Institutionen för miljöanalys
SLU, Uppsala
Sven Bråkenhielm   2002-03-25

Effects of global warming on trees and understorey plants at Swedish IM sites – a tentative approach

by

Sven Bråkenhielm [1] **and Martin Köchy** [2]

[1] Institutionen för miljöanalyst, SLU, Box 7050, 750 07 Uppsala
[2] Abteilung für Vegetationsökologie und Naturschutz, Institut für Biochemie und Biologie, Universität Potsdam, Postfach 60 15 53, 144 15 Potsdam

INTRODUCTION

A multitude of papers deal with the large- and small-scale effects of global warming on biomes (Sykes & Prentice 1996b, Sykes et al. 1999), habitats and organisms (Holten & Carey 1992, Prentice et al. 1993, Sykes & Prentice 1995, Sykes et al. 1996, Sykes & Prentice 1996a and 2000, Woodwell et al. 1999). Relatively few of them are concerned with the understorey vegetation in forest as compared with those dealing with trees (Sykes et al. 1996) or plants growing in other habitats than forest (Gottfried et al. 1999, Holten 1990).

The distribution of low-growth plant species at high latitudes is essentially governed by their different sensitivity to temperature during the cold season, snow cover and water availability. Besides these, a canopy of shrubs and trees exerts a major influence. Global warming with increasing average temperatures will change the current geographical range of plant species. In forest the conditions for the understorey vegetation may change dramatically if the dominant tree species is exchanged. This change is particularly pronounced if there is a change from deciduous to evergreen or vice versa, i.e. from a canopy that lets in full light in early spring and late autumn to one that is constantly shading or opposite. Such change will favour some species, especially mosses and lichens and early-sprouting vascular plants. Other factors of importance that could change are the character of the litter, the density of the leafage and the depth of the root system. In general, evergreen tree species may have a lower growth rate and be more economic under harsh conditions than deciduous species and may be outcompeted by the latter when growth conditions improve (Aerts 1995).

Mathematical models predict that in Sweden both conifers and southern deciduous trees will extend their ranges northwards and upwards, the conifers at the same time withdrawing from the south (Sykes & Prentice 1995, 1996a, 2000) (Figure 1 in Appendix). Pine, being little shade tolerant, is replaced faster by deciduous trees than spruce, site conditions being favourable. Thus, several pure coniferous stands are replaced by pure deciduous or mixed stands consisting of deciduous trees and spruce. The invasion of deciduous trees in the south may to some degree increase soil nutrients, soil pH and light, the latter at least before leafing and after leaf fall (Aerts 1995; Saetre 1999). However, under beech and oak the nutrient increase may be slight, mainly due to the slow turnover of the litter. Those understorey species that are more competitive under the new conditions will slowly replace the former residents. At those sites in the mountains where there is subalpine birch forest the change will be reversed since conifers may invade the birch forest (Holten 1990). Generally there will a shift from coniferous forest communities to deciduous forest ones in the south

and from deciduous birch to conifers in the mountains. The replacement speed will depend on the species' dispersal ability (Matlack 1994, Eriksson et al. 1995, Brunet & Oheimb 1998). Due to the persistence of spruce and old pine and consequently of their companions, there will be a mosaic of forest floor vegetation types during a long transitional period in Sweden south of the future taiga borderline (cf "Limes Norrlandicus"(Sjörs 1956)). This will presumably result in higher species richness and biodiversity than in pure coniferous forests. From the continent, i.e. Denmark, Germany, Poland and the Baltic states, new species will migrate into south Sweden and spread northward.

The time aspect in the change of vegetation is crucial. It makes a great difference in the vegetation if 100, 500 or 1000 years have elapsed after the temperature has stabilised – if it does at all. Assuming, as is commonly done, a doubling of the present concentration of CO_2 in the atmosphere various general circulation models predict that the global temperature should rise by between 2-4 degrees centigrade, more at higher latitudes than near the equator (Pastor & Post 1988).

In this paper we present a simplified approach to the prediction of understorey vegetation change at IM reference sites in Sweden following the changes in forest tree distributions under two scenarios of winter temperature given as maps in Sykes & Prentice (1995, 2000). These tree distribution maps are suitable tools for testing a simple prediction method based on the relation between the tree canopy and the undergrowth. It is one of the aims of the ICP-IM programme, under the UN ECE Convention on Long-range Transboundary Air Pollution, to assess the biological and other effects of climate change. IM runs several sites in northern Europe covering the region involved in Sykes & Prentice´s studies.

The aim of this paper is to test to which extent it is possible to base prediction of forest undergrowth on correlation, species by species, with tree canopy composition and density. The correlation should then be applied to predict the abundance of the understorey species at IM sites as a result of predicted tree canopy changes caused by global climate change.

METHODS

We used two sets of tree distribution maps produced by Sykes & Prentice (1995 and 2000) (Figure 1 a-e in Appendix), in their turn based on two climate change scenarios calculated by general circulation models (GCM), both assuming doubled CO^2 in the atmosphere (IPCC 1996). One is based on the mean of four climatic models (GFDL, OSU, UKMO, GISS) predicting 5 –15°C increased winter temperature

in south-central Sweden after 100 years (Sykes & Prentice 1995). In this report the four-model case is called the ***GOUG** scenario* according to the initials of the four models. The other is based on the Hamburg ECHAM 3 climate model which predicts a rise in winter temperature of 1-2°C (Bengtsson et al. 1995). This case is called the ***HHE3** scenario*. The tree distribution maps mentioned above (Figure 1 in Appendix) were produced using the bioclimatic STASH model which was constructed for regional scale modelling of tree distributions (Sykes et al. 1996). We predicted future cover of understorey species by calculating regressions of species cover on tree abundance under present conditions at 33 sites in northern Europe and applying the equations to future tree abundance at 26 sites in Sweden. We used two alternative measures of tree abundance: per cent canopy cover and number of living stems with DBH 15 cm per hectare.

For the regressions we used the data from forested, protected reference sites in Sweden (20 coniferous/4deciduous) (Figure 2), Estonia (1/0), Germany (1/1), Latvia (3/0), and Lithuania (3 mixed) monitored by the former PMK (Bernes 1990) and present IM programmes (Kleemola & Forsius 2000). Cover of understorey species was estimated according to the "Manual for Integrated Monitoring" (Anon. 1998) on mainly 16 or 32 permanent quadrats (50x50 cm) on 40x40 m plots. Cover of each species was averaged across quadrats and years.

Tree diameter at breast height of all trees was measured on the same plot as understorey cover for Swedish sites and in adjacent plots in the other countries. For Swedish sites, we calculated tree density from the original data. For the other countries we had only the mean number of stems per hectare and and their mean diameter. We used regression equations based on the Swedish data to calculate the number of big stems in the other countries ($R^2 > 0.66$). When the calculation resulted in a negative number we replaced it by zero.

Both crown and stem diameters in Sweden were measured on plots adjacent to the understorey plots. Based on the relation between these two variables we calculated the cover of each tree on the understorey plots. Canopy overlaps of the same species was counted only once.

Picea abies and *Pinus sylvestris* were treated by species and *Betula spp.* as one group. The broadleaf tree species *Fagus sylvatica*, *Quercus petraea*, *Q. robur*, *Alnus glutinosa*, *Fraxinus excelsior*, and *Ulmus glabra* were lumped together in order to create a large enough group suitable for regression and indication of changed climate. These species have a similar continental distribution with regard to temperature (Ellenberg et al. 1991).

Figure 2. Reference sites of PMK/IM in Sweden treated in the text.

The STASH model predicts future tree distributions as likelihood of establishment and how well the species might do. The shading on the maps says something about how productive a species could be. We estimated the future tree cover and density of stems (DBH 15 cm) for Swedish reference sites based on the tree distribution maps (Figure 1 in Appendix) using long-term personal field-experience and detailed knowledge of environmental characteristics of each site. Tree numbers/covers on the plots were predicted setting the following limitations:

- The plots have been permitted to develop freely under stable climatic conditions and negligible air pollution for several hundred years.
- The sites are protected, i.e. not subject to any direct anthropogenic influence such as silvicultural management.
- There is no indirect anthropogenic influence such as "unnatural" species grown near the site, disseminating propagules onto it.

– The tree stand is regenerating successively without fire or severe windfelling. This means, among others, that pine will be at a disadvantage at regeneration except at very poor and dry sites. At more normal sites spruce and beech if available will prevail. In gaps birch will be able to grow up and will be present almost everywhere but in small numbers due to their relatively short life-span. Oak is able to compete successfully with the other trees at comparatively dry and nutrient-poor sites, preferably with rock outcrops.

– The hunting pressure and thus wildlife browsing is of about the same extent as at present. This means that e.g. rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and sallow (*Salic caprea*) have small chances of reaching the canopy. However, they are represented by one tree on each plot.

– Reindeer browsing and trampling is a little less than at present.

– The mountain birch has reached the two alpine plots with only a few scattered trees.

For each understorey species we calculated the linear regressions of their present cover on the density or cover of birch, spruce, pine, and broadleaf species using a stepwise regression approach. We retained regressions with an $R^2 > 0.50$, at least 3 degrees of freedom, and all variables significant at P   0.10 (Table 1). We used these regression equations to predict the future cover of understorey species at Swedish sites based on the STASH-predicted tree distributions of the GOUG and HHE3 climate scenarios (Table 2 and 3 in Appendix).

Since the results of the regression runs, using both tree stem density and canopy cover, largely coincided, only one of them – tree stem density – was applied to both climate scenarios. Predicted canopy cover was used only with the HHE3 scenario.

RESULTS

Of the 83 common undestorey species occurring at more than four of the 37 sites, we obtained strong correlations with tree density or tree cover for 25 species (Table 2 in Appendix). These did not include typical dominants like *Vaccinium myrtillus*, *Pleurozium schreberi*, *Hylocomium splendens* or *Dicranum polysetum*. Only *Vaccinium vitis-idaea* was a more abundant species at several sites. Since most of the 25 species have low cover at present, their predicted change is small in absolute terms. Therefore, the regressions are more useful in describing the predicted geographical ranges of the species rather than their possible future abundances. The

small predicted change in cover also precludes the comparison between the HHE3 and the GOUG scenarios.

Table 1. Regression and p-values for species attaining R^2 0,50 relative to canopy trees.

Species	ou	Stem density [*] R^2	n	param.	P	ou	Canopy cover (%) R^2	n	param.	P
Vascular plants										
Calamagrostis arundinacea	x	0,98	6	+Q	0,0002					
Deschampsia flexuosa	x	0,5	23	+PS	0,0002	x	0,6	22	+PS	0,0001
Gymnocarpium dryopteris		0,61	7	+BZ	0,04		0,7	7	+BZ	0,02
Juniperus communis		0,85	8	+BZ	0,001		0,62	7	+BZ	0,04
Linnaea borealis		0,5	9	+PA	0,03					
Lycopodium annotinum		0,53	11	+Q	0,01					
Melampyrum pratense						x	0,83	18	+PS	0,0001
Melampyrum sylvaticum		0,62	10	+BZ	0,007					
Picea abies		0,71	26	+Q	0,0001		0,85	24	+Q	0,0001
Vaccinium vitis-idaea		0,51	25	+PS	0,0001		0,59	22	+PA-PS	0,0002
Mosses										
Brachythecium salebrosum	x	0,68	8	+BZ	0,04					
Brachythecium sp.		0,69	7	+BZ	0,02					
Dicranum majus		0,62	19	+PA+PS	0,0004					
Dicranum montanum	x	0,6	6	+Q	0,01	x	0,95	5	+BZ	0,004
Dicranum sp.		0,7	5	+PA	0,08					
Hypnum cupressiforme		0,64	10	-PA	0,005		0,8	10	+PA+PS+Q	0,02
Plagiothecium laetum	x	0,61	6	+PA	0,07					
Plagiomnium affine						x	0,97	6	+PS	0,0004
Polytrichum commune	x	0,74	13	+Q	0,0002	x	0,7	13	+PS	0,0003
Polytrichum juniperinum		0,92	8	+BZ-PA	0,002	x	0,97	6	+BZ-PS	0,005
Rhodobryum roseum		0,77	6	-PA	0,02					
Rhytidiadelphus loreus	x	0,75	5	-PA	0,06					
Sphagnum girgensohnii		0,84	5	+PA	0,03					
Tetraphis pellucida							0,83	5	+PS	0,03
Lichens										
Cladonia furcata		0,82	5	+PA	0,03					
Cladonia gracilis		0,55	6	-BZ	0,09					
Cladonia squamosa		0,56	7	-BZ	0,05					

[*] n:o stems >15 cm dbh /ha

Column "ou":
x: regression affected by outlier
Column n: number of sites

Column "param.":
+: positive correlation with species abundance
–: negative correlation with species abundance
BZ: Betula spp.
PA: Picea abies
PS: Pinus sylvestris
Q: broadleaf trees

Most of the 25 species were correlated with the density of tree stems rather than tree cover. Only three species were correlated exclusively with tree cover and not with tree density.

Juniperus communis will continue to be present throughout Sweden except the far South. In southern and central Swedish forests it is usually a relict from the time when the landscape was more open, e.g. as open or lightly wooded pasture. The correlation with birch is presumably a coincidence that does not reflect common climatic requirements. It rather reflects joint dominance in clearings and dry habitats.

Linnaea borealis under the HHE3 scenario is predicted to extend its range southward, whereas the GOUG scenario seems to imply an increase in the north. The positive correlation with spruce seems reasonable as *L. borealis* is typical of Swedish blueberry-spruce forests.

Picea abies seedlings in the understorey are predicted to increase at all sites. Under GOUG a stronger increase is predicted than under HHE3. The abundance of young *Picea* individuals is positively correlated with that of broadleaf trees where the growth conditions are good, at least for seedlings and young plants.

Vaccinium vitis-idaea is predicted to decrease at most sites according to the tree density regression, but by the tree cover regression it will increase except in the extreme north. *Melampyrum pratense* will establish itself as a subordinate plant at several sites where it is missing today, particularly in south Sweden. *Gymnocarpium dryopteris* and *Lycopodium annotinum* will behave largely in the same way, *Lycopodium* developing more cover in the south than *Gymnocarpium*.

The mosses will behave in diverse ways, some of them being or becoming dominants. *Dicranum majus* is predicted, from presence at practically every site except in the north and the south, to disappear from all but a couple of them. *Dicranum sp.* will appear and almost dominate – from its current absence in the southern half of Sweden – at most sites in central and southern Sweden, preferably under the HHE3 scenario. Several species will spread in the country but have very small abundance, e.g. *Brachythecium salebrosum, B. sp.*, *Dicranum montanum*, *Hypnum cupressiforme*, *Plagiothecium laetum*, *Polytrichum juniperinum* and *Rhodobryum roseum*, today being present at only around six sites each. *Polytrichum commune* is predicted to advance both geographically and quantitatively.

Cladonia furcata is predicted to disappear from several sites in the south and appear in central Sweden. Both *C. gracilis* and *C. squamosa*, under both scenarios, will increase their occurrences, especially in south Sweden, but their covers will be as negligible as it is today.

According to the model two species,*Calamagrostis arundinacea* and *Rhytidiadelphus loreus*, are predicted to increase strongly both in distribution and abundance under both scenarios.

DISCUSSION

The regression models allowed us to predict the cover of 25 species with >50% accuracy based on their correlation with the tree layer composition. This, however, is only a fraction of the nearly 400 species observed at all sites and does not include the most frequent dominant species (*Hylocomium splendens*, *Deschampsia flexuosa*, *Dicranum polysetum*, *Pleurozium schreberi*, *Vaccinium myrtillus*). Apparently, the abundance of tree species in Swedish forests tells us little about what the understorey looks like. This may indicate that the distribution and abundance of most understorey species are not primarily conditioned by climate or light conditions. Experimental evidence shows that competition for belowground resources in rooted plants is stronger than competition for light (Riegel et al. 1992). Future models to predict the change of the understorey should consider site conditions and the competitiveness of species in relation to them.

There is a contradiction between the predicted retreat of *Picea abies* trees from south towards north on one hand and the increased abundance of seedlings and young spruce on the other. It is questionable whether seedlings will reach maturity in a dense deciduous forest composed of e.g. *Fagus* or *Ulmus* and *Fraxinus*. Most probably they will succumb early and, as new seeds will not be produced in the vicinity, the species will disappear.

The predicted spread in geographical range and abundance of *Calamagrostis arundinacea* and *Rhytidiadelphus loreus* is apparently due to the effect of outliers in the regressions of the present understorey cover on tree abundance. Both species are currently present at few sites, 6 and 5 respectively, and it is highly improbable that they should increase as much as indicated. *Calamagrostis arundinacea* is a common grass in the southern half of Sweden, missing in the north and particularly abundant at clear-felled sites (Sjörs 1956). The abundance given by the regression, at several sites between 50 and 92% under both scenarios, could possibly be achieved in a clear-felled area but not in an undamaged stand. *Rhytidiadelphus loreus* is a moss with a restricted southwestern distribution in Sweden, favoured by a maritime climate (Hallingbäck1996, Sjörs 1956). In these two cases we do not attribute much biological significance to the predicted distribution and cover values, even though the GOUG scenario brings with it great changes.

With higher annual temperatures, species from the warm-temperate zone are expected to extend their ranges northward into Sweden. Sixty-seven species at the Central European sites were not recorded at the Swedish sites, although they are all to be found in Sweden. Most of them had low mean cover (<1.5 %) at the Central European sites except *Lamium galeobdolon* (1.6 %), *Cladina rangiferina* (1.7 %), *Circaea alpina* (2.2 %), *Brachythecium oedipodium* (4.7 %), and *Festuca rubra* (10.3 %). These would be the most likely candidates for invasion. On the other hand, species with a cold-boreal distribution may be lost. More than two hundred species were recorded in Sweden but not in Central Europe. Although this high number is largely due to the larger number of Swedish sites, it includes many frequently occuring lichens (*Cladonia spp.*) and mosses (*Barbilophozia spp.*) that could be affected by a drier, warmer climate.

The mean cover of species was similar at temperate Swedish and Central European sites (Figure 3). The greater deviations suggest that *Vaccinium vitis-idaea*, *V. myrtillus*, and *Dicranum polysetum* may decrease, while *Hylocomium splendens* and *Ptilium crista-castrensis* may increase. The southern limit of all dominant species in Sweden extends to
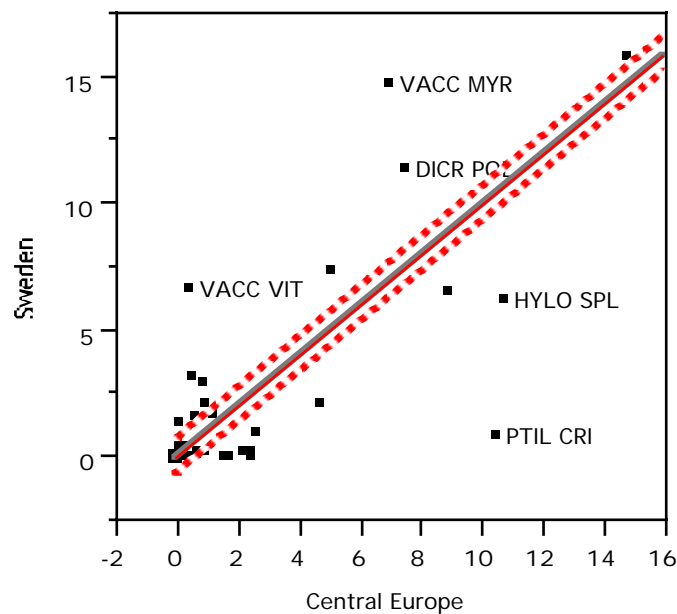

Figure 3. Comparison of cover of species occuring at both Swedish and Central European sites (DICR POL=Dicranum polysetum, HYLO SPL=Hylocomium splendens, PTIL CRI=Ptilium crista-castrensis,.VACC MYR=Vaccinium myrtillus, VAC VIT=V. vitis-idaea).

at least Central Europe. Therefore it is unlikely that even a dramatic climate change will cause their southern limits to retreat into Sweden, although their abundancies may decrease. On the other hand their northern limits could move northward. Thus, one may assume that these species will continue to dominate even under a changed climate though farther north. The most dramatic changes are predicted for those forests that shift from coniferous to mixed or deciduous and vice versa, i.e. in the extreme south and the northwestern mountain-range. Unfortunately the small number of deciduous stands did not allow to make predictions for the establishment of their characteristic understorey species. These underlying conditions made some of the results obtained relatively uncertain. However, the regression models were applied strictly and the results were analysed as objectively as possible.

CONCLUSIONS

– The hypothesis that it is possible to base a reasonably accurate prediction of forest understorey vegetation on correlation, species by species, with tree canopy composition and density has apparently to be rejected under the conditions at hand.
– Apart from a few special cases rather small effects of the climate change are predicted using the canopy/undergrowth correlation – even with the GOUG scenario.
– The most dramatic changes in spread and abundance, e.g. *Calamagrostis arundinacea*, *Rhytidiadelphus loreus* and *Polytrichum commune* are affected by extreme values and do not seem very realistic.
– The species composition of the tree canopy – as different from the density – has apparently only partial influence on the understorey species.
– Few species considered are bound to a particular tree stand type.
– The data available from deciduous stands is probably too small for reliable regressions to be established. From coniferous stands the basis is broader.

ACKNOWLEDGEMENTS

REFERENCES

Anon.(1998). "Manual for Integrated Monitoring". UN ECE Convention on Long-range Transboundary Air Pollution. Finnish Environment Institute. Helsinki.(Unpublished.)

Aerts, R. (1995). "The advantages of being evergreen." TREE **10**: 402-407.

Bengtsson, L., Botzet, M. & Esch, M. (1995). "Hurricane-type vortices in a general circulation model". Tellus 47A: 1751-1796.

Bernes, C. (1990). "Environmental Monitoring in Sweden". Monitor 1990. Swedish Env. Prot. Agency Informs. Stockholm. 180 pp.

Brunet, J. & von Oheimb, G. (1998). "Migration of vascular plants to secondary woodlands in southern Sweden." Journal of Ecology **86**: 429-438.

Ellenberg, H., Webert, H.E., Düll, R., Wirth, V., Werner, W. & Paulissen, D. (1991). "Zeigerwerte von Pflanzen in Mitteleuropa". Scripta Geobotanica **18**. Göttingen,

Eriksson, O., Ehrlén, J, Telenius, A. & Froborg, H. (1995). "Dynamics and abundance of field layer plants in a deciduous wood at Tullgarn, province of Sodermanland." Svensk Botanisk Tidskrift **89**: 91-107.

Ertsen, A.C.D., Alkemade, J.R. M. & Wassen, M.J. (1998). "Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in the Netherlands." Plant Ecology **135**: 113-124.

Gottfried, M., Pauli, H., Reiter, K. & Grabherr, G. (1999). "A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming." Diversity and Distributions **5**: 241-251.

Hallingbäck, T. 1996. "Ekologisk katalog över Mossor." [The bryophytes of Sweden and their ecology.] Artdatabanken, SLU, Uppsala.

Holten, J. (ed.). (1990). "Biologiske og økologiske konsekvenser av klimaforandringen i Norge." Bidrag til Den interdepartementale klimautredningen. Norsk Institutt for Naturforskning (NINA). Trondheim.

Holten, J. & Carey, P.D. (1992). "Responses of climate change on natural terrestrial ecosystems in Norway". Norsk Institutt for Naturforskning (NINA). Trondheim.

IPCC. (1996). "Climate change 1995, impacts, adaptations and mitigations of climate change: scientific-technical analyses." In: Warson, R.T., Zinyowera, M.C., Moss, R.H. & Dokken, D.J. (Eds, Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, 878 pp.

Kleemola, S. & Forsius, M. (2001). "10th Annual Report 2001". UN ECE Convention on Long-range Transboundary Air Pollution: ICP Integrated Monitoring. Finnish Environment Institute. Helsinki.

Matlack, G.R. (1994). "Plant species migration in a mixed-history forest landscape in eastern North America." <u>Ecology</u> **75**(5): 1491-1502.

Pastor, J.P., & Post, W.M. (1988). "Response of northern forests to CO2-induced climate change." <u>Nature</u> **334**: 55-58.

Prentice, I.C., Sykes, M.T. & Cramer, W. (1993). "A simulation model for the transient effects of climate change on forest landscapes." <u>Ecological Modelling</u> **65**: 51-70.

Riegel, G.M., Miller, R.F. and Krueger, W.C. (1992). "Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon." - <u>Ecological Applications</u> **2**: 71-85.

Saetre, P. (1999). "Spatial patterns of ground vegetation, soil microbial biomass and activity in a mixed spruce-birch stand." <u>Ecography</u> **22**: 183-192.

Schlesinger, M.E., & Zhao, Z.C. (1989). "Seasonal climate changes induced by doubled CO2 as simulated by the OSU atmospheric GCM/mixed layer ocean model." <u>J. Climate</u> **2**: 459-495.

Sjörs, H. (1956). "Nordisk växtgeografi." Scandinavian University Books. Svenska Bokförlaget/Bonniers. Stockholm.

Sykes, M.T. (1997). "The biogeographic consequenses of forecast changes in the global environment: Individual species´potential range changes". <u>In:</u> B. Huntley (ed.) p. 427-440. Berlin Heidelberg, Springer-Verlag.

Sykes, M.T. & Prentice, I.C. (1995). "Boreal forest futures: Modelling the controls on tree species range limits and transient responses to climate change." <u>Water, Air and Soil Pollution</u> **82**(1-2): 415-428.

Sykes, M.T. & Prentice, I. C. (1996a). "Climate change, tree species distributions and forest dynamics: A case study in the mixed conifer/northern hardwoods zone of northern Europe." <u>Climatic Change</u> **34**:161-177.

Sykes, M.T. & Prentice, I.C. (1996b). "Carbon storage and climate change in Swedish forests: a comparison of static and dynamic modelling approaches." <u>NATO ASI Series</u> **I 40**: 70-78.

Sykes, M.T. and Prentice, I.C. (2000). "Modelling the effect of climate change on Swedish forests". Swedish Environmental Protection Agency. Stockholm.

Sykes, M.T., Prentice, I.C. & Cramer, W. (1996). "A bioclimatic model for the potential distributions of north European tree species under present and future climates." <u>Journal of Biogeography</u> **23**: 203-233.

Sykes, M.T., Prentice, I.C. & Laarif, F. (1999). "Quantifying the impact of global climate change on potential natural vegetation." <u>Climatic Change</u> 41:37-52.

Woodwell, G.M., MacKenzie, F.T., Houghton, R.A., Apps, M., Gorham, E. & Davidson, E. (1999). "Biotic feedbacks in the warming of the earth." <u>Climatic Change</u> **40**: 495-518.

APPENDIX

Figure 1 a-e. Tree distribution maps under three scenarios, calculated by the STASH model. Species: birch, Norway spruce, Scots pine, beech and oak.

Table 2. Cover of plants in relation to tree stand density under three scenarios.
Table 3. Cover of plants in relation to canopy cover under two scenarios.

Appendix

Figure 1 a. Tree distributions of birch calculated by the STASH bioclimatic model under current conditions and two predicted scenarios of 1-2 °C (HHE3) and 5-15 °C (GOUG) winter temperature increase respectively. The shading expresses the expected degree of productivity.

Appendix
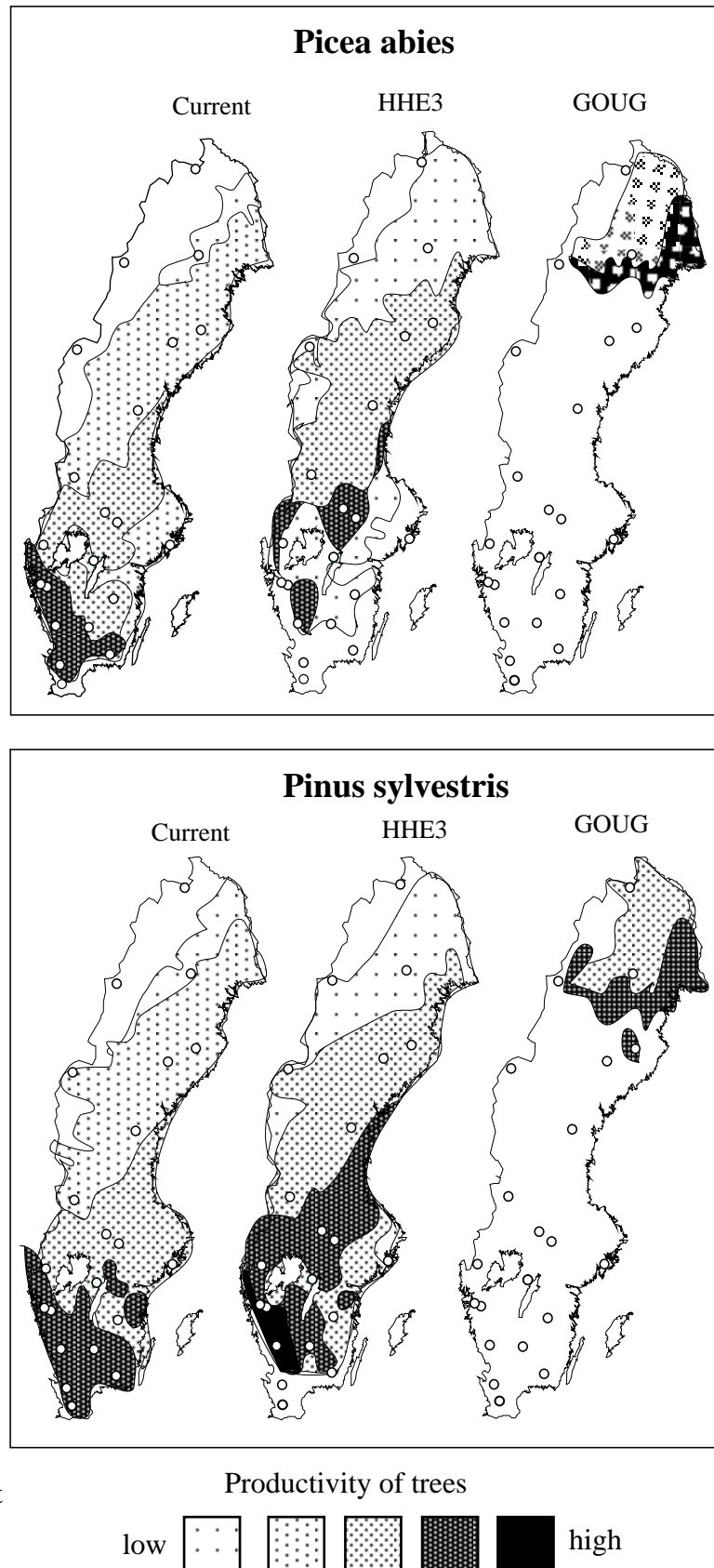
Figure 1 b and c. Tree distributions of Norway spruce and Scots pine calculated by the STASH bioclimatic model under current conditions and two predicted scenarios of 1-2 °C (HHE3) and 5-15 °C (GOUG) winter temperature increase respectively.
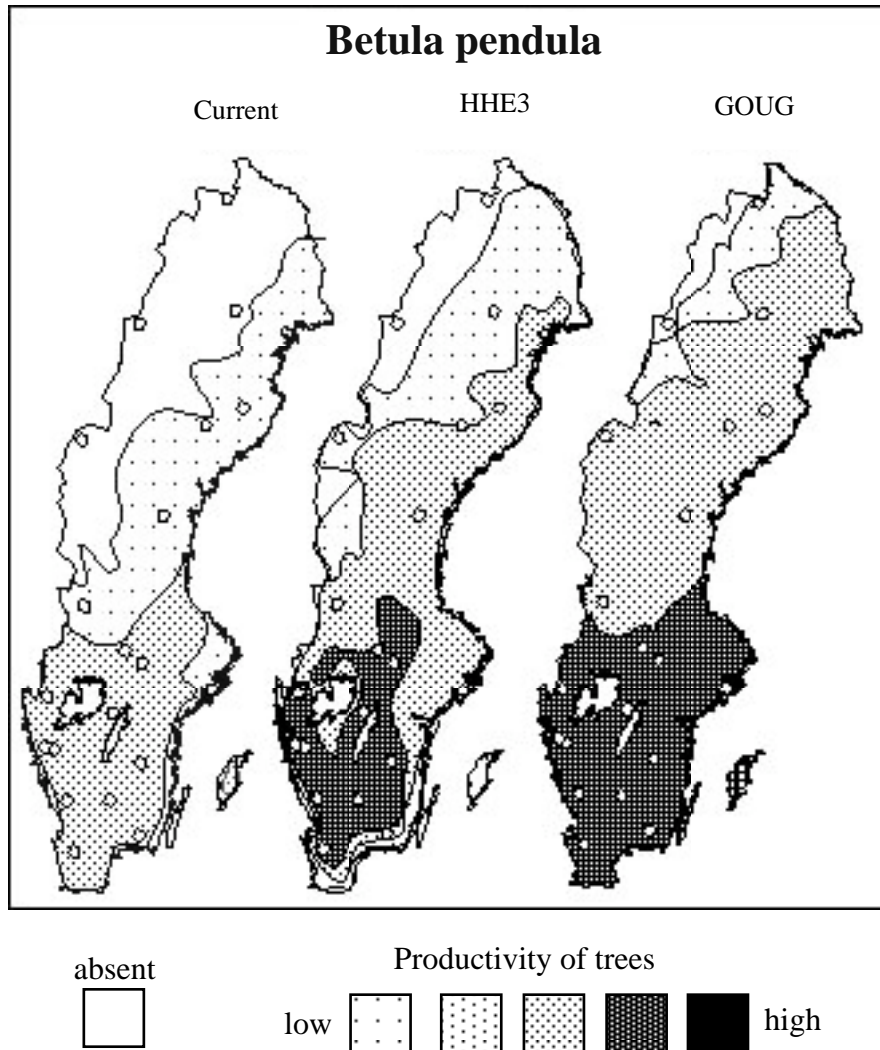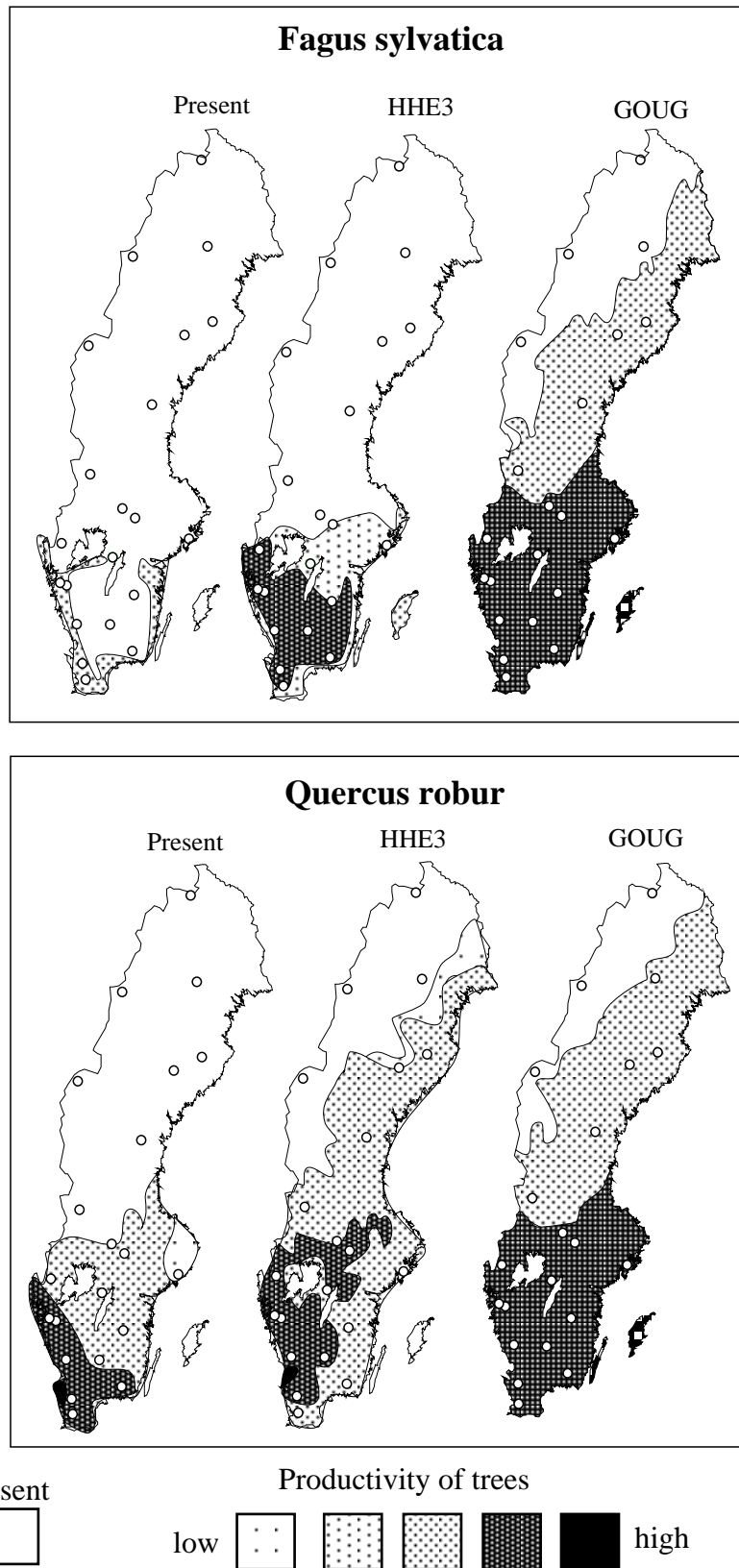
Appendix

Figure 1 d and e. Tree distributions of beech and oak calculated by the STASH bioclimatic model under current conditions and two predicted scenarios of 1-2 °C (HHE3) and 5-15 °C (GOUG) winter temperature increase respectively.

Appendix

Table 2. Cover of plants under present conditions and after stabilisation of changes in the tree **stand density** (nu... model applied to two climate scenarios – one predicting 1-2 °C increase in winter temperature (HHE3), the other...

location	scenar	Betula spp. (1)	Pice abies (2)	Pinus sylvestris (3)	broadleaf trees (4)	Juniperus communis (5)	Linnaea borealis (6)	Picea abies (7)	Vaccinium vitis-idaea (8)	Melampyrum sylvaticum (9)	Calamagrostis arundinacea (10)	Deschampsia flexuosa (11)	Gymnocarpium dryopteris (12)	Lycopodium annotinum (13)	Brachythecium salebrosum (14)	Brachythecium sp. (15)	Dicranum majus (16)	Dicranum montanum (17)	Dicranum sp. (18)	Hypnum cupressiforme (19)	Plagiothecium laetum (20)	Polytrichum commune
Abisko alpine	present					1	0		3					0					8			
	HHE3	31				0		0	1	0	1		1	0	0	0		0		1	0	
	GOUG	188			188	2		2	1	1	45		5	2	1	1		2		1	0	
Abisko birch	present	178				3	0		1	2		3	1	0	1	1			0			
	HHE3	188				2		0	1	1	1		5	0	1	1		0		1	0	
	GOUG	63	125		63	1	1	1	1	1	15		2	1	0	0		1	6	1	0	
Ammarnäs alpine	present								0		10				0							
	HHE3	31				0		0	1	0	1		1	0	0	0		0		1	0	
	GOUG	188			188	2		2	1	1	45		5	2	1	1		2		1	0	
Ammarnäs birch	present	258				3	0		2	1		3	9	0	1							
	HHE3	281		6		3		0	1	2	1		8	0	2	1		0		1	0	
	GOUG	156	125		156	2	1	2	1	1	37		4	2	1	1		1	6	1	0	
Reivo coniferous	present	6	247				1		5	0		2					0					
	HHE3	13	250	6		0	2	0	1	0	1		0	0	0	0		0	14	0	0	
	GOUG	6	250		6		2	0	1	0	2		0	0	0			0	14	0	0	
Vindeln, Svartb. coniferous	present	28	303	197		0	4		11			2		0				2	25			
	HHE3	31	219	31	6	0	2	0	2	0	2	0	1	0	0	0		0	12	1	0	
	GOUG	31	281	188	38	0	2	1	4	0	9	6	1	0	0	0	6	0	16	0	0	
Vindeln, Kulbäcksl. coniferous	present	13	316	50		0	4	0	8	0		6	1						16		0	
	HHE3	31	250	31	6	0	2	0	2	0	2	0	1	0	0	0		0	14	0	0	
	GOUG	31	313	31	31	0	3	1	2	0	8	0	1	0	0	0	4	0	18	0	0	
Gammtratten coniferous	present	31	225	50		1	0	0	2			1		0				1				
	HHE3	31	219	13	6	0	2	0	1	0	2		1	0	0	0		0	12	1	0	
	GOUG	31	219	63	38	0	2	1	2	0	9	1	1	0	0	0		0	12	1	0	

Appendix

location	scen.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Sandnäset mixed	present	106	200				0	0	1	1		2	6	0	0	0	0		1		
	HHE3	94	188	6		1	1	0	1	1	1		3	0	1	0		0	10	1	0
	GOUG	125	188		125	1	1	2	1	1	30		4	1	1	1		1	10	1	0
Stormyran coniferous	present	31	175	169			2	2	7	0		1		0	0	0	1				
	HHE3	31	250	31	13	0	2	0	2	0	3	0	1	0	0	0		0	14	0	0
	GOUG	31	63	125	100	0	0	1	3	0	24	4	1	1	0	0		1	2	1	0
Tandövala coniferous	present	28	238	13		0		0	3			2		0							
	HHE3	31	188	6	6	0	1	0	1	0	2		1	0	0	0		0	10	1	0
	GOUG	219	63	19	231	2	0	3	1	1	55		6	2	1	1		2	2	1	0
Kindla coniferous	present	38	863	25				0	0			1					50				0
	HHE3	31	375	6	31	0	3	1	1	0	8		1	0	0	0	8	0	21	0	0
	GOUG	31	25	6	138	0		2	1	0	33		1	1	0	0		1	0	1	0
Grimsö coniferous	present		197	175			2	1	3	0	1	1	0				2				
	HHE3	31	281	25	31	0	2	1	2	0	8		1	0	0	0	1	0	16	0	0
	GOUG	19	13		156	0		2	1	0	37		1	2	0	0		1		1	0
Tyresta coniferous	present	66	366	94		0		0	2	0	9	0	0	0		0	2	0			
	HHE3	31	31	6	219	0		3	1	0	52		1	2	0	0		2	0	1	0
	GOUG	31			356	0		4	1	0	84		1	3	0	0		3		1	0
Tresticklan pine	present	48	13	660	34			0	9							0	0				
	HHE3	31	13	63	188	0		2	2	0	45	1	1	2	0	0		2		1	0
	GOUG	19			206	0		2	1	0	49		1	2	0	0		2		1	0
Tresticklan spruce	present	53	459	200				0	1								3			0	
	HHE3	19	188	31	125	0	1	2	2	0	30	0	1	1	0	0		1	10	1	0
	GOUG	25			275	0		3	1	0	65		1	3	0	0		2		1	0
Tiveden coniferous	present	19	183	292	216			0	6	0		0					0				
	HHE3	13	94	63	250	0	1	3	2	0	59	1	0	2	0	0		2	4	1	0
	GOUG	19			219	0		3	1	0	52		1	2	0	0		2		1	0
Gårdsjön coniferous	present	56	338	81				1	1			2				0	9			0	
	HHE3	19	63		350	0	0	4	1	0	83		1	3	0	0		3	2	1	0
	GOUG	13			325	0		4	1	0	77		0	3	0	0		3		1	0
Svartedalen coniferous	present	225	383	129				0	1			2					8			0	
	HHE3	25	125	31	219	0	1	3	2	0	52	0	1	2	0	0		2	6	1	0
	GOUG	19			331	0		4	1	0	78		1	3	0	0		3		1	0
N Kvill spruce	present		292					0		1	0						0	0		0	0
	HHE3	13	63		188	0	0	2	1	0	45		0	2	0	0		2	2	1	0
	GOUG	13			325	0		4	1	0	77		0	3	0	0		3		1	0
N Kvill pine	present	6	75	396				0	3								0				
	HHE3	13	31	63	188	0		2	2	0	45	1	0	2	0	0		2	0	1	0
	GOUG	13			213	0		3	1	0	50		0	2	0	0		2		1	0

Appendix

location	scen.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Aneboda coniferous	present		464	203	6			0				3					50	0		0	0	
	HHE3	13	313	31	156	0	3	2	2	0	37	0	0	2	0	0	4	1	18	0	0	
	GOUG	13			325	0		4	1	0	77		0	3	0	0		3		1	0	
Berg mixed	present		350	110	247			0				3	0	0		0	0	0		0	0	
	HHE3	13		6	338	0		4	1	0	80		0	3	0	0		3		1	0	
	GOUG				313			4	1	0	74		0	3	0			3		1	0	
Sännen coniferous	present		423	96				2	0			0					3	0		0		
	HHE3	13		31	338	0		4	2	0	80	0	0	3	0	0		3		1	0	
	GOUG	13			325	0		4	1	0	77		0	3	0	0		3		1	0	
Tostarp southern deciduous	present				225			0												1		
	HHE3				269			2	1	0	45		0	2	0			2		1	0	
	GOUG				313			3	1	0	52		0	2	0			2		1	0	
Dalby southern deciduous	present				300										0							
	HHE3				375			3	1	0	59		0	2	0			2		1	0	
	GOUG				394			4	1	0	92		0	4	0			3		1	0	

Table 3. Cover of plants under present conditions and after stabilisation of changes in the tree **canopy**
model applied to a climate scenario predicting 1-2 °C increase in mean winter temperature (HHE3). 0=

		Cover %				Cover %			Cover %			
		canopy trees				shrubs			other vasculars			
location	scenario	Betula spp.	Picea abies	Pinus sylvestris	broadleaf trees	Juniperus communis	Picea abies	Vaccinium vitis-idaea	Melampyrum pratense	Deschampsia flexuosa	Gymnocarpium dryopteris	Dicranum montanum
		1	2	3	4	5	6	7	8	9	10	11
Abisko alpine	present					1		3				
	HHO3	5				0	0	2	0	1	1	0
Abisko birch	present	24				3		1		3	1	
	HHO3	30	1			2	0	2	0	1	5	1
Ammarnäs alpine	present							0		10		
	HHO3	5				0	0	2	0	1	1	0
Ammarnäs birch	present	49				3		2	1	3	9	
	HHO3	50				3	0	2	0	1	8	1
Reivo coniferous	present	1	20					5		2		
	HHO3	2	30				0	4	0	1	0	0
Vindeln, Svartberget coniferous	present	5	33	25		0		11	0	2		
	HHO3	3	50	5		0	0	7	1	3	1	0
Vindeln, Kulbäcksl. coniferous	present	3	34	12		0	0	8	1	6	1	
	HHO3	3	50	1	2	0	1	6	1	1	1	0
Gammtratten coniferous	present	12	34	8		1	0	2	1	1		
	HHO3	10	40	2		0	0	6	1	2	2	0
Sandnäset mixed	present	17	24				0	1	1	2	6	
	HHO3	5	40			0	0	5	0	1	1	0
Stormyran coniferous	present	15	35	30	5		2	7	0	1		
	HHO3	10	70	5		0	0	9	1	3	2	0
Tandövala coniferous	present	16	20	1		0	0	3	1	2		
	HHO3	10	40	1	1	0	0	5	1	1	2	0

Appendix

location	scenario	1	2	3	4	5	6	7	8	9	10	11
Kindla coniferous	present	7	61	5			0	0	0	1		
	HHO3	10	50		1	0	0	6	0	1	2	0
Grimsö coniferous	present	1	33	28			1	3	1	1	0	
	HHO3	10	60	1	5	0	1	7	1	1	2	0
Tyresta coniferous	present	13	50	13	13	0	0	2	1	0	0	0
	HHO3	10	50		22	0	2	6	0	1	2	0
Tresticklan pine	present	14	3	63			0	9	0			
	HHO3	5	30	15	25	0	2	6	2	5	1	0
Tresticklan spruce	present	14	58	21			0	1				
	HHO3	5	60	2	25	0	2	7	1	2	1	0
Tiveden coniferous	present	3	19	37			0	6	1	0		
	HHO3	5	20	10	30	0	3	5	1	4	1	0
Gårdsjön coniferous	present	18	54	13	1		1	1	0	2		
	HHO3	5	2	5	75	0	7	3	1	3	1	0
Svartedalen coniferous	present	43	62	22			0	1		2		
	HHO3	5	2	5	75	0	7	3	1	3	1	0
N Kvill spruce	present		34				0		1			0
	HHO3		1		80		7	2	0	1	0	0
N Kvill pine	present		14	47			0	3	0			
	HHO3	1		10	55		5	3	1	4	0	0
Aneboda coniferous	present		60	46			0			3		0
	HHO3	1			90		8	2	0	1	0	0
Berg coniferous	present		59	21	5		0			3	0	0
	HHO3		2		95		8	2	0	1	0	0
Sännen coniferous	present	1	65	23	1		2	0		0		0
	HHO3				85		7	2	0	1	0	0
Tostarp southern deciduous	present				63		0					
	HHO3				80		7	2	0	1	0	0
Dalby southern deciduous	present				62							
	HHO3				80		7	2	0	1	0	0