathered in e.g. Ellenberg et al. (1991) gave good indications whether a species should be regarded as shadow tolerant or shadow intolerant. In accordance with the methods used in Urban (1990) i.e. the ZELIG model and Levine et al. (1993), the curves were established. It is acknowledged here that the exact bend of the curve is not known and cannot be assessed from actual data at this moment.

Peak standing crop

Data to determine peak standing crop as a ceiling of achievable biomass, were gathered in a selectively sampling experiment. Based on relations found in literature concerning height and biomass, it was assumed that the peak standing crop could be assessed at that specific spot in the vegetation patch, where the highest cover and height were achieved. The biomass sampling experiment data were assessed in a short time period (end June-beginning July) with the aim to cover the maximum summer biomass. However, it remains uncertain whether the summer maximum biomass is really sampled and for each species this moment varies slightly. Furthermore, these data rely on the weather circumstances of the year in which the sampling was carried out. Winter '93/'94 was mild and very wet with a short cold period in February. Spring was wet and summer was extremely hot. On these dry sites, the abundant winter and spring rains will probably have stimulated the growth, whereas the drought of the summer must have had its effect on growth. It is difficult to determine how representative the sampled biomasses of '94 were for the herb layer. The cover-biomass

relations at the stand level are in accordance with data found in literature (see Appendix A).

The results in Figures 3.9 to 3.15 do not always present a clear trend in peak standing crop in relation to stand basal area due to the limited number of data for each combination of site and tree species. Trends for wavy hair-grass, heather, purple moor-grass, blueberry and cowberry and absolute maxima for all herb layer species were distilled.

Height-biomass relations
The height-biomass relations at the sub-plot level are good for A. capillaris, C. vulgaris, high D. flexuosa, P. aquilinum, V. myrtillus and V. vitis-idaea. They are weak for low D. flexuosa and M. caerulea. The presented functions gave the highest explanatory values. The limited number of data probably causes the limited explanatory value for purple moor-grass function. Surprisingly, a clear distinction could be made for D. flexuosa under 30 cm and above 30 cm height. This coincides with respectively infertile and fertile D. flexuosa. This clear distinction in two height classes is mainly caused by the method of recording the height. Because the top height of the plant was recorded, including the plant's spike, these two height classes coinciding with infertile and fertile wavy hair-grass originated from the data. The presented relations show a linear relation between height and biomass for the investigated range in height except for bracken. The results should not be extrapolated far beyond the range of heights that was covered by the data. The presented results differ from the ones given by Wallis de Vries (1980) in that most of his relations curve of at a certain amount of biomass. This can be caused by the fact that he investigated plants in the open field and by the fact that he used a light disc which he lowered on top of the vegetation to measure the height. However, when applied to wavy hair-grass, the method with the light disc did not seem to give reliable results. It was therefore decided to measure the top height of all plant species.

Cover-biomass relations at two levels
By using a selective sampling method, the number of samples per stand could be kept limited. The stratified sampling method according to average height, allowed an extrapolation of the data to the stand level. The upscaled results are in accordance with other herb layer biomass data from Oeffelt and Oostveen (1985), Wallis de Vries (1989), Jongman & Ruyter (1976), Aerts (1994) and Van Wieren (1988) for Dutch circumstances and with Kellomäki 1974 & 1975 for boreal circumstances.

The cover-biomass relations at the sample plot level give satisfactory results. The results cannot directly be extrapolated to the stand level unless the given cover is representative for the whole stand. Stratification according to height classes did not result in clear stratification of the data. Upscaling was done taking into account the cover in the whole stand. E.g. linear upscaling of the sub-plot-level biomass of M. caerulea to the stand level, would give a maximum total aboveground biomass of approximately 7000 kg ha^{-1}. But figure 3.30 shows that when the cover at the stand level is taken into account, the maximum biomass amounts to only 1000 kg ha^{-1}.

The biomass-cover relations at the stand level can generally be described as good for four species, although quite some residual variance remained. The correlations were good for D. flexuosa, M. caerulea, V. myrtillus and V. vitis-idaea. Too few data were gathered for the other species.

A. capillaris occured and was sampled in two stands. It occurs however more frequent in forest edges and on forest roads. The recorded biomass amounted only a few kg ha^{-1} in stands with basal areas of in between 25 and 30 m^{2}ha^{-1}. Open field measurements presented by Wallis de Vries (1989) gave dry matter data for summer grazed vegetation of 950 and 1800 kg ha^{-1} and for summer long (ungrazed) vegetation of 3250 and 5150 kg ha^{-1}.

C. vulgaris was only recorded and sampled in five stands. In three of them, heather only had a very small cover, resulting in total aboveground biomass figures of only a few kg ha^{-1}. However, a large set of open field biomass measurements of C. vulgaris exists, both valid for the United Kingdom (Chapman et al. 1975, Miller 1979) and for The Netherlands (Jongman & Ruyter 1976, Aerts 1989, Prins et al. 1991, Berendse 1990, Aerts 1994, Diemont 1994, Diemont and Oude Voshaar 1994). 25 years after burning and sod cutting, the dwarf shrub can reach total aboveground biomasses of 14000 kg ha^{-1} on Betulo-Quercetum sites with peak annual production values of 2500 kg ha^{-1} at an age of 9 years (Diemont & Oude Voshaar 1994).

Indications for higher productivity on Fago-Quercetum sites were found in Diemont (1994). Recovery of productivity from sod cutting was found to start again within a decade on a Fago-Quercetum site, while it was still reduced to 1-2 ton ha^{-1} on the Betulo-Quercetum site after 10 years. Data which clearly show higher total aboveground biomass and production on Fago-Quercetum sites, were not found. Satisfying curves, describing the build-up of total aboveground biomass and the annual rate of increment of heather in The Netherlands are given in Figure 3.5. This curve was chosen based on the wide variety of data available. A maximum total aboveground biomass of 12500 kg ha^{-1} seemed reasonable for heathlands which are not affected by excessive grass growth.

The presented results indicate that the total aboveground dry matter of D. flexuosa can reach a total aboveground biomass of almost 2500 kg d.m. ha^{-1}. Oeffelt & Oostveen (1985) found under open field situations an average summer maximum above-ground dry matter of 4056 kg ha^{-1} with the maximum at 7820 kg ha^{-1} and the minimum at 1980 kg ha^{-1}.

Results from this study gave total biomass values for M. caerulea that were all under 1000 kg ha^{-1}. Aerts (1994) presented an aboveground summer maximum total biomass of M. caerulea in an open field of 650 g m^{-2} in September, resulting in 6500 kg ha^{-1}, when this sample plot is assumed to be representative for a larger area. Wallis de Vries (1989) carried out repeated sampling in two open field Molinia sites. Summer maximum total aboveground dry matter amounted (upscaled to one hectare) 3836 and 3916 kg

ha⁻¹ both reached in August. It is not clear what caused this big difference between these two studies.

Maximum aboveground biomass of P. aquilinum can range from 10000 kg ha⁻¹ in an open field situation to 410 kg ha⁻¹ in a woodland floor community in the United Kingdom (Al-Mufti et al. 1977). The number of data obtained during the biomass sampling experiment, was too limited to fit a model. Den Ouden (pers. comm., WAU) mentioned that he found total aboveground biomass figures on the Veluwe ranging from 3150 kg ha⁻¹ in an "open" larch stand to 1000 kg ha⁻¹ in a "dark" oak forest belonging to the forest type of crooked deciduous trees. Based on the relation between height and biomass and the fact that bracken seldomly reaches heights of more than 1.5 m under forest in The Netherlands, it is assumed that the maximum total aboveground biomass is approximately 6000 kg ha⁻¹, assuming 100% cover.

Additional data concerning biomass of V. myrtillus under forest for Dutch circumstances were found in Jongman & Ruyter (1976).

Table 4.1 Total aboveground biomass of V. myrtillus sampled under varying forest types and circumstances on 't Loo, The Netherlands. Values in kg ha⁻¹ dry matter (Jongman & Ruyter 1976).

	spring	autumn	ungrazed	simulated grazing
Scots pine, open	1905	2355	5427	4767
oak staddles	1440	1355	1788	-
oak staddles	1295	2138	2725	4815
Scots pine with oak	3700	5223	6800	9645
Scots pine with oak and birch	1463	1723	2920	4075

*: stand densities were not presented

Jongman and Ruyter's (1976) data recorded in autumn on Fago-Quercetum sites, are comparable to the data presented in this study, where total aboveground biomass of V. myrtillus reached 1500 to 2000 kg ha⁻¹. Only the Scots pine-oak site has a much higher total aboveground biomass of V. myrtillus. According to them, total aboveground biomass increased on all sites, when grazing was prevented. In simulations of grazing, total biomass increased again compared to the ungrazed plots on three out of five sites.

All of the stands where V. vitis-idaea occured had a basal area of more than 20 m²ha⁻¹. The highest total aboveground biomass of approximately 4000 kg ha⁻¹ was found at a stand basal area of 33 m² ha⁻¹.

Assessment of edible part

Determination of the edible part of total aboveground biomass depends strongly on the ungulate species. The presented percentages were usually assessed based on distinction that was made between green and non-green parts during biomass sampling experiments. Although arbitrary, it was assumed that all the green parts of the plant could be regarded as edible to red deer, cattle and pony. An extra reduction factor will be laid upon the module to take into account the edible part for roe deer.

4.2 Comparison with existing models

4.2.1 Overstorey - understorey cover relations in literature

Various functions that describe the herb layer biomass or productivity from overstorey characteristics are available in literature. Support was found to assume that basal area of the stand can be used as an indirect measure of the light level reaching the forest floor in Bredemeier & Dohrenbusch (1984), Lieffers & Stadt (1993). Bredemeier & Dohrenbusch (1984) present a negative exponential relation between the basal area of a Norway spruce stand and the relative light level reaching the herb layer. Lieffers and Stadt (1994) found that light transmittance to the herb layer was positively correlated to hardwood basal area and negatively correlated to softwood basal area! McLaughlin (1978) studied basal area and three measures of canopy cover as predictors of both throughfall and light in ponderosa pine forest. Overhead canopy accounted for the largest proportion of the variance in throughfall. The amount of open canopy accounted for the largest proportion of variance in light. Basal area appeared to be the poorest predictor, although it was for almost 80% correlated to canopy cover. Bojorquez Tapia et al. (1990) present a review of regression models of understorey-overstorey relations for ponderosa pine stands in Arizona. Three log-linear models in which the basal area of the stand was the predictive variable, performed very well.

From natural regeneration trial tests in The Netherlands, some information on overstorey-understorey relations is available from Oosterbaan and Van Hees (1989, 1991). In one thinning experiment carried out in a beech-sessile oak forest, the control, light thinning and heavy thinning resulted in basal areas of resp. 23.0, 17.4 and 12.5 m^2ha^{-1} (crown cover of resp. 90-100, 70, 40-50%). Among the species of which the cover increased strongly under decreasing crown cover are: V. myrtillus, C. vulgaris and D. flexuosa. V. myrtillus however did not occur in plots where the crown cover was 90% or more and C. vulgaris occured only at places where the crown cover was less than 70%, with an optimum in plots with 40% crown cover.

In another natural regeneration experiment in a beech stand near Ede, basal areas were reduced to 25.6 (=control), 22.6, 16.1 and 0 m^2ha^{-1}. This resulted in light intensities (photosynthetically active radiation) of resp. 50, 50, 400 and 750 μmol $m^{-2}s^{-1}$ measured in July on a cloudless day around noon. Six years after establishment of the experiment, the ground vege-

tation coverages were resp. 25, 40, 90 and 100%. Of the relevant species, D. flexuosa showed the most significant reaction and increased from 1% in the clearcut plot in 1984 to up to 5-12% in the clearcut plot in 1988. The strongest reaction however gave Rubus fruticosus that increased from 1% in all plots in 1984 to 75% in the heavy thinning and clearcut plots in 1989.

Bojorquez-Tapia et al. (1990) investigated forest overstorey-herbage production relation in Arizona ponderosa pine forests which are managed for both cattle and timber production. Basal area of the stand appeared to be a good predictive variable.

Dodd et al. (1972) found that herbage productivity can be estimated from estimates of tree crown cover in lodgepole pine and Douglas-fir stands. The output of the model was very well in accordance with the measurements made of the herbage production. Ford and Newbould found that during a coppice cycle of Castane sativa, the ground vegetation production decreased logarithmically in relation to increase in total tree amount. Tree variables as total biomas, basal area and leaf biomass all explained the ground vegetation production.

Validity of the assumption to use basal area as an indirect measure of the light level reaching the forest floor was also found in the Woodlands data set published by DeAngelis et al. (1981).
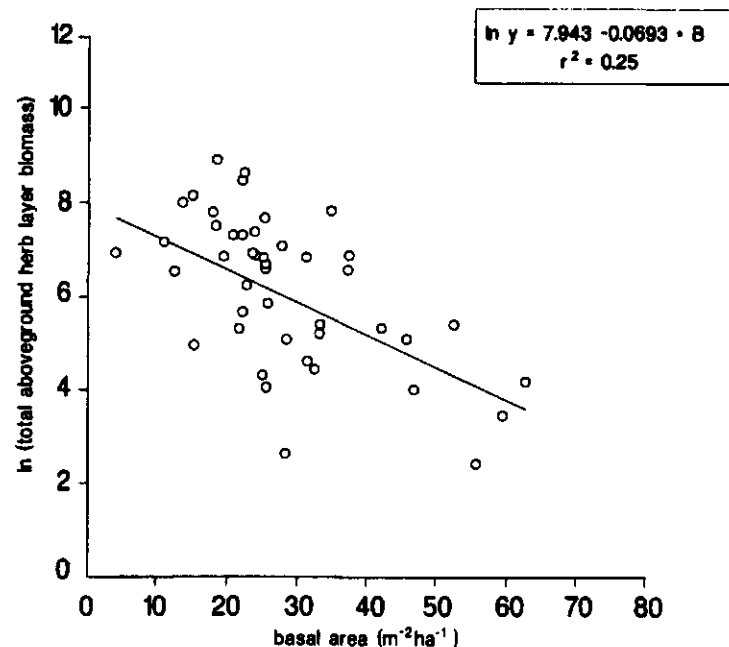
Figure 4.1   Effect of stand basal area on herb layer biomass in forests of the temperate zone. Data obtained from the "Woodlands data set", published by DeAngelis et al. 1981. Y is the biomass of the herb layer (kg ha⁻¹ d.m.) and BA is the basal area of the stand (m² ha⁻¹).

Sakura et al. (1985) showed that under Japanese larch plantations in N.E. Scotland, D. flexuosa was the most persistent. It had the greatest capacity to persist both under dense stands, and to become dominant in those of lesser density. The number, cover and flowering of herb layer species increased as stand density decreased.

The above given list of publications indicates that often some relation between stand density and herb layer cover is found in the way that increasing stand density reduces herb layer cover, biomass and/or production. Varying characteristics for the stand are used: crown cover, basal area, number of stems, amount of open canopy and precipitation throughfall. The correlations with the herb layer are also found for a variety of herb layer parameters as cover, biomass, productivity, height and spring biomass. The causality of the relations is often poorly studied and understood.

It can be concluded that although the causal relation between overstorey and understorey is sometimes questioned, basal area of the stand can be used as an indirect measure to estimate the herb layer biomass or productivity. Non-linear and log-linear models seem to give the best results.

4.2.2 Comparison with existing models

Aim of this paragraph is to give an overview of existing herb layer simulation models which simulate the herb layer species composition and growth/-biomass dynamically in relation to the forest dynamics. Both models which showed similar and different approaches were included.

A description of the selected models is given in Table 4.2. The selection of models is certainly not complete. Many more, especially in the plant physiological field exist. Models that were comparable concerning goal or approach with the present module were selected.

Table 4.2 Overview of simulation models which simulate the herb layer species composition and growth/biomass in relation to the overstorey characteristics.

	Kellomäki & Väisänen (1991)	Armstrong et al. (in press)	Qarro & De Montard (1992)	Msika (1993)	Pakeman et al. (19-94)	Jorritsma (in prep)
Aim	Dynamic simulation of the succession of the herb layer in relation to the stand	To improve sheep grazing in the UK hill areas, a model that predicts seasonal biomass and digestibility was made	To assess a model which explains dry matter production of the herb layer in relation to climate, soil and tree cover	To model changes in forage supply in relation to forest stand growth and levels of clearing	A physiological model of the growth of bracken to predict the effects of control measures	To develop a dynamic forage supplying module in relation to stand characteristics
Approach	Dynamic approach; abundance of grasses, herbs, mosses and lichens is modified by the availability of light and nitrogen in the forest floor, which is controlled by gap dynamics	Non-dynamic; production is calculated on the basis of a set of functions which give the relation between NPP and temperature zone, altitude, past and future fertiliser rates, summer rainfall and soil water capacity.	Non dynamic; herb layer production is related through multiple regression to precipitation, soil nutrients, soil physical characteristics, seasonal radiative energy, tree cover and number of leguminous plants	Dynamic; the predictive model relates canopy cover and meso-climatic factors to forage supply. It includes the moisture balance of the herb layer and active periods of the herb layer species. Species composition changes can not occur.	Mechanistic physiological model which describes the yearly cycle based on various processes.	Dynamic; cover and biomass of herb layer species is modified by the site and availability of light at the forest floor, which is controlled by gap dynamics
Validity	Boreal forests; parametrized for Myrtillus site, Finland	Hill area in the UK; heathland, reseeded pasture and indigenous pastures	Middle Atlas and central Plateau; oak and cedar forests	Parametrized for oak coppice and Austrian black pine in the Pre-alpes in France	Bracken in temperate forests; parametrized for the UK	Temperate forests (parametrized for The Netherlands
Scale	100 m²	1 ha	1 ha	100 ha	1 m²	1 ha

Table 4.2   Continue 1

			rough pastures		Pteridium aquilinum	
Herb layer species	Many species belonging to grasses, herbs, dwarf shrubs, mosses and lichens	Calluna, Lolium perenne, Trifolium repens, Festuca, Agrostis, Molinia, Nardus.		Sylvopastural sites, many species e.g. Carex spp., Festuca spp., Galium spp., Poa spp.		Agrostis capillaris, Calluna vulgaris, Deschampsia flexuosa, Molinia caerulea, Pteridium aquilinum, Vaccinium myrtillus, V. vitis-idaea
Site factors	light nitrogen	Temperature zone, altitude, past and future fertiliser rates, past management, summer rainfall and soil water capacity	precipitation, soil nutrients, soil physical characteristics, seasonal radiative energy, tree cover and number of leguminous plants	tree cover, mesoclimate, herb layer moisture balance, radiative energy	degree days, light level, frost, control measures, soil temperature,	light level reaching the forest floor and to a lesser degree site quality
Aggregation level for vegetation	Species are grouped as pioneer, intermediate and climax.	species	communities	communities	species	species
No. of plant compartments	1	1	1	1	3; frond biomass, rhizome tissue biomass, rhizome carbohydrate	1

Table 4.2   Continue 2

Variables	biomass, potential growth, growth multiplier, death rate	monthly growth, (NPP), senescence, litterfall, seasonal biomass digestibility to sheep, sward height	Net Primary Production	Net Primary Production, total aboveground biomass, timber production	rhizome respiration, tissue senescence, photosynthesis, fluxes between compartments	Total above-ground biomass, relative growth rate, peak standing crop
Simulation period (yr)	500	1	1	150	30	100
Formulation -of plant growth	Net Primary Production minus death rate, the potential growth (g m⁻² yr⁻¹) is limited by a growth multiplier.	Net seasonal dry matter production minus rates of senescence and litter fall. The effect of grazing on production is not yet included.	Functions describing the relation between tree cover and Net primary Production of the herb layer.	Net Primary Production. Effect of grazing on regrowth not included.	Gross Primary Production, respiration, Net Primary Production, senescence.	Monthly net relative growth as a result of growth rate in relation to the light level. The peak standing crop serves as an asymptotic level. The relative growth level is not affected by grazing.
Output	Biomass per species and species group (kg 100 m⁻²)	Annual and monthly dry matter production, total biomass, digestibility to sheep, sward height	Abundance of leguminous plants, Net Primary Production, relative light level	Total available dry matter, timber production	Total aboveground biomass, frond biomass, rhizome tissue biomass, rhizome carbohydrate	Seasonal forage supply, cover, height, total aboveground biomass

Of the dynamic forest gap models available (e.g. ZELIG, JABOWA, FOREST), not many include the dynamics of the herb layer. They are usually restricted to the tree and shrub layers. In the short review of models as presented above, only the model published by Kellomäki & Väisänen (1991) and the one under preparation by Jorritsma (this study) show an approach of a dynamic simulation model for the herb layer in a forest gap model. The other models included in Table 4.2, are a non-dynamic approach for hill pastures (Armstrong et al. in press), a non-dynamic approach for the herb layer under forest (Qarro & De Montard 1992), a semi-dynamic simulation of the herb layer biomass in relation to tree cover and management (Msika 1993) and a mechanistic plant physiological model for bracken (Pakeman et al. 1994).

From the above presented reviews, it appears that the light level (determined by tree cover) is often considered an important site factor determining the growth and total aboveground biomass of the herb layer species. All models except the one from Armstrong et al. consider the light level. The model from Kellomäki & Väisänen (1991) is closest to the present study. The herb layer biomass is simulated dynamically in relation to the light level. Their potential growth being limited by two growth multipliers which are laid upon on the basis of general ecological knowledge concerning the effect of light and nitrogen. The present study simulates monthly growth on the basis of a combination of potential relative growth rates and growth reduction curves in relation to the light level. Growth can furthermore be curved off by the peak standing crop that can be attained on the specific site.

Completely different approaches from the present study are published by Armstrong et al. (in press) and Pakeman et al. (1994). The first combines a set of functional relations between productivity and site factors and does not include the effect of tree cover. This in contrast to the functional relations presented by Qarro & De Montard (1992). The model from Pakeman et al. (1994) is a plant physiological model and was only included because it deals with a species of relevance for the present study.

The model published by Msika (1993) is less dynamic in the tree stratum and the species composition of the herb layer, but includes many more environmental variables. Tree cover determines a wide set of mesoclimatic factors in their model. Site factors explaining the production of phytomass are:
- cumulative radiation;
- cumulative daily maximum temperatures;
- maximum temperatures divided by the square root of the radiation;
- number of active days;
- evapotranspiration;
- available soil moisture.

With this set of site factors he is able to simulate the development of the production of the herb layer in the course of stand development of black pine (Pinus nigra var. nigra) and dawny oak (Quercus pubescens). The present study which assumes that herb layer development can be simulated

mainly by the light level could be expanded with some of these other site factors in forthcoming studies.

4.3 Applicability in practice

The presented functions can also be used in a practical method to estimate the forage supply of a given area of forest on dry sandy soils in The Netherlands. With simple data as height and cover of the herb layer species it is possible to assess an estimate of the forage supply. One has to keep in mind that forage supply is determined by various menu components (e.g. also overhanging branches, roots and mast) from various species. This practical method only determines the forage supply of the seven most important herbaceous species of the herb layer. Both summer maximum and winter minimum can be determined with this method. It is assumed that a fast change in vegetation cover or species composition is undesirable.

The principle is as follows: amounts of total aboveground dry matter can be assessed with the functions as given in paragraph 3.5.2. from data as height and cover of each herb layer species per stand in the summer. From annual curves of aboveground dry matter, the winterminimum can be calculated. With the reduction factors for the edible part as given in paragraph 3.5.3, the edible amount of biomass can be calculated. If height and cover data are not available, the method foresees in standard descriptions of the herb layer under various types of forest. Furthermore, the method assumes that at the maximum 10% of the total aboveground biomass can be eaten to allow for the necessary regrowth in the next year. This practical method also foresees in a table with daily required amounts of dry matter of red deer, roe deer, cattle and ponies. At this time (Jan 1995) this method is being developed and it will be published in a seperate report.

4.4 Priorities for future data collection

Major uncertainties in parametrizing the dynamic module of the herb layer development appeared to be representative annual growth curves of the relative growth rate assessed under optimal field circumstances and assessment of good light response curves. Furthermore, the relative importance of each site factor and the relation between basal area and light level on the forest floor remained unclear. Initial species composition, initial herb layer cover, peak standing crop and translation functions were assessed satisfactory.

A wide variety of data of the herb layer does exist, but they usually consist of once-only or twice-only executed biomass sampling experiments. Representative annual curves of the total aboveground biomass (or growth rate) are scarce, and site characteristics are often not available. Exceptions are heather and purple moor-grass that have been intensively studies during the 1980's acidification reserach programmes. Seedling relative growth rates under optimal experimental conditions are usually available, but for improve-

ment of the module, relative growth rates have to be assessed under varying light levels in field circumstances. The module could also be improved by incorporating more site factors.

5 SAMENVATTING EN TOEPASBAARHEID IN DE PRAKTIJK

Als onderdeel van het Nationaal Bosbegrazingsonderzoek wordt gewerkt aan het ontwikkelen van een bosontwikkelingsmodel welk de effecten van diverse maten van begrazing kan simuleren. Het bosontwikkelingsmodel is geldig voor bos op droge, arme zandgronden. Onderdeel van dit bosontwikkelingsmodel is de voedselaanbodmodule. Het voedselaanbod voor grote grazers in bossen wordt bepaald door een groot aantal menu-componenten van een groot aantal plantesoorten. De menu-componenten zijn: niet-houtige kruidlaagsoorten, houtige kruidlaagsoorten (zaailingen), struiken en jonge bomen in de struiklaag, afhangende takken, mast en wortels. Dit rapport beschouwt de zeven belangrijkste niet-houtige kruidlaagsoorten en geeft de benodigde relaties om de voedselaanbodmodule te kunnen bouwen. In een ander rapport (Van Hees in prep) wordt het voedselaanbod van de zaailingen en de struiken en jonge bomen van de struiklaag beschreven. Het derde rapport in deze serie beschrijft de voedselaanbodmodule, en geeft model resultaten (Jorritsma in prep).

De kruidlaagbiomassa en soortensamenstelling worden in de voedsel-aanbodmodule van de kruidlaag op een dynamische wijze gesimuleerd. De module begint met een opgelegde kruidlaagsoortensamenstelling en biomassa welke horen bij het uitgangsbostype en welke zijn verkregen uit bestaande gegevens. De groei van de 7 relevante kruidlaagsoorten wordt vervolgens berekend per maand en per plot van 400 m². De groei wordt berekend in termen van g kg⁻¹ staande biomassa. Hierbij wordt gebruik gemaakt van gegevens over groeisnelheden in relatie tot het lichtniveau en van maximaal te bereiken staande biomassa onder de gegeven omstandigheden.

In dit deelrapport worden de functies en parameterwaarden die nodig zijn voor het module gepresenteerd. Deze bestaan uit:
- Initiële biomassa van de relevante kruidlaagsoorten onder diverse omstandigheden;
- groeisnelheden in relatie tot het lichtniveau;
- maximaal te bereiken biomassa onder diverse omstandigheden;
- functies die een vertaling mogelijk maken van totale biomassa naar hoogte en bedekking en van totale biomassa naar eetbare biomassa.

De weergegeven relaties zijn behalve in de module goed te gebruiken voor het bepalen van het voedselaanbod in een praktijksituatie. Op dit moment (jan 1995) wordt gewerkt aan het verder uitwerken van deze praktijkmethode. Met eenvoudig te bepalen gegevens als hoogte en bedekking van de kruidlaagsoorten per opstand is het mogelijk voor een beheerder om het voedselaanbod te bepalen tijdens het zomermaximum, maar ook tijdens het winterminimum. De methode is vrij grof en moet gezien worden als een indicatie van de draagkracht van een terrein. We gaan er daarbij van uit dat sterke aantasting of verandering van de vegetatie ongewenst is.

Het principe van de methode is als volgt (zie ook Wallis de Vries 1989, Van der Grift & Huijser 1991 en Jongman & Ruyter 1976): met bedekking en

hoogte gegevens per kruidlaagsoort per opstand, zijn uit de gegeven relaties staande biomassa's te bepalen. Deze staande biomassa's moeten dan vermenigvuldigd worden met een reductiefactor waarmee het eetbare deel verkregen wordt. Mochten deze bedekking en hoogtegegevens niet aanwezig zijn, dan voorziet de methode in een standaardsamenstelling en biomassa van de kruidlaag voor diverse bostypen. Om het winterminimum te verkrijgen, zijn seizoenscurven van staande biomassa en eetbaar deel opgenomen. Verder gaat de methode er van uit dat slechts 10% van de staande biomassa opgevreten mag worden, om het volgende jaar weer een gelijke hergroei te krijgen. De methode geeft verder een tabel met de dagelijkse behoefte aan droge stof van ree, edelhert, paard en ponie.

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APPENDICES

A List of definitions
B Peak standing crop data assessed in the biomass sampling experiment
C CANOCO output

Appendix A: List of definitions

Aboveground biomass: the total dry organic matter of a living organism that is present above the surface of the soil and in case of a forest site, above the top of the litter layer.

Basal area: Sum of all stem surfaces of a stand, expressed in m^2 ha^{-1}.

Betulo-Quercetum: a type of Potential Natural Vegetation. An oak forest with some co-dominant birches that may develop on dry poor sandy soils in The Netherlands.

Biomass: total dry organic matter or stored energy content of living orga nisms that is present at a specific time in a defined unit (community, ecosystem, crop etc.) of the earth's surface.

"Dorschkamp" forest type: a forest type classification developed primarily for The Netherlands that discriminates on the land-use/soil type at the time of afforestation, the period in which the afforestation was carried out and on the primary goal of the afforestation. E.g. Estate forest established on wet heathland between 1800 and 1850.

Fago-Quercetum: a type of Potential Natural Vegetation. A beech forest with some co-dominant oak trees that may develop on dry loamy sandy soils in The Netherlands.

Field layer: identical to herb layer

Forest floor: (identical to litter layer) organic matter on top of the mineral soil that has accumulated there because the rate of litterfall exceeds the rate of decomposition. The thickness can vary from 1 cm up to 50 cm.

Growth: equivalent to Net Primary Production. A vague term, better to specify growth as net growth, net primary production or net ecosystem production.

Herb layer: a horizontal layer in a forest that streches from the top of the litter layer to the top of the dwarf shrubs and grasses, usually less than 50 cm in height. Grasses, herbs and dwarf shrubs occupy this layer.

Living biomass: not an official term, identical to biomass

Model: in the present study, the term model is used for the overall forest development model that consists of a forest module, a diet choice module and a forage supply module. However, model can also refer to a standardisation of a certain process or species composition.

Module: in the present study the term module is used for the forage supply module that is part of the forest development model.

Net growth: the net increase or decrease in biomass of an organism (in the present study: a green plant or a herb layer species on a specified area) between two points in time. This is the result of the total production of biomass minus losses as litterfall or grazing. Identical to net growth rate

Net primary Production: the part of the gross primary production that remains stored in the producer organism (primarily green plants) after deducting the amount used during the process of respiration.

Net Relative Growth Rate (NRGR): a way to express the net growth rate in relation to the amount of total aboveground biomass. This includes the net increase or decrease in biomass of the plant. The unit is g kg^{-1} d^{-1}.

Overstorey: the top layer in a forest, that is formed by the canopy of the trees.

Production: a vague term, better to speak of net primary production or net growth rate.

Relative Growth Rate (RGR): a way to express the growth rate in relation to the amount of total aboveground biomass. The unit is g kg^{-1} d^{-1}. This includes the net increase or decrease in biomass of the plant plus all losses.

Site: the environment in which (in this case) a plant germinates, lives and dies.

Site factor: the environment in which a plant lives, consists of many components (factors) that determine the success of a plant. Examples are: soil type, soil moisture, light (total and diffuse), litter layer etc.

Understorey: a rather vague term that is sometimes used for the herb layer alone and sometimes for all the layers under the overstorey canopy. In the present study, this term was used to specify the herb layer alone.

Appendix B Peak standing crop data of seven herb layer species assessed in the biomass sampling experiment.

Betulo-Quercetum

Dominant tree species	basal area (m² ha⁻¹)	Peak standing crop (g 0.1m⁻²)						
		A. capillaris	C. vulgaris	D. flexuosa	M. caerulea	P. aquilinum	V. myrtillus	V. vitis-idaea
Scots pine	3		228.5	11.0			67.8	
	5			4.3			175.0	66.1
	15			31.4				
	15		63.0	18.0	111.9		176.7	
	16			20.0				
	17			21.3				
	18			24.8				
	21		35.5	24.5				
	21			11.9			90.5	24.5
	22			11.3			63.7	
	23			22.0				
	24		153.1	4.2			78.5	44.3
	26			20.0			130.2	11.9
	27			12.1			49.8	
	28	10.0	3.2	10.0				
	34			34.4			137.7	112.9
	40			11.1			83.6	
	45			9.0			145.3	18.1
oak	15			12.8			84.4	
	18			4.1			64.3	
	22			15.1			97.8	
	24			7.0		69.3	57.6	
	24			6.6			37.1	
	26			9.8			50.0	
Douglas-fir	7			3.3	29.0		42.9	
beech	12			5.7			1.4	
	18						3.7	
	30			1.8				

Appendix B continued

Fago-Quercetum				Peak standing crop (g 0.1m⁻²)					
Dominant tree species	basal area (m² ha⁻¹)	A. capillaris	C. vulgaris	D. flexuosa	M. caerulea	P. aquilinum	V. myrtillus	V. vitis-idaea
Scots pine	17			14.0			70.3	
Douglas-fir	18			6.6			55.3	
	27			0.9				
	29			5.4			34.3	
	36			3.2			10.0	
	38			9.5				
	41			10.9			92.4	
	47			7.7				
Japanese larch	21			14.5	70.0			
	29		26.5	13.2				
	35			10.9			30.1	
oak	16			6.1				
	27			12.0	60.6			
	32		4.1					
	37			1.8	20.5		43.0	
beech	13	1.5		0.6				
	25	0.6						
	29			7.6				
birch	19				34.8	215.3	143.6	

Appendix C. CANOCO output

Program CANOCO Version 3.11 November 1990 - written by Cajo J.F. Ter Braak
Copyright (c) 1988-1990 Agricultural Mathematics Group DLO
Box 100, 6700 AC Wageningen, The Netherlands.
CANOCO performs (partial) (detrended) (canonical) correspondence analysis,
principal components analysis and redundancy analysis.
CANOCO is an extension of Cornell Ecology program DECORANA (Hill,19-79)

*** Type of analysis ***
Model   Gradient analysis
               indirect   direct   hybrid
linear   1 = PCA   2 = RDA   3
unimodal   4 = CA   5 = CCA   6
    ,,   7 = DCA   8 = DCCA   9
               10 = non-standard analysis
Type analysis number
Answer = 5

*** Data files ***
Species data   : veg1.cnd
Environmental data : omgzbom1.cnd
Number of samples   216
Number of species   144
Number of occurrences   1987

Total inertia in species data =
Sum of all eigenvalues of CA =   10.11426

**** Start of forward selection of variables ****

N	Name	Extra fit
5	JL	0.03
3	ZD	0.03
12	DD	0.05
8	AE	0.06
9	BU	0.09
16	S	0.10
2	GD	0.11
4	DG	0.12
6	PS	0.12
7	EI	0.13
14	PN	0.18
13	DK	0.23
11	OL	0.33

Environmental variable   11 tested

*** Unrestricted permutation ***
Seeds: 23239   945
Number of permutations =   99

P-value 0.010 (variable   11; F-ratio =   6.39; number of permutations = 99)
Environmental variable   11 added to model
Variance explained by the variables selected: 0.33
"   "   "   all variables   :   1.37

Environmental variable   13 tested
P-value 0.010 (variable   13; F-ratio =   4.18; number of permutations =   99)
Environmental variable   13 added to model
Variance explained by the variables selected: 0.54
"   "   "   all variables   :   1.37

P-value 0.020 (variable   4; F-ratio =   2.46; number of permutations =   99)
Environmental variable   4 added to model
Variance explained by the variables selected: 0.66
"   "   "   all variables   :   1.37

P-value 0.030 (variable   6; F-ratio =   2.34; number of permutations =   99)
Environmental variable   6 added to model
Variance explained by the variables selected: 0.78
"   "   "   all variables   :   1.37

P-value 0.020 (variable   7; F-ratio =   2.20; number of permutations =   99)
Environmental variable   7 added to model
Variance explained by the variables selected: 0.89
"   "   "   all variables   :   1.37

P-value 0.010 (variable   14; F-ratio =   1.94; number of permutations =   99)
Environmental variable   14 added to model
Variance explained by the variables selected: 0.98
"   "   "   all variables   :   1.37

P-value 0.010 (variable   16; F-ratio =   1.72; number of permutations =   99)
Environmental variable   16 added to model
Variance explained by the variables selected: 1.07
"   "   "   all variables   :   1.37

P-value 0.050 (variable   9; F-ratio =   1.67; number of permutations =   99)
Environmental variable   9 added to model
Variance explained by the variables selected: 1.15
"   "   "   all variables   :   1.37

P-value 0.110 (variable   2; F-ratio =   1.38; number of permutations =   99)
Environmental variable   2 added to model
Variance explained by the variables selected: 1.21

      "   "   "   all variables   :   1.37

P-value 0.460 (variable 12; F-ratio = 0.93; number of permutations = 99)
Environmental variable   12 added to model
Variance explained by the variables selected: 1.26
    "   "   "   all variables   :   1.37

P-value 0.680 (variable 5; F-ratio = 0.80; number of permutations = 99)
Environmental variable   5 added to model
Variance explained by the variables selected: 1.30
    "   "   "   all variables   :   1.37

P-value 0.600 (variable 8; F-ratio = 0.79; number of permutations = 99)
Environmental variable   8 added to model
Variance explained by the variables selected: 1.34
    "   "   "   all variables   :   1.37

P-value 0.500 (variable 3; F-ratio = 0.67; number of permutations = 99)
Environmental variable   3 added to model
Variance explained by the variables selected: 1.37
    "   "   "   all variables   :   1.37

No more variables to improve fit
*** End of selection ***

N name	(weighted) mean	stand. dev	inflation factor
1 SPEC AX1	0.0000	1.2018	
2 SPEC AX2	0.0000	1.2033	
3 SPEC AX3	0.0000	1.2878	
4 SPEC AX4	0.0000	1.4865	
5 ENVI AX1	0.0000	1.0000	
6 ENVI AX2	0.0000	1.0000	
7 ENVI AX3	0.0000	1.0000	
8 ENVI AX4	0.0000	1.0000	
2 GD	7.8818	9.9482	1.5709
3 ZD	0.1375	0.9669	1.0626
4 DG	2.1758	7.0202	1.4488
5 JL	1.4603	5.1382	1.1969
6 PS	0.7936	3.5025	1.0983
7 EI	4.0658	7.2401	1.3288
8 AE	0.2330	1.0342	1.1998
9 BU	0.7837	3.4005	1.1292
11 OL	1.9396	4.1241	1.4026
12 DD	0.1619	0.5272	1.1229
13 DK	30.8068	39.8555	1.1713
14 PN	60.6042	18.7581	1.4557
16 S	2.4553	0.8591	1.1142

**** Summary ****

Axes   1   2   3   4 Total inertia

Eigenvalues   : 0.364 0.249 0.164 0.109   10.114
Species-environment correlations : 0.832 0.831 0.777 0.673
Cumulative percentage variance
  of species data   : 3.6 6.1 7.7 8.8
  of species-environment relation: 26.6 44.8 56.8 64.8

Sum of all unconstrained eigenvalues   10.114
Sum of all canonical   eigenvalues   1.369

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