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Colonizing Landscapes :

Human Apropriation of Net Primary Production and its Influence of Standing Crop and Biomass Turnover in Austria

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ABSTRACT

Human land use significantly influences important properties of terrestrial ecosystems, e.g. energy flow, standing crop and biomass turnover. The socio-economic interference with ecological energy flows may be studied empirically by calculating the „human appropriation of net primary production“ (in short: „NPP appropriation“) resulting from two processes: The change in average primary productivity of ecosystems caused by land use and the harvest of biomass from ecosystems. NPP appropriation is defined as difference between the NPP of the potential vegetation and the proportion of the actual NPP remaining in ecosystems after harvest. Land use also influences the amount of biomass and carbon stored in live vegetation. Changes in land use can thus lead to significant net carbon flows between the vegetation and the atmosphere. By comparing the standing crop of the potential vegetation and the actually prevailing vegetation we demonstrate the human impact on standing crop and the amount of carbon stored in live vegetation. By relating standing crop and NPP we estimate the impact of land use on biomass turnover. We discuss these concepts using empirical results for the aboveground vegetation in Austria calculated from statistical data and from land use and land cover models derived from remote sensing data. According to our calculations the human appropriation of aboveground NPP in Austria amounts to 51% today and has gradually declined to this value from 53% in 1950. The standing crop of the actually prevailing vegetation is about 64% lower than that of the potential vegetation. Biomass turnover has been accelerated by a factor of 2.4.

Key words: Land use and cover change, net primary production, standing crop, carbon flows, remote sensing, human impact on ecosystems.

INTRODUCTION

Much effort is currently devoted towards understanding ecosystem functioning – e.g., net primary production (NPP), carbon storages and fluxes, nutrient fluxes and other biogeochemical processes – on a large scale (e.g., Cramer et al. 1997, Kaduk and Heimann 1996, Schimel 1995, Schimel 1991, Schimel et al. 1997). The impact of human activities on these and related ecosystem processes is already significant and continues to increase (Schlesinger 1997, Walker and Steffen 1996).

Human activities influence ecosystem functioning at least in two ways: First, global ecological change, e.g., climate change and increasing atmospheric levels of CO_2, potentially affect fundamental ecosystem processes; e.g., NPP, nutrient and carbon cycling. These issues are currently analyzed in on-going research programs (Walker and Steffen 1996) and will not be treated in this paper. Second, human societies transform terrestrial ecosystems around the globe at an increasing pace through a variety of activities encompassed in the notion of „land use“ (Meyer 1996, Meyer and Turner 1994). These changing patterns of human land use and the changes they induce in land cover influence fundamental ecosystem properties.

In an attempt to quantify the impact of land use on ecosystem functioning, this paper assesses the effects of land use on three fundamental ecosystem properties: net primary production, standing crop and biomass turnover. To achieve this, we compare actually observable ecosystem patterns (i.e., properties of the current vegetation) with those which would be expected in the absence of human activities (i.e., the ecosystem properties of the potential natural vegetation). This difference between actual and potential conditions can be used as an indicator of the human impact on ecosystem functioning.

To assess the human impact on ecological energy flows, we use a concept developed by Vitousek and others which can be called „appropriation of net primary production“ or „NPP appropriation“ (Vitousek et al. 1986, Wright 1990). The notion of NPP appropriation refers to the observation that, by using the land, humans alter ecological energy flows. For example, agriculture and forestry aim at harnessing biomass energy for socio-economic purposes and reduce the amount of NPP remaining in ecological food chains. Other types of land use, e.g. soil sealing, alter ecosystems and impact on net primary productivity even if no biomass is harvested. Thus, the indicator „NPP appropriation“ – defined as the aggregate effect of land use-induced changes in productivity and biomass harvest on the energy availability in ecosystems – can be used to assess the effect of land use on the availability of biomass energy in ecosystems (Haberl 1997).

Land use also influences the standing crop; i.e., the biomass stock, of ecosystems (Houghton et al. 1983, Houghton 1995, Schimel 1995). Converting forests to cultivated land reduces the amount of carbon in living vegetation and accelerates biomass turnover. Additionally, a conversion of pristine forests into managed forests leads to a net carbon release, even if forest management techniques include regrowth after harvest (Harmon et al. 1990). A reduction of standing crop changes the amount of carbon in living vegetation and results in net carbon fluxes from the vegetation into the atmosphere, contributing to increasing atmospheric CO_2 levels.

Meanwhile, appraisals of the human impact on general ecosystem properties are important for land use and land cover research. For example, changes of satellite-derived estimates of the NPP of forests have been used to estimate rates of deforestation (Jang et al. 1996). We discuss how studying the human impact on general properties of terrestrial ecosystems can contribute to the analysis of the interrelations between land use patterns, industrial resource use, and their ecological consequences. For example, there is evidence that a reduction of ecological energy flows may threaten biodiversity (Brown 1991, Wright 1983). Moreover, such studies also have practical implications, e.g., as they call into question the biological sustainability of strategies aiming at a substitution of biomass for fossil fuels in order to combat global warming.

The empirical example used in this paper is Austria, a highly industrialized Central European country with medium population density (area 83.000 km^2, population 7.8 million). Since 1995 Austria is a member of the European Union. Forests cover over 45 % of its area, a rather high percentage for Central European standards (EU average: 40 %) due to the mountainous landscape.

MATERIALS AND METHODS

As a result of the International Biological Programme (IBP), there are quite reliable data on the aboveground NPP of many vegetation units. However, data on belowground NPP and belowground standing crop still are rather uncertain. Current studies show that the belowground NPP of forest ecosystems was significantly underestimated in most of the IBP research in the Seventies, when it was usually estimated at 15 to 30 % of the aboveground NPP. In contrast, more recent work revealed that the belowground productivity may, in some cases, even surmount 100 % of the aboveground NPP (Melillo and Gosz 1983, Vogt et al. 1982, Vogt et al. 1986). Similarly, data on the belowground standing crop are uncertain. The belowground standing crop is seasonally highly variable and difficult to measure (Waring and Schlesinger 1985, Vogt et al. 1986, Sing et al. 1984). Due to these uncertainties and the lack of reliable data syntheses we restrict ourselves to aboveground NPP (abbreviated as ANPP), aboveground standing crop and aboveground turnover. The calculations were performed with respect to dry matter, carbon and energy. For converting dry matter to energy, we used calorific values for different plants or different parts of plants, respectively (decidous forests, coniferous forests, shrubs, grains and shoots of crop plants, grassland, etc.; for reference see Haberl 1995). For converting dry matter to carbon we used a conversion factor of 0.45 (Schlesinger 1997).

Definition of NPP appropriation

NPP appropriation is defined as the difference between the NPP of the potential natural vegetation and the amount of NPP remaining in nature. The former property is termed NPP_0, i.e. the NPP of the vegetation that would prevail in the absence of human interference. The NPP remaining in nature is termed NPP_t, i.e. the amount of biomass currently available in ecological cycles.

Two processes contribute to the appropriation of net primary production: (1) Land use changes the average productivity of ecosystems. (2) Harvest extracts NPP from ecosystems. Both processes reduce the amount of energy available as an input to heterotrophic food chains. We denote the NPP of the actual vegetation as NPP_{act}, and harvest as NPP_h. With these conventions, NPP appropriation can be defined as follows (Haberl 1997):

$$NPP_a = NPP_0 - NPP_t \quad \text{with} \quad NP_P = NPP_{act} - NPP_h$$

While this definition is straightforward for grasslands and cultivated land, it raises some problems with wood harvest from forests; i.e., from long-accumulated biomass stocks. In treating the harvest of wood in a larger region as a percentage of the NPP of all forested ecosystems in this region, it tacitly assumes that logging occurs in forests which are allowed to regrow after harvest.

Whereas this actually is the case in Austria, the concept would have to be extended if it should be applied to regions where deforestation plays an important role. In this case, it would be necessary to distinguish harvest from continually managed forests or wood plantations from destructive harvest (Wright 1990).

As we restrict our work to aboveground NPP, we count every removal of biomass from the aboveground component as NPP appropriation. Thus, agricultural residues remaining on a field and ploughed into the soil after harvest are regarded as „appropriated".

Land Use and Land Cover Data

The appraisal of NPP appropriation requires the calculation of NPP_0, NPP_{act} and harvest. To assess the first two properties and the estimates of potential and actual standing crop in Austria, we used the following sources of land use and land cover data:

1. „*Statistical data*": Land use and land cover data of the Austrian Central Statistical Office, based on agricultural statistics, forestry statistics and land use statistics (real estate statistics).

2. „*Corine data*": Land cover data visually derived from satellite imagery, aerial photography and topographic maps by the Environmental Agency Austria (EEA) in the European „Corine land cover" program (Aubrecht 1998, Liebel and Aubrecht 1996).

3. „*ARCS data*": This land cover model was automatically derived from Landsat TM-images by the Austrian Research Centre Seibersdorf (ARCS). These data have a high spatial resolution and were used to derive maps of productivity, NPP appropriation, and standing crop.

The *statistical data* refer to municipalities (n = 2350) as the smallest spatial unit and allow a discrimination between about 40 land use categories. Agricultural areas and grasslands are finely differentiated, distinguishing 17 main crops and 8 types of grasslands. There are also data on built-up area, vineyards, gardens etc. The minimum area recorded in land use statistics is 1 ha (104 m^2). In real estate statistics – which we used to assess built-up land and other urban areas – there is no such lower limit. There is some spatial distortion due to the fact that a parcel of land is allocated to the municipality where the owner of the parcel resides, even if the parcel itself is located in another municipality (ÖSTAT 1992, Schieler et al. 1996, Gerhold 1992). Statistical data are the only available source for time-series calculations. The land cover data derived from statistics we used are compiled in Table 1.

Table 1: Land use and land cover in Austria 1950-1995, according to statistical data.

Year	Urban areas	Agriculture	Grasslands	Forests	Alpine area
			[km²]		
1950	1 689	15 109	20 346	34 778	10 958
1960	2 067	15 707	19 367	34 627	10 972
1970	2 459	15 046	18 380	35 959	10 950
1980	2 926	15 129	17 070	36 737	10 964
1990	3 266	14 354	15 499	38 735	10 964
1995	3 417	13 014	16 378	39 036	10 968

Source: compiled from various data sources of the Austrian Central Statistical Office.

The *Corine data* distinguishes 44 different land cover classes, 26 of which apply to Austria. Data source are Landsat TM images collected in summer 1995 and 1996 with a spatial resolution of 30 m which were repeated every 16 days. The interpretation of satellite images was supported by topographic maps (1:50 000), infrared aerial photography and statistical data. Objects had to have a minimum size of 25 ha to be recorded; longitudinal objects had to be at least 100 m broad. The Corine land cover data was only available for this study as a table of land use class areas for the 99 Austrian districts not suitable for mapping.

The *ARCS data* set was derived using 12 cloud-free Landsat TM scenes covering the entire area of Austria with a geometric resolution of 30 m (one pixel represents an area of 30 x 30 m) and a spectral resolution of 7 different channels describing the reflectance of the solar radiation in wave-length classes ranging from visible light to far infrared. The images were all acquired between 5 August 1991 and 5 October 1991, except one quarter scene which was taken in August 1992. In addition to the image data, a digital elevation model (DEM) with a resolution of 50 m was used for geocoding the image data set in mountainous terrain. Geocoding is the geometric transformation process that recalculates the image coordinates to map coordinates. Through the geocoding process, the spatial resolution of the image was enhanced from 30 m to 25 m.

The land cover classification was performed after geocoding. The goal of the classification was to gain 15 land use classes adapted from the Corine land cover nomenclature Level II, as described in Table 2. The spectral classification process starts with an unsupervised pre-classification performed by cluster analysis that discriminates 50 significant spectral classes for every scene. These spectral classes were aggregated to the Corine land cover classes described in Table 2. Some classes - e.g. „mixed build up area“ and „vineyards“ - were classified by supervised classification with training areas. Grassland classes above the timberline were defined as „alpine pasture“ using the DEM with specific elevation levels as threshold. The final classification and aggregation of primary classes was performed by a spatial postclassification algorithm using moving windows (4x4 pixels and 8x8 pixels) on the pre-classification grid derived from the geocoded satellite images. The postcassification algorithm is based on rules considering the frequency of sub-classes to be found within one „moving window“. Usually, the majority of primary classes and class combinations within one moving window is used to define the final land use class. The final classification using the 15 level II Corine land cover classes was generated with a spatial resolution of 100 x 100 m (Steinnocher 1996). For validation of the classification results, KFA-1000 analogue infrared photographs were used as reference information. These photographs (resolution approximately 7 m) cover 80 % of the Austrian territory and were acquired by the Russian MIR-satellite in 1991.

Table 2: Land use nomenclature as used in the ARCS land cover model

I. Artificial surfaces	I.1. High density urban
	I.2. Low density urban
	I.3. Green urban
	I.4. Industrial/commercial/traffic
	I.5. Mineral extraction sites
II. Agricultural areas	II.1. Arable land
	II.2. Vineyards
	II.3. Pastures
	II.4. Heterogenous agricultural areas
III. Natural areas	III.1. Forest
	III.2. Natural vegetation
	III.3. No vegetation
	III.4. Glacier
IV. Wetlands	IV. Wetlands
V. Water	V. Water

Source: adapted from the Corine 1993 inventory (Aubrecht 1996, Liebel and Aubrecht 1996).

Net Primary Productivity

The aboveground production of the potential vegetation ($ANPP_0$) was calculated on the basis of a digital elevation model (DEM). The DEM was used to reflect changes in productivity related to elevation. Because Austria is a small country, there is comparatively little variation in the vegetation type usually predominating in an elevation class. The Austrian climate is humid (600-1200 mm precipitation), and precipitation is positively correlated with elevation. Thus, with rising elevation, NPP is limited by shorter growing seasons and lower temperature. We used the function for the dependence of productivity from elevation displayed in Table 3 (p.5). The productivity data used reflect climax vegetation communities occuring in Austria: forests, alpine shrubs and alpine pastures. Which climax community was assumed depended on elevation; i.e., if the pixel was located below or above the timberline.

Table 3: Values of the aboveground productivity of potential vegetation and forests per unit area as used in the calculation of ANPP0 and ANPPact. Which productivity value is used between 1700 m and 2100 m elevation depends on the region (see text).

Elevation	Typical potential vegetation	Forests [$MJ.m^{-2}.yr^{-1}$]	Alpine Tundra [$MJ.m^{-2}.yr^{-1}$]
100	Mixed decidous forests	21,60	
200		21,40	
300		21,20	
400		21,00	
500		20,60	
600		20,36	
700	Mixed decidous / coniferous forests	20,09	
800		19,78	
900		19,45	
1000		19,09	
1100		18,70	
1200		18,28	
1300		17,83	
1400		17,33	
1500	Subalpine coniferous forests / shrubs	16,73	
1600		16,03	
1700		15,23	
1800		14,33	9,60
1900	Subalpine forests (mainly coniferous) / shrubs / alpine tundra	13,33	8,66
2000		12,13	7,52
2100		10,83	6,50
2200		9,43	5,28
2300	Nival vegetation		4,34
2500			2,20
3000			0,50
3800			0,20

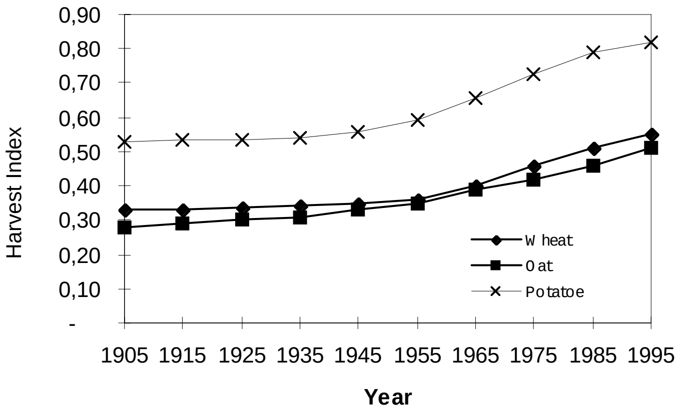
Sources: Cannell 1982, Walter and Lieth 1973 and the literature review documented in Haberl 1995

In Austria, the timber line is up to 450 m higher in the central alps than in the peripheral alpine regions. In order to reflect this we developed a spatial timberline model with a continually increasing timberline from peripheral to central alpine regions, essentially based upon the existing timberline, but considering the fact that the actual timberline is reduced significantly through alpine land use. While the „forest“ value (Table 3) was used below the timberline, the „alpine tundra“ value was used above the timberline. The data in Table 3 were obtained using regression analyses on the relation between mean annual temperature, precipitation, and productivity in forest ecosystems using data from literature reviews and data compilations (e.g., Cannell 1982, DeAngelis et al. 1981, Haberl 1995) and climate data (Walter and Lieth 1973).

The $ANPP_{act}$ was calculated on the basis of the three land use and cover data sets described above. In forests we assumed that the actual productivity was equal to that of the potential vegetation. This assumption was cross-checked with the Austrian forest inventory (Schieler et al. 1996): the difference between estimates of the ANPP based on the forest inventory and the estimates reported here was only 2 %.

To calculate the actual productivity of agricultural areas and harvested meadows we used harvest factors of the form NPP = H x F where H is the commercial harvest and F an appropriate factor to extrapolate aboveground productivity. Plant breeding aims at an increase of the proportion of the edible parts to the total plant biomass which tends to lower harvest factors. For calculating the time-series, we performed a literature review to assess the change in harvest indices for the most important cultivars over time (e.g., Austin et al. 1980, Donald and Hamblin 1976, Donald and Hamblin 1984, Feil 1992, Riggs et al. 1981, Sing and Stoskopf 1971). The development of harvest indices for important crops are displayed in Figure 1. However, it is important to note that harvest data are only available with a spatial resolution of districts (n=99) which can cause artificial boundaries in maps in some cases (see section „Results“).

Figure 1: Harvest indices for various crops 1950-1995 as used in calculating ANPPact.



Sources: Austin et al. 1980, Donald and Hamblin 1976, Donald and Hamblin 1984, Feil 1992, Riggs et al. 1981, Sing and Stoskopf 1971

The productivity of other land cover classes was calculated on the basis of literature reviews and held constant throughout Austria (for reference see Haberl 1995, Schulz 1999).

Harvest was calculated according to agricultural and forestry statistics (ÖSTAT 1992, Gerhold 1992). Agricultural biomass was converted to dry matter and calorific value using standard tables on nutritive value of the materials under consideration. Wood was treated alike, based on tables on species-specific dry matter content and calorific value. Additionally, estimates for biomass harvest in urban areas (e.g., management of parks, horticulture in gardens etc.) and grazing on alpine pastures was taken into account, based on estimates per unit area.

Standing Crop

The appraisal of the standing crop of the potential Austrian vegetation was based on vegetation data – e.g., distribution of tree species in the potential vegetation (Mayer 1974) – and data on elevation and climate. The potential vegetation was assumed to consist of climax vegetation; i.e., we assumed old-growth forests (Reichle 1975, Sprugel 1985, Shugart 1984). Above the timber line, alpine shrubs were assumed to prevail, except on glaciers and rocky grounds. The standing crop of old-growth stands of the tree species occuring in the potential vegetation of Austria (*Fagus sylvatica, Quercus sp., Abies sp. Picea abies, Pinus sp.* and other temperate decidous forests) was calculated using logistic regressions for the standing crop of the respective species depending on stand age (Figure 2, S. 7) using the formula

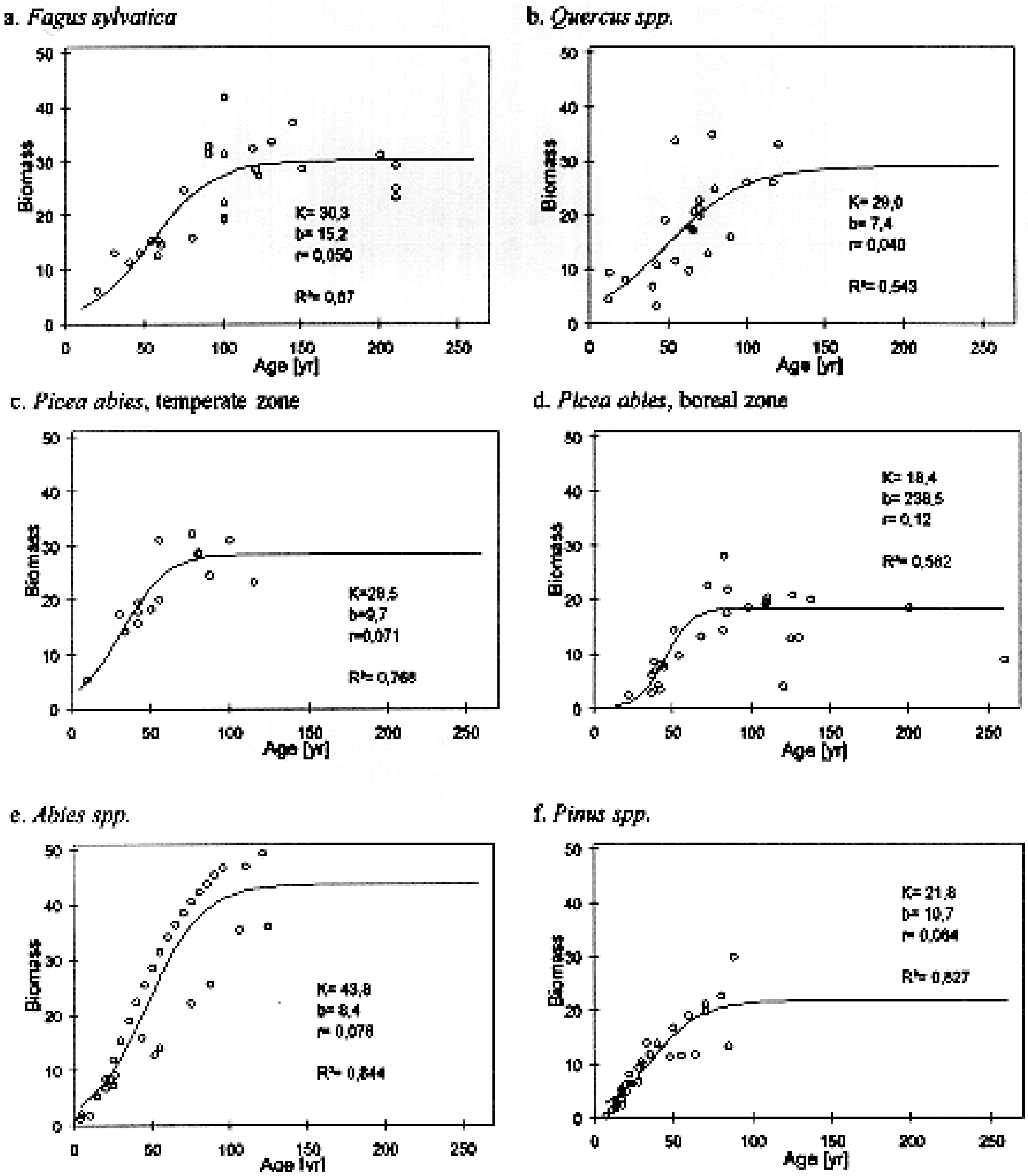
$$SC(t) = K / (1 + b \cdot e^{-r \cdot t})$$

where SC denotes standing crop, t stand age, K the standing crop of old-growth stands of the respective species, b a regression factor, and r a growth factor.

These regressions yielded comparably satisfactory fits ($0{,}54 < r^2 < 0{,}83$, depending on the tree species), whereas regressions between standing crop, temperature and precipitation failed to produce satisfactory results. Alpine communities were assessed on the basis of a literature review (Ajtay et al. 1979, Franz 1979, Paulsen 1995; for more detail see Erb 1999). Standing crop estimates of different vegetation units as used in our calculations are displayed in Table 4 (S. 8).

While the ANPP of actual forests is similar to that of the potential forests, there are significant differences in standing crop: forest management reduces the average stand age and thus the standing crop of actual forests, compared to the potential vegetation (Harmon et al. 1990). In order to account for the reduction of standing crop through forest management, we calculated

Figure 2. Logistic regressions for the standing crop of the main forest species of Austria, depending on stand age.



„Biomass" is the aboveground standing crop in kg/m². We only included study sites with a mean annual temperature between 4°C and 14°C and a yearly mean precipitation of more than 450 mm. The regressions result in K-values for Oak (*Quercus spp.*) of 29,0 kg/m², for beech (*Fagus sylvatica*) of 30,3 kg/m², for fir (*Abies spp.*) of 43,8 kg/m², for montane spruce (*Picea abies*, temperate zone) of 28,5 kg/m², for subalpine spruce (*Picea abies*, boreal zone) of 18,4 kg/m² and for Pine (*Pinus spp.*) of 21,8 kg/m².

Sources: Cannell 1982, Walter and Lieth 1973 and others; for reference see Erb 1999.

Table 4: Standing crop of typical vegetation units of the potential vegetation in Austria as used in the calculations.

Vegetation unit	Standing crop		
	Dry matter [kg.m-2]	Carbon [kgC.m-2]	Energy [MJ.m-2]
Oak *(Quercus sp.)*	29.0	13.1	560
Beech *(Fagus sylvatica)*	30.3	13.6	585
Fir *(Abies sp.)*	43.8	19.7	863
Montane spruce *(Picea abies)*	28.5	12.8	562
Subalpine spruce *(Picea abies)*	18.4	8.3	370
Alpine shrubs	1.0	0.5	20
Glaciers, rocky grounds	no veget.	no veget.	No veget.

Source: own calculations.

the standing crop of the Austrian forests based on the forest inventory (Schieler et al. 1996). The forest inventory only contains data on usable timber which we used to obtain estimates of standing crop using „expansion factors" based on data from the literature (Cannell 1982, Burschel et al. 1993) to reflect branches and twigs, leaves, fruits, blossoms and understorey. These expansion factors depended on stand age (Körner et al. 1993, Mitscherlich 1975, Paulsen 1995). Vegetation gaps and bush areas were also considered (Dörflinger et al. 1994, Sattler 1990). The standing crop of agricultural areas was assessed as the peak biomass of fields – i.e., the standing biomass at the time of harvest – assessed on the basis of the harvest factors described above. The standing crop of most grassland types was estimated at 0.55 kg.m^{-2} (Erb 1999); exceptions were fallows (0.38 kg.m-2) and alpine pastures above 1700 m elevation (0.42 kg.m-2. We assumed that the standing crop of alpine shrubs was equal to that of the potential vegetation.

RESULTS

Appropriation of aboveground NPP

According to our calculations, the aboveground NPP of the potential vegetation is 1 481 PJ.yr^{-1} which is an average of 17.7 MJ.m^{-2}.yr^{-1} or a dry matter production of about 0.9 kg.m^{-2}.yr^{-1} (about 0.4 kg C.m^{-2}.yr^{-1}). Table 5 shows a breakdown of the ANPP to six elevation classes, revealing that mixed decidous forests below 600 m elevation account for 47.5 % of the ANPP$_0$. Most most urban and agricultural land use is situated in this elevation class. A previous study (Haberl 1997) had showed that Lieth´s „Miami" model (Lieth 1975), based on mean annual precipitation and long-term temperature averages (corrected for belowground NPP), yielded only 3 % lower values than the method used here, but appeared to over-estimate the productivity in high alpine regions.

Table 5: Aboveground net primary production of the potential vegetation in Austria

Elevation	Typical vegetation	Area [Km²]	ANPP Dry matter [Mt.yr-1]	Carbon [MtC.yr-1]	Energy [PJ.yr-1]
<600 m	mixed decidous forests	33 834	36.1	16.2	704
600-1400 m	mixed decidous / coniferous forests	26 135	26.2	11.8	510
1400-1700 m	subalpine coniferous forests	9 691	8.4	3.8	163
1700-2200 m	subalpine forests / shrubs	8 098	4.8	2.2	94
2200-2800 m	alpine shrubs	4 228	0.5	0.2	10
>2800 m	nival vegetation	719	0.0	0.0	0
Total	(without inland water areas)	82 761	76.0	34.2	1.481

Source: own calculations.

The three different data sets on land use and cover result in similar estimates of the overall $ANPP_{act}$ (see Table 6). The statistical data produce the lowest estimate of the ANPP (1 276 $PJ.yr^{-1}$). The two land use and cover models based on satellite imagery yield similar values of 1 284 $PJ.y^{r-1}$ and 1 287 $PJ.yr^{-1}$, respectively. All three hest estimate of class „II agricultural areas", resulting in the highest ANPP, whereas ARCS data are lowest. The estimate of the area (and ANPP) of the land cover class „III-natural areas" is highest according to the ARCS data and lowest according to the Corine data.

Table 6: Aboveground NPP of the actual vegetation in Austria around 1990 according to three different sets land use and cover data in energy units – breakdown by actual land cover.

	ARCS data		Corine data		Statistical data	
	area [km^2]	ANPP [$PJ.yr^{-1}$]	area [km^2]	ANPP [$PJ.yr^{-1}$]	area [km^2]	ANPP [$PJ.yr^{-1}$]
I.1 High density urban	75	0	71	0	942	0
I. 2 Low density urban	1 513	18	1 232	15	2314	28
I.3 Green urban	16	0	32	0	n.d.	n.c.
I.4 Industr., comm., traffic	112	0	104	0	n.d[1]	n.c.
I.5 Mining	38	0	62	0	n.d.	n.c.
Total I ("artificial surfaces")	1 753	19	1 500	16	3 256	28
II.1 Arable land	11 500	213	11 421	215	12 532	230
II.2 Vineyards	696	9	586	8	582	8
II.3 Pastures	5 177	85	8 842	145	8 368	138
II.4 Heterog. agric. areas	10 271	127	9 594	123	8 160	83
Total II ("agricult. areas")	27 644	434	30 444	491	29 642	458
III.1 Forest	41 377	782	38 955	736	38 898[2]	741
III.2 "Natural veget."	7 490	36	5 590	27	4 584	22
III.3 Alpine / no vegetation	4 256	10	6 028	15	5 607	27
III.4 Glacier	464	0	566	0	719	0
Total III ("natural areas")	53 587	828	51 139	777	49 807	790
IV Wetlands	200	3	151	3	n.d.	n.d.
V Inland water	667	n.c.	640	n.c.	1 153	n.c.
Austria total	83 851	1 284	83 874	1 287	83 859	1 276

n.d. ... no data, n.c. ... not considered
1 included in I.1, high density urban
2 excluding forests above 1 700 m elevation (which were considered in productivity estimate of the class III.2 „natural vegetation")
Sources: ARCS land cover data based on Landsat TM images (Steinnocher 1996), Corine land cover data (Aubrecht 1996, Liebel and Aubrecht 1996, Umweltbundesamt 1998), Statistical land cover data compiled by H. Haberl, N. Schulz, and F. Krausmann.

models show that the ANPP of the actual vegetation is significantly lower than that of the potential vegetation. The „prevention" of ANPP induced by land use may be estimated between 13.0% and 13.3% of the $ANPP_0$. However, while total $ANPP_{act}$ estimates are similar, there are marked differences between the three data sets for different land cover classes. The land cover class „I artificial surfaces" covers most area in the statistical data and the smallest area in the Corine data. Both sources relying on remote sensing (ARCS data and Corine data) give much lower estimates for „I.1 high density urban" areas than the statistical data. Statistical data for the classes I.3-I.5 are not available. Corine data yield the hig-

Only one data set on harvest, relying mainly on agricultural and forestry statistics, was considered (Table 7, p. 10). Harvest in „urban areas" includes the mowing of lawns, gardening in parks and harvest in private gardens. Agriculture (including urban areas) accounts for 64 % of the harvested biomass energy, including cropland (39 %) and grasslands (16 %). Forests contribute 34 % of the harvested energy.

Table 8 (p. 10) summarizes the results for the socio-economic appropriation of ANPP in Austria. The three data sets result in estimates of overall ANPP appropriation between 50.7 % and 51.4 % of the $ANPP_0$. Land cover data relying

Table 7: Harvest of biomass in Austria in 1990.

Land use class	Harvest			
	Dry matter [Mt.yr-1]	Carbon [MtC.yr-1]	Energy [PJ.yr-1]	Distribution [% of total]
Urban areas	0.74	0.33	14	2 %
Arable land	11.90	5.35	215	39 %
Vineyards	0.39	0.17	7	1 %
Grasslands	5.12	2.30	92	16 %
Heterogeneous agricultural areas	2.04	0.92	37	7 %
Grazing on alpine pastures	0.17	0.08	3	1 %
Total agriculture	19.62	8.82	354	64 %
Forests[1]	9.65	4.34	188	34 %
Total Austria	30.00	13.50	557	100.0 %

[1] Average of the years 1988-1992.
Sources: Gerhold 1992, ÖSTAT 1992, own calculations

Table 8: Appropriation of aboveground NPP in Austria around 1990 in energy units: Aboveground productivity of the potential vegetation (ANPP0), of the actual vegetation (ANPPact), harvest of ANPP, ANPP remaining in ecosystems (ANPPt) and ANPP appropriation (ANPPA).

	Unit	ARCS data	Corine data	Statistical data
$ANPP_0$	[PJ.yr-1]	1 481	1 481	1 481
$ANPP_{act}$	[PJ.yr-1]	1 284	1 287	1 276
Harvest	[PJ.yr-1]	557	557	557
$ANPP_t$	[PJ.yr-1]	727	730	720
$ANPP_A$	[PJ.yr-1]	754	751	762
$ANPP_A$	[% of $ANPP_0$]	50.9%	50.7%	51.4%

Source: Own calculations.

on satellite imagery tends to produce lower estimates of NPP appropriation than statistical data.

The ARCS data was used to produce maps of primary production processes in Austria. Figure 3a (annexe) visualizes the spatial distribution of the ANPP of the potential vegetation. The potential vegetation was assumed to consist of climax forests below the timberline which in Austria is between elevations of 1800 m and 2250 m, with the highest values in the central alps and the lowest values on the edge of the alpine region. Above the timberline, alpine shrubs and alpine pastures were assumed to prevail. Thus, Figure 3a (annexe) mainly reflects elevation, with the highest productivity in the lowlands and lowest in the high alpine regions.

Figure 3b (annexe) shows the spatial distribution of the ANPP of the actual vegetation. Yellow areas in the lowlands depict the larger Austrian cities. Dark blue indicates the areas where forests remained intact in the lowlands. The fragmentation of forests is clearly visible. Green and light blue colored low-lying areas (see Figure 3a for comparison) refer to different agricultural land cover classes (cropland, grasslands, etc.). Their productivity was modelled based upon harvest data available on the spatial level of provinces (n=99); i.e., all grid cells of an agricultural land cover class within one district were assumed to be equal. This can lead to artificial boundaries between adjacent districts (see the north-eastern parts of the map in Figure 3b, annexe).

Figure 3c (annexe) visualizes the spatial distribution of the proportion of the ANPPact actually remaining in ecosystems; i.e., the $ANPP_t$. It shows that the amount of energy available in intensively harvested areas and the centers of cities is nearly as low as in highly alpine areas, whereas the highest $ANPP_t$ values are encountered in forested areas. Essentially, Figure 3c (annexe) distinguishes between forests (green), urban and agricultural areas (yellow) and alpine areas (yellow or white, depending on elevation and land cover).

ecosystems covering these areas more or less constant, the increase in forested areas more than offsets the growth in urban areas. As a consequence, ANPP appropriation in Austria slightly decreases from 53 % in 1950 to 51 % in 1995.

Table 9: Time-series of the aboveground net primary production (ANPPact) and biomass harvest in Austria 1950, 1970 and 1995 in energy units – breakdown to land use classes.

	$ANPP_{act}$ [PJ.yr^{-1}]			Biomass harvest ($ANPP_h$) [PJ.yr^{-1}]		
	1950	1970	1995	1950	1970	1995
Urban areas	14	21	29	7	11	15
Agriculture	155	249	237	125	215	213
Grasslands	170	227	203	81	126	112
Forests	657	679	741	134	117	199
Alpine areas	47	47	47	3	3	3
Total	1042	1223	1257	350	472	542

Source: own calculations.

Figure 4 (annexe) shows the spatial distribution of aboveground NPP appropriation in Austria. It shows that NPP appropriation is highest in the lowlands currently used as croplands and other intensively managed agricultural ecosystems. The lowest levels of NPP appropriation are encountered in high alpine regions. However, in the high regions there are some plots with a very high NPP appropriation, appearing as red dots. These presumably are regions in which the timberline has been reduced and forests have been replaced with alpine pastures.

Time-series of NPP appropriation 1950-1995

The calculations of $ANPP_{act}$ and biomass harvest for the period of 1950 to 1995 rely solely on statistical data. The productivity of the potential vegetation was assumed to be constant. In this period, the aboveground productivity of the Austrian vegetation increased by 20.6 % while harvest rose by 54.9 % (Table 9). Two trends are responsible for the increase in productivity: (1) Forested areas (with the highest productivity per unit area) increased by 12 % at the expense of less productive agricultural and grassland areas. (2) The productivity of agricultural areas and grasslands grew considerably, due to agricultural intensification (e.g., more fertilizer and irrigation), in turn allowing for higher harvests. As Figure 5 (p. 12) shows, both harvest and $ANPP_{act}$ grew parallel until 1985 and remained more or less constant afterwards. While increases in the $ANPP_{act}$ of agricultural areas appear to allow for increased harvests, but leave the ANPP remaining in the

Aboveground standing crop and biomass turnover

The calculations of the aboveground standing crop were based upon the statistical data. Table 10 (p. 12) displays the results for the standing crop of the potential Austrian vegetation. The total standing crop is estimated at 2.2 billion tons dry matter (994 MtC) with a calorific value of 43.2 EJ. Forests account for the bulk of this biomass (99.8 %), the remainder being alpine tundra. Coniferous forests account for 26.7 % of the biomass, decidous forests for 45.5 %, mixed forests for 27.7 %. We mapped the spatial distribution of the standing crop of the potential vegetation in Austria (Figure 6a, annexe), based upon the ARCS land cover data. Whereas there is a monotonously declining gradient of ANPP from low to high altitudes, the aboveground standing crop is highest in medium altitudes. The decidous tree species dominating at low elevations (e.g., *Fagus sylvatica*, *Quercus spp.*) reach considerably lower standing crop maxima than firs (in Austria: *Abies alba*) which play an important role in the potential vegetation in alpine forest communities (see Figure 2a,b,e). Thus, while lowlands generally fall between 13 and 14 kgC.m^{-2}, the aboveground standing crop surpasses 15 kgC.m^{-2} in peripheral alpine regions. The standing crop of high alpine forests and especially that of vegetation units above the timber line, of course, is much lower.

Table 11 (p. 12) reveals that the standing crop of the actual Austrian vegetation is significantly smaller than that of the potential vegetation. The

Figure 5: Human appropriation of aboveground net primary production in Austria (excluding the province of Burgenland) from 1950 to 1995: ANPP of the actual vegetation (ANPPact), ANPP remaining in ecosystems (ANPPt) and harvest of ANPP (ANPPh). ANPP appropriation (ANPPa) was calculated assuming a constant value of the ANPP of the potential vegetation (ANPP0 = 1404 PJ.yr-1).

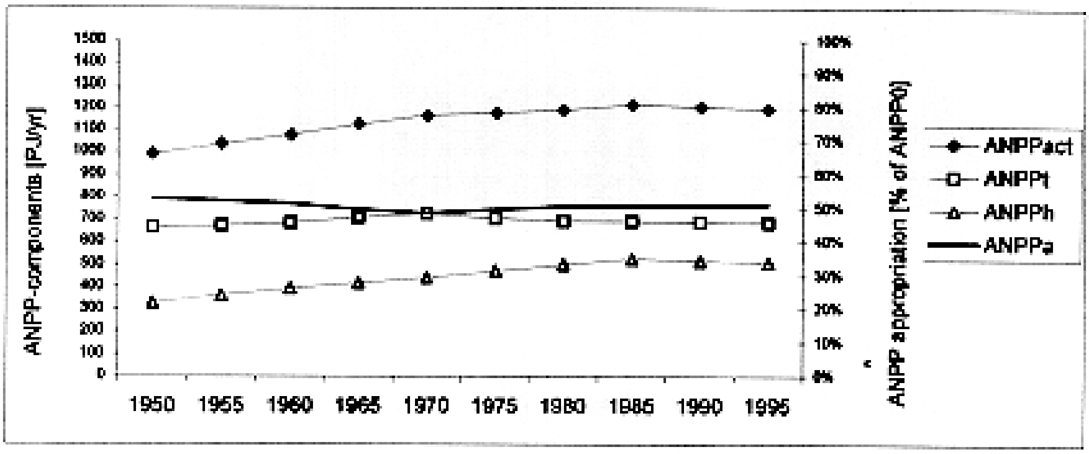


Table 10: Standing crop of the potential Austrian vegetation.

Vegetation type	Area	Dry Matter		Standing crop Carbon		Energy	
	[km²]	[Mt]	[kg.m⁻²]	[MtC]	[kgC.m⁻²]	[EJ]	[MJ.m⁻²]
Decidous forest	33 823	1 004	29.7	452	13.4	19.4	573
Coniferous forest	25 160	590	23.4	265	10.5	11.7	465
Mixed forest	17 850	611	34.2	275	15.4	12.0	674
Total forest	76 832	2 204	28.7	992	12.9	43.1	561
Alpine Tundra	5 139	5	1.0	2	0.5	0.1	20
Area with vegetat.	82 690	2 209	26.7	994	12.0	43.2	523
Total of Austria	83 857		26.3		11.9		515

Table 11: Standing crop of the actual vegetation in Austria 1990.

Vegetation type	Area	Dry matter		Standing crop Carbon		Energy	
	[km²]	[Mt]	[kg.m⁻²]	[MtC]	[kgC.m⁻²]	[EJ]	[MJ.m⁻²]
Coniferous forest	23 669	428	18.1	193	8.1	8.4	354
Decidous forest	2 080	43	20.7	19	9.3	0.8	406
Mixed forest	14 040	300	21.3	135	9.6	5.9	418
Forest total	39 789	770	19.4	347	8.7	15.1	379
Alpine Tundra	5 607	6	1.0	3	0.5	0.1	20
Agriculture	13 384	11	0.9	5	0.4	0.2	16
Grasslands	15 288	8	0.5	4	0.2	0.2	10
Alpine pastures	4 584	2	0.4	1	0.2	0.0	8
Horticulture	0 969	5	4.7	2	2.1	0.1	92
Built-up area	2 349	0	-	-	-	-	-
Total vegetation	79 622	802	10.1	360	4.5	15.7	200
Veget.+built-up area	82 687		9.7		4.4		190
Austria total	83 859		9.6		4.3		187

Source: own calculations

actual standing crop totals 802 million tons dry matter or about 15.5 EJ, which is 64 % less than that of the potential vegetation. Forests predominate as they account for 94.8 % of the total actual standing crop. Agriculture contributes 2.3 %, all other vegetation units 2.9 %. Figure 6b shows the spatial distribution of the actual standing crop, revealing the fragmentation of forests (6-10 $kgC.m^{-2}$) due to agricultural land use (below 1 $kgC.m^{-2}$) and urban areas (between these classes).

Table 12 compares the actual standing crop of main currently prevailing vegetation classes in Austria with the standing crop of the potential vegetation that would be expected to grow on the respective area. On the average, the standing crop of the actually prevailing vegetation is 36 % of that of the potential vegetation. Depending on land cover class, between 0 % and 77 % of the initially existing standing crop remain. The percentage of remaining standing crop is highest in forests (62-77 %) and lowest in agricultural areas, grasslands and built-up areas (0-3 %). Forest management reduces the average standing crop on the currently forested areas by 30 %, compared to old-growth stands. That the reduction in standing crop values is highest in mixed coniferous / decidous stands results from the significant reduction of the density of firs (Abies alba).

Table 13 (p. 14) and Figure 6c (annexe) show the acceleration of the turnover (NPP/Standing crop) which is a result of the land use-induced changes in ecosystem functioning described above. Whereas the average turnover of the potential vegetation is 29.2 years, the average turnover of the actual vegetation is 12.1 years – an average acceleration by a factor 2.4. However, the acceleration may even reach factors between 28-42 in land cover classes in which there is a very high reduction in standing crop.

DISCUSSION

A first calculation in the early 1970ies concluded that the amount of biomass harvested for human food was only 0.8 % of the global NPP (Whittaker and Likens 1973). This order of magnitude hardly raised concern, however, the calculation included only food consumed by humans and thus neglected the NPP foregone because of reduced productivity or used by human society for other purposes than human nutrition. A paper by Vitousek et al. (1986) estimated the global human appropriation of the products of photosynthesis between 24 and 39%. Wright (1990), using essentially the same data, but distinguishing between destructive harvest (i.e., wood harvest resulting in deforestation) and harvest from continually managed ecosystems, narrowed the range to 20 to 30%. Neither of these two calculations attempts to analyze the spatial distribution of NPP appropriation; both calculate total NPP but rely on problematic estimates as far as belowground NPP is concerned (see section „Materials and Methods“).

Table 12: Comparison of the carbon content of the potentially and actually prevailing vegetation in Austria – breakdown by actual land cover.

	Area [km²]	Potential vegetation [MtC]	Actual vegetation [MtC]	Remaining portion (d.m.) [%]
Actual land cover				
Coniferous forest	23 669	250	192	77%
Decidous forest	2 080	28	19	70%
Mixed forest	14 040	216	135	62%
Forest total	39 789	493	347	70%
Alpine Tundra	5 607	6	3	44%
Agriculture	13 384	194	5	3%
Grasslands	15 288	222	4	2%
Alpine pastures	4 584	31	1	3%
Horticulture	969	14	2	15%
Built-up area	2 349	34	-	0%
Total vegetation	79 622	994	361	36%
Veget.+ built-up area	82 690	994	361	36%
Austria total	83 859	994	361	36%

Source: own calculations

Table 13: Acceleration of the turnover as a result of standing crop reduction in Austria.

	turnover of the potential vegetation [yr]	turnover of the actual vegetation [yr]	Acceleration of turnover [factor]
Current vegetation			
Coniferous forest	27.4	20.9	1.3
Decidous forest	27.6	19.5	1.4
Mixed forest	34.5	21.4	1.6
Forest total	31.1	18,1	1.5
Alpine Tundra	11.0	4.1	2.7
Agriculture	28.7	0.9	32.0
Grasslands	28.7	0.7	41.5
Alpine pastures	29.6[1]	1.0	28.6
Horticulture	28.7	5.4	5.3
Built-up area	28.7	no veg.	no veg.
Austria total	29.2	12.1	2.4

1 potential vegetation: alpine tundra
Source: own calculations.

The calculations we present here show that the appropriation of aboveground NPP in Austria is higher than the estimates of global NPP appropriation. Moreover, NPP appropriation presumably is much higher in many central European countries than in Austria due to their considerably higher population density and their much lower proportion of forested area.

The estimate of NPP appropriation is also higher than that of a previous study by one of the authors (Haberl 1997). A large part of the difference is due to differences in definitions: whereas the previous study counted only actually harvested biomass as appropriated, we here regarded all biomass removed from the aboveground compartment as appropriated (see section „Materials and Methods"). This increases ANPP appropriation, because all ANPP on cropped areas not consumed during growth (about 5 %) is regarded as appropriated. Moreover, in-depth literature reviews carried out for this study (see section „Materials and Methods") revealed that the harvest factors used for the older study had been overly conservative; i.e., tended to under-estimate ANPP appropriation.

Modeling strategy

As described in the section „Materials and Methods", we modeled ecosystem functioning based upon average productivities or standing crop values of land cover types obtained by regression analyses and harvest factors. That is, instead of using one formal model we used various approaches depending on available input data. Basically, our modeling strategy was statistical, not process-oriented.

Currently, much effort is currently devoted to biosphere models which are able to calculate terrestrial productivity, carbon fluxes and storage, etc., in a process-oriented approach (Cramer et al. 1997, Kaduk and Heimann 1996, Schimel 1995, Schimel 1991, Schimel et al. 1997). Most of these models are primarily developed to examine past or future changes in carbon fluxes or storage or to test hypotheses on the causes of these changes (Cramer et al. 1997). One of the most important motivations is to assess the response of the terrestrial biota to elevated atmospheric CO_2 levels. To our knowledge, biosphere models have not yet been used to perform calculations like those presented here. Process-oriented modeling could provide important additional insights for studies of human NPP appropriation; e.g., it would enable us to consider the effect of climate change on the potential vegetation. Additionally, the results on the spatial distribution of $ANPP_0$ (Figure 3a) could probably be improved for some of the low regions in the eastern parts of Austria, where NPP could be expected to be limited by low precipitation in summer.

However, our modeling strategy was very flexible and made possible to incorporate a wealth of data from statistical sources. For example, for assessing the ANPP of croplands and some grassland types, we considered data for 99 districts and about 40 different crops and cross-checked the results for forests with forestry inventories – an amount of „ground truthing“ usually not possible in formal modeling. The data of agricultural statistics are generally regarded as very reliable, because there is a tradition of almost 200 years in Austria of statistical accounting for agricultural production and forestry which has lead to a highly refined and elaborated design of data collection. Moreover, until now most biosphere models are „calibrated“ to much the same NPP database we used for our calculations (Cramer et al. 1997). Therefore, while we would expect that our results could be refined and improved by using biosphere models, we would not expect fundamentally different patterns if biosphere models were used.

Differences between land cover data

The three different land cover data yield astonishingly similar results for $ANPP_{act}$ and, as we used constant values for potential productivity and harvest, ANPP appropriation. One of the reasons for this was that we tried to standardize the input data with respect to productivity (i.e., $ANPP.m^{-2}.yr^{-1}$) for comparable land cover classes; that is, we used essentially the same productivity estimates for all three calculations. The three calculations (Table 6) should, therefore, not be interpreted as a sensitivity analysis with respect to other factors than different sources of land cover data. Moreover, some of the differences at lower levels of aggregation (see Table 6) appear to offset one another. Thus, the values are more different between different data sources at lower level of aggregation than are the totals. For example, „agricultural areas“ produce 434 $PJ.yr^{-1}$ according to the ARCS data but 491 $PJ.yr^{-1}$ according to the Corine data, whereas „natural areas“ produce 828 $PJ.yr^{-1}$ according to the ARCS data but only 777 $PJ.yr^{-1}$ according to the Corine data.

An important difference is that of the estimates of urban and industrial areas, as summarized in the land cover class „artificial surfaces“. Here, the statistical data are about 2 times higher than ARCS data and Corine data. The reason is that in order to be classified, objects must have some minimum area in remotely sensed data sets (see section „Materials and Methods“), whereas real estate statistics keeps track of all parcels of land and all officially approved buildings, not depending on their size. The higher estimate of forested area in the ARCS data set is the result of a tendency of the automatic classification procedure to overestimate forested areas in alpine regions, especially in narrow valleys (Steinnocher 1996).

Human society as an ecosystem component

One conclusion of the fourth Cary Conference, hosted by the Institute of Ecosystem Studies, Millbrook, New York (McDonnell and Pickett 1997), was that better understanding the impacts of human society on ecosystems requires to regard humans as integral compartment of ecosystems rather than as a disturbance to the „natural“ evolution of ecosystems. This not only requires to outgrow the widely held preoccupation in ecology towards pristine or remote areas as study objects (Likens 1997), it also requires to develop a complex, interdisciplinary perspective on how human societies and ecosystems interact (e.g., Boyden 1992, Boyden 1993, Fischer-Kowalski and Weisz 1998, Sieferle 1997).

Comparing the processes that could be expected if the – albeit hypothetical – potential vegetation would prevail with those that can be currently observed is an approach to relate ecosystem processes to socio-economic processes. Following this kind of argument, human appropriation of NPP and the human impact on the standing crop of ecosystems and biomass turnover can be seen as measures of the „size“ of the human compartiment compared to natural processes (Daly 1992).

However useful, this approach hides changes which are not visible in the aggregate indicator „NPP appropriation“. The time-series displayed in Figure 4 reveals that NPP appropriation was more or less constant from 1950 to 1995, whereas in the same period there were significant changes in land use and land cover. For example, built-up area more than doubled and forests grew by 12 %, both at the expense of cultivated land and grasslands. At the same time, the ANPP on agricultural areas grew by 53 %, that on grasslands by 19 %. In total, biomass harvest rose by 55 % and the ANPP increased by 21 %. This increase in productivity on agricultural land was made possible through agricultural intensification; i.e., using more fertilizers, pesticides, machinery, irrigation and, hence, fossil energy.

A dynamic picture of the interrelations between human society and ecosystems, which many believe to be essential (e.g., Boyden 1992, Cronon 1997), could be promoted by regarding land use as „colonization“ of terrestrial ecosystems by human society (e.g., Bittermann and Haberl 1998, Fischer-Kowalski et al. 1997, Fischer-Kowalski and Haberl 1997). In ecology it is usual to denote the invasion of new habitats by animal or plant species as colonization. Since Elton´s classic study (Elton 1958) the ecology of invasions – e.g., the changes in ecosystems caused by invading species – has developed into an important field in ecology. We argue that it can be useful to use this notion also for human society.

There are, however, important differences. While it may be interesting to study the effect of humans invading new habitats, this process is currently more or less completed. However, what is changing is the number of people and their modes of subsistence. Thus, for analyzing the interrelations between human society and ecosystems it is not sufficient to study, for example, the significance of the metabolism of humans for ecosystem processes – the flows of materials and energy induced by human society are quantitatively much larger than that. In establishing accounts of the socio-economic flow of energy and materials the approach of „socio-economic metabolism" (Ayres and Simonis 1994, Fischer-Kowalski et al. 1997, Fischer-Kowalski 1998) is looking upon society as an ecosystem compartment exchanging water, air and a wealth of other materials (minerals, fossil fuels, biomass, etc.) with its natural environment. This includes human metabolism, metabolism of livestock and the materials and energy consumed by machinery and artifacts. The difference between Whittaker and Likens´ (1973) calculation of NPP appropriation and those of Vitousek et al. (1986), Wright (1990) and the present paper exemplarily shows the importance of not only considering human metabolism for analyzing the effects of humans on ecosystems.

In this context, indicators like those presented in this paper can be used to quantitatively analyze the colonization of ecosystem processes by human society – i.e., through land use and its effects on land cover – in a spatial as well as temporal perspective. This could contribute to current research in the field of land use and land cover change (Meyer and Turner 1994, Turner et al. 1994).

Significance for Carbon Balances

The difference between the standing crop of the potential Austrian vegetation and the actual vegetation is 1 419 Mt biomass (dry matter) or about 640 Mt carbon. This amount of carbon has been released to the atmosphere in the past 1000 to 2000 years of agricultural and industrial socio-economic development in Austria. For comparison it may be noteworthy that Austrian CO_2 emissions from fossil fuel combustion are about 16 $MtC.yr^{-1}$. A buildup of standing crop, e.g. due to increasing forested areas or reducing logging, could, therefore, temporarily lead to a net CO_2 absorption. This, however, is only possible because of the reduction of the standing crop in the past. A periodical monitoring of the standing crop would be a prerequisite for determining the amount of absorbed CO_2 and would, thus, contribute to clarifying the currently much debated question of carbon sinks (Houghton 1995, Schimel 1995).

Possible effects on biodiversity

There is evidence that NPP appropriation and the human impact on standing crop may be important for biodiversity. The reduction of standing crop may be relevant because it is an indicator for the loss of structural diversity occuring when forests are converted to intensively used land. The hypothesis that NPP appropriation may impact on biodiversity is grounded in the so-called species-energy theory dating back to G.E. Hutchinsons famous „Homage to Santa Rosalia" (Hutchinson 1959) and recently revived by several authors (Brown 1991, Brown 1995, Wright 1983, Wright 1987).

The species-energy theory predicts that the number of species which can inhabit a certain environment increases with the amount of energy available; conversely, the number of species is supposed to decrease if the energy flow is reduced. The rationale behind this is that in habitats with abundant resources rivaling species will be able to specialize with respect to more gradients and thus can avoid extinction due to Gauses´ principle of competition exclusion (Brown 1991). The species-energy theory has been shown to be an extension of species area-theory (Wright 1983) based upon the theory of island-biogeography by Mac Arthur and Wilson (MacArthur and Wilson 1967). Species-energy theory claims that this assertion can be explained by the fact that ceteris paribus bigger islands provide more energy, and predicts that among islands of the same size more productive ones will support a higher number of species. The species-energy theory is able to explain the gradient of species diversity from the poles to the equator and there is some empirical evidence to support it (Wright 1987, Currie and Paquin 1987, Turner et al. 1987, Turner et al. 1988).

However, the species-energy theory is challenged on the grounds that there are counter-examples, empirical examples are not convincing, and is difficult to explain mechanistically (Rosenzweig 1971, Rosenzweig 1995). Calculations like those presented below, allowing spatially highly resolved comparisons of patterns of ecological energy availability and species diversity, could contribute to the design of studies aimed at generating better empirical evidence.

CONCLUSIONS

The impact of human land use on ecological patterns and processes is significant. In Austria, the aboveground NPP of the actual vegetation is about 13 % lower than that of the potential vegetation, reflecting climatic and edaphic conditions, would be expected. Additionally, about 44 % of the actual aboveground NPP is harvested. When NPP appropriation is defined as the difference between the NPP of the potential vegetation and the amount of NPP actually remaining in ecological cycles, and, thus, available as energy input for ecological food chains, we conclude that about 51 % of the potential aboveground NPP is „appropriated“ by humans in Austria. The same land use processes result in a considerable reduction of the standing crop: the standing crop of the actual vegetation is about 64 % lower than that of the potential vegetation, resulting in a considerable net release of carbon to the atmosphere which occurred during cultivation. The standing crop is reduced much more than the productivity of the vegetation, due to the fact that land use favors herbaceous plants at the expense of woody species. This results in a considerable increase of biomass turnover: The average turnover (NPP/standing crop [yr]) has been accelerated by a factor of 2.4.

Comparing actually prevailing ecosystem patterns and processes with potential patterns and processes is an approach to generate indicators for the „size“ of a human society vis-a-vis its natural environment. This approach is useful for developing environmental indicators (Bittermann and Haberl 1998, Munasinghe and Shearer 1995) and it also has practical implications. For example, current strategies to substitute biomass for fossil fuels could be problematic if they increase NPP appropriation and induce land use changes lowering the amount of carbon stored in live vegetation. The practical importance of these considerations could increase if the currently anecdotal evidence for a relation between energy flows and biodiversity would be confirmed. To further analyze this „species-energy“ hypothesis, empirical data like those presented in this paper could be essential because they could make possible a comparison of the spatial distribution of energy availability in ecosystems with patterns of biodiversity.

Conceptualizing human society as an ecosystem compartment is an useful approach for analyzing the interactions between human societies and their natural environment (McDonnell and Pickett 1997). Current analyses of the „socio-economic metabolism“ (Ayres and Simonis 1994, Fischer-Kowalski et al. 1997, Fischer-Kowalski 1998) conceptualize society (socio-economic systems) as an ecosystem compartment maintaining material and energy flows with its environment (including water, air, minerals, fossil fuels biomass, etc.). In order to maintain these material and energy flows, human can be regarded as „colonizing“ terrestrial ecosystems – a process which can be empirically analyzed with indicators like those discussed in this paper. Our historical analysis has shown that that primary productivity is increasingly controlled by socio-economic activities. In the last 45 years, the aboveground productivity of the Austrian vegetation rose by 21 % due to agricultural intensification. Biomass harvest increased by 55 %, whereas ANPP appropriation declined slightly due to the increasing area of forests.

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ANNEXE

Figure 3: Maps of the aboveground net primary production in Austria as influenced by society:

a) ANPP0 – Productivity of the potential vegetation;

b) ANPPact – productivity of the actually prevailing vegetation;

c) ANPPt – biomass remaining in ecosystems after harvest. Source: own calculation based on the land cover model of the ARCS, derived from Landsat-TM data (see text, p. 11).

Figure 4: The spatial distribution of the human appropriation of net primary production in Austria as percentage of the ANPP of the potential vegetation. Source: own calculations based on the ARCS land cover model, derived from Landsat-TM data (see text).

Figure 6: Standing crop of the Austrian vegetation and acceleration of turnover:

a) standing crop of the potential vegetation,

b) standing crop of the actually prevailing vegetation,

c) acceleration of turnover. Source: Derived from the land cover model of the ARCS (see text, p. 14).

Figure 3

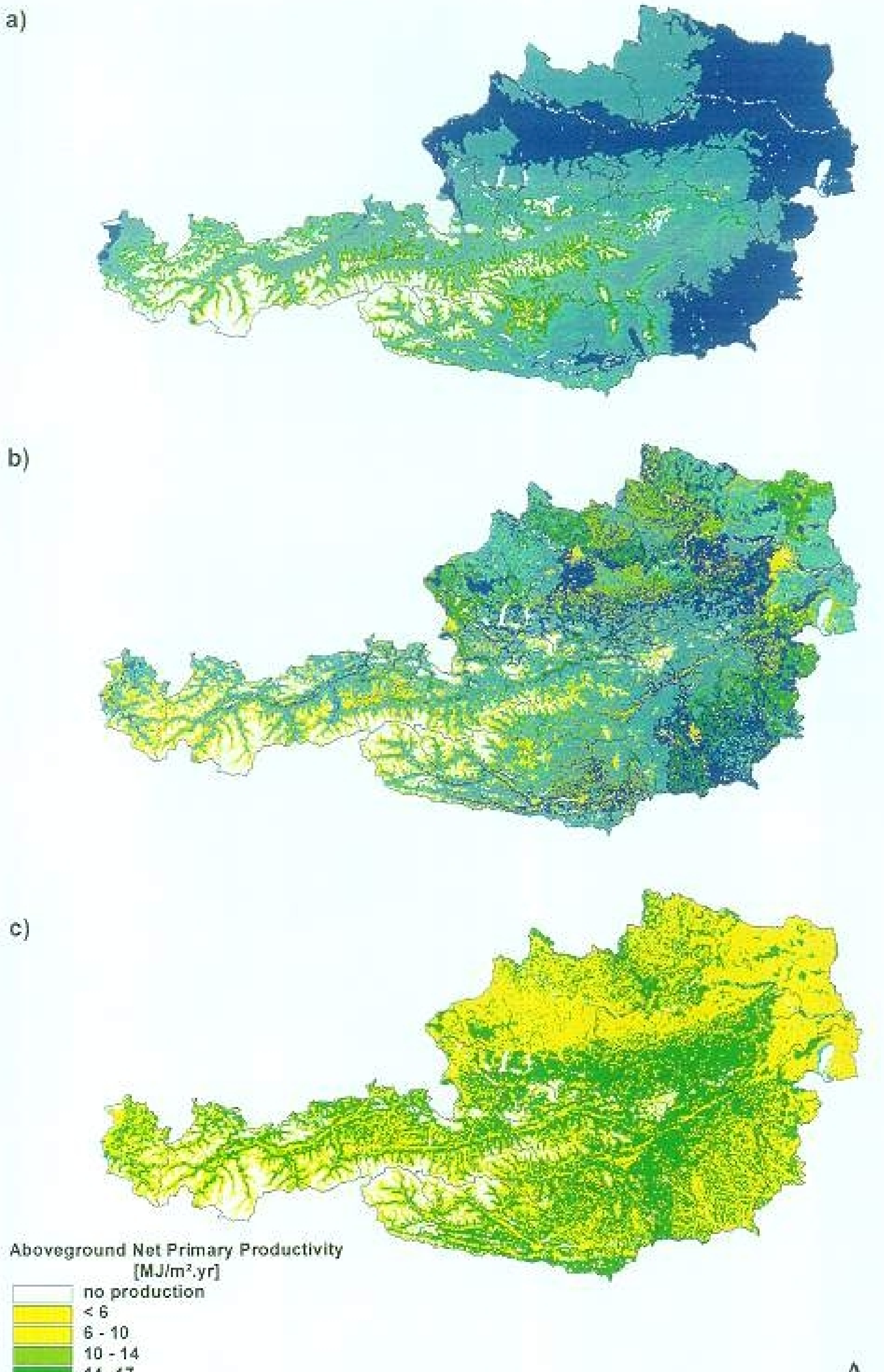
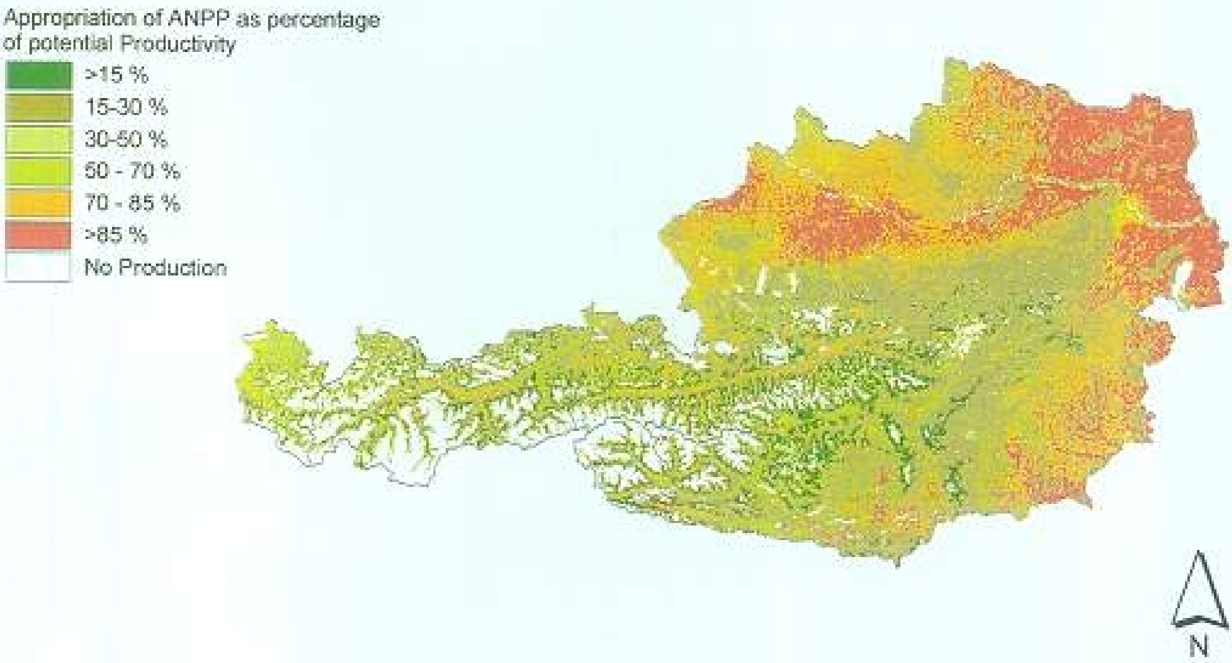
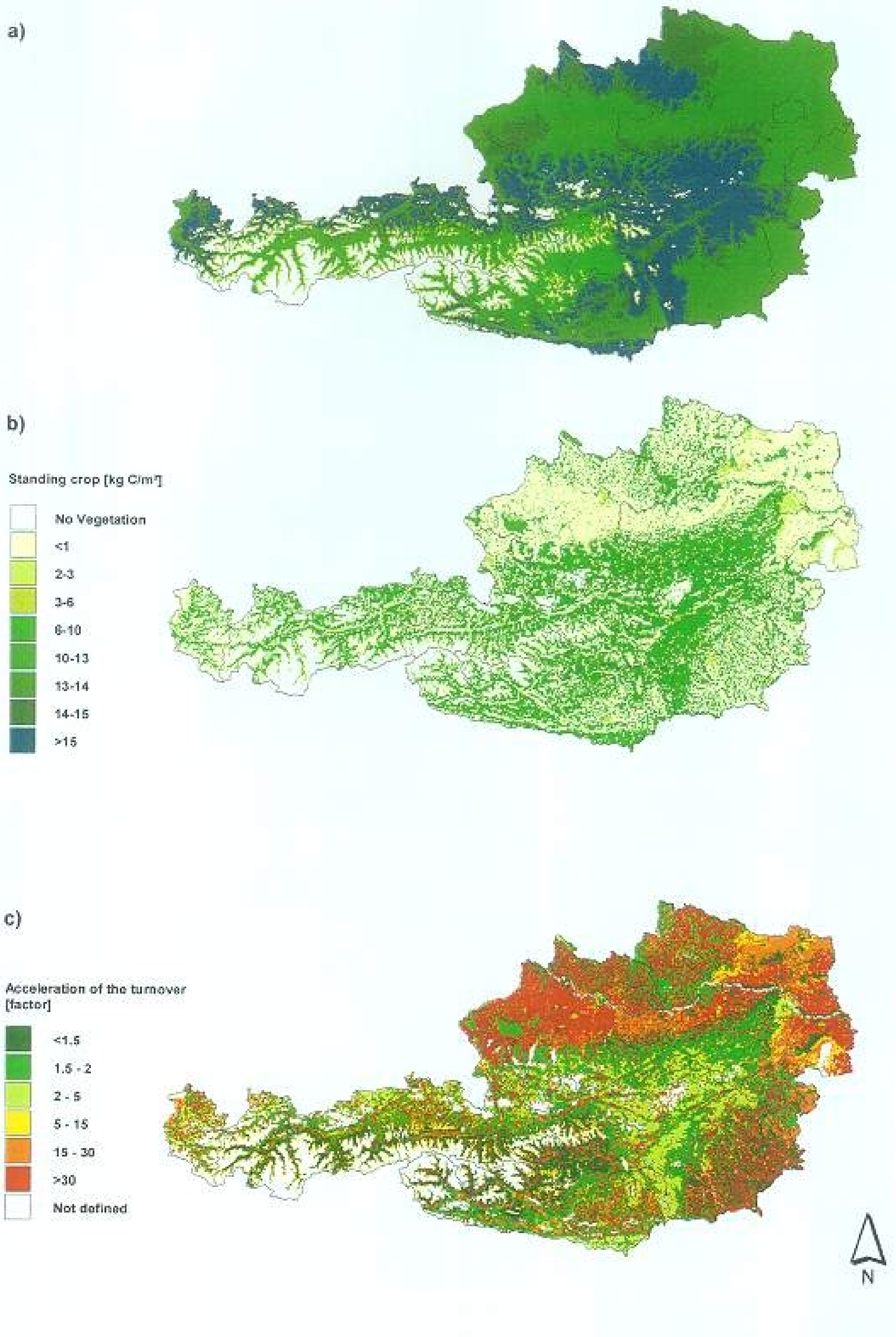

a)
b)
c)
Aboveground Net Primary Productivity
[MJ/m².yr]
no production
< 6
6 - 10
10 - 14
14 -17
17 - 19
19 - 20,5
> 20,5
N

Figure 4



Appropriation of ANPP as percentage of potential Productivity
>15 %
15-30 %
30-50 %
50 - 70 %
70 - 85 %
>85 %
No Production
N

Figure 6



a)
b)
Standing crop [kg C/m^2]
No Vegetation
<1
2-3
3-6
6-10
10-13
13-14
14-15
>15
c)
Acceleration of the turnover [factor]
<1.5
1.5 - 2
2 - 5
5 - 15
15 - 30
>30
Not defined
N