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The consequences of urban land transformation on net primary productivity in the United States

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Abstract

We use data from two satellites and a terrestrial carbon model to quantify the impact of urbanization on the carbon cycle and food production in the US as a result of reduced net primary productivity (NPP). Our results show that urbanization is taking place on the most fertile lands and hence has a disproportionately large overall negative impact on NPP. Urban land transformation in the US has reduced the amount of carbon fixed through photosynthesis by 0.04 pg per year or 1.6% of the pre-urban input. The reduction is enough to offset the 1.8% gain made by the conversion of land to agricultural use, even though urbanization covers an area less than 3% of the land surface in the US and agricultural lands approach 29% of the total land area. At local and regional scales, urbanization increases NPP in resource-limited regions and through localized warming "urban heat" contributes to the extension of the growing season in cold regions. In terms of biologically available energy, the loss of NPP due to urbanization of agricultural lands alone is equivalent to the caloric requirement of 16.5 million people, or about 6% of the US population.

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1. Introduction

As we begin to recognize the scope of human influence on Earth's ecosystems, it is important to understand how specific forms of human-induced land transformation affect the dynamics of Earth's biological systems. Land transformation due to human activity has taken many forms historically starting with fire management, herding practices, the development of agriculture, and culminating with urbanization including industrial development (Daily & Ehrlich, 1992; Ehrlich & Ehrlich, 1992; Kates, Turner, & Clark, 1990). Past studies of human impacts to the biosphere estimate that between one third to one half of the planet's land surface has been transformed by human action (Vitousek, Mooney, Lubchenco, & Melillo, 1997) and that between 10-55% of the yearly products of photosynthesis are appropriated by human beings (Rojstaczer, Sterling, & Moore, 2001; Vitousek, Ehrlich, Ehrlich, & Matson, 1986). DeFries, Field, Fung, Collatz, and Bounoua (1999) estimate that the potential photosynthetic production of the planet has been reduced by 5% due to the increase in agricultural land conversion in the last couple of centuries. Recently, more attention is being paid to urbanization as it is a particularly disruptive form of land transformation in terms of its ecological impact and the extent of its influence is growing along with increasing population and material requirements (Keilis-Borok, 1994; Wackernagel & Yount, 1998). While the actual amount of land area in urban use appears small (urban lands in the US occupy about 3% of the land surface), recent studies have shown that urban development is taking place on the most fertile and productive land-a trend that holds true even at continental scale

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comparisons (Nizeyaimana et al., 2001). At local or regional scales, the loss of fertile land to urbanization has reached notable proportions (15% of the best agricultural soils in California are urbanized) and may have significant implications for local food security, climates, and environments (Imhoff, Lawrence, Stutzer, & Elvidge, 1997a).

While there are numerous issues that could be addressed concerning urban influences on the biosphere ranging from the conversion of the land itself to a broader context of the ecosystem services required for recycling urban metabolic byproducts (Folke, Jannson, Larsson, & Constanza, 1997), we focus specifically on how the conversion of land to urban use affects the net primary productivity (NPP) of the landscape. NPP is the amount of solar energy converted to chemical energy through the process of photosynthesis (production minus respiration) and represents the primary source of food for Earth's heterotrophic organisms (organisms that require preformed organic compounds for food energy) including human beings. Measures of photosynthetic production such as NPP, net ecosystem productivity (NEP), or net biome productivity (NBP) are useful as a "common currency" for quantifying the impact of land transformation across a broad spectrum of issues in Earth system science and global change research (e.g., Bounoua, DeFries, Imhoff, & Steininger, 2003). Human influence over the capacity of the Earth to produce products of photosynthesis and the fate of those products affect changes in the composition of the atmosphere (Schimel, Melillo, & Tian, 2000), modulate important ecosystem services such as fresh water availability (Postel, Daily, & Ehrlich, 1996), impact biodiversity (Pimm & Raven, 2000; Sala et al., 2000), and affect the input rate and allocation of the energy supply within the food web (Field, 2001).

In this study, we use a unique combination of daytime and nighttime satellite data and a biophysical model to derive estimates of NPP for three broad categories of urban-influenced land cover and compare the relative impact of urbanization on photosynthetic production as a function of the degree of urbanization. We focus specifically on NPP rather than other productivity measures as it represents the initial input of carbon to the biosphere, fits the temporal scale of available data, and compares to other NPP-based land use and human impact studies (Defries et al., 1999; Rojstaczer et al., 2001; Vitousek et al., 1986).

We present our results in terms of an annual cycle showing differences in net primary production between classes of urbanization and estimate the reduction of NPP due to urban land transformation from a potential pre-urban condition. We also perform a separate analysis and present the results in terms of food energy focusing on the loss of food products due to conversion of agricultural lands to urban use. Presentation of NPP in caloric terms is useful in the context of reaching a broader audience in conservation biology and food resource studies that use food energy as a basis for modeling and analysis.

2. Methods

We used a combination of satellite data, information extraction techniques, and geo-spatial data from map sources to carryout the analysis. Nighttime images from the Defense Meteorological Satellite's Operational Linescan system were used to create a thematic map portraying the extent and spatial distribution of urbanized, peri-urban, and non-urban areas in the coterminous United States. The DMSP-based urban categories were geo-registered to a 12-layer map of monthly maximum normalized difference vegetation index (NDVI) values derived from the advanced very high resolution radiometer (AVHRR) satellite and a digital land cover map generated by Hansen, DeFries, Townshend, and Sohlberg (2000). We estimate urban impact on NPP by using the NDVI data as input to the Carnegie Stanford Ames (CASA) productivity model and using the co-registered data sets to make a spatially explicit seasonal and annual comparison of NPP for the urban, peri-urban, and non-urban areas. The NDVI data are independent from the vegetation classification.

2.1. Satellite mapping of urbanization

There is no internationally standardized definition of "urbanized land," and map data representing this form of land cover at regional or super-regional scales are rare. As such, there is need of a methodology for identifying urban land use and mapping it synoptically. We used a previously derived map of urban areas created using a series of nighttime images from Defense Meteorological Satellite Program's Operational Linescan System for this study (Imhoff, Lawrence, Stutzer, & Elvidge, 1997b). Originally designed to map moon-lit cloud cover for nighttime aircraft navigation and weather forecasting for the United States Air Force, the DMSP/OLS operates at extreme sensitivity collecting image data at a moderate spatial resolution (2.7 km pixel) across a broad visible to near infrared band (0.4-1.1 μm) (Elvidge, Baugh, Kihn, Kroehl, & Davis, 1997a). The resulting images show a dramatic picture of urbanization through the detection of city lights during cloud-free acquisitions. Previously, DMSP/OLS data have been used to estimate population (Sutton, Roberts, Elvidge, & Meij, 1997) and indicate energy consumption (Elvidge, Baugh, Kihn, Kroehl, & Davis, 1997b).

The DMSP/OLS data used were collected from October 1, 1994 to March 31, 1995, between 20:30 and 21:30 local time. The data were screened for cloud cover and ephemeral light sources, and re-projected onto a 1-km grid to conform to other global databases.

The DMSP-derived urban map product identifies three classes of urban land use: (1) urban, (2) peri-urban, and (3) non-urban land. Urbanized areas exhibited high levels of nighttime light emission and occupy approximately 3% of the landscape; peri-urban areas exhibited considerable but unstable illumination and make up about 15% of the land

surface. Non-urban lands were never observed as being lit indicating no or little development and represent 82% of the land surface in the United States. These classes and their areas compare well with independently derived census data estimating urban and non-urban areas in the United States (Imhoff et al., 1997b), have been shown to represent phenologically different environments (Imhoff, Tucker, Lawrence, & Stutzer, 2000), and have been positively linked to urban warming effects in the long-term climate record for the US (Hansen et al., 2001).

2.2. Calculation of NPP

Photosynthetic productivity of the land surface was estimated using a combination of satellite observations, climate information, and a biophysical model. Satellite observations of photosynthetic parameters were obtained from a global monthly composite of NDVI data set from the AVHRR. These were used with a vegetation classification map derived by Hansen et al. (2000) to provide a measure of intercepted photosynthetically active radiation (IPAR) for input to the carbon model. Monthly NDVI data have been shown to provide accurate estimates of absorbed photosynthetically active radiation (APAR) (Asrar, Fuchs, Kanemasu, & Hatfield, 1984; Asrar, Kanemasu, Jackson, & Pinter, 1985; Asrar, Kanemasu, Liller, & Weiser, 1986; Los et al., 2000), are strongly correlated to biomass (Asrar et al., 1985; Tucker, Holben, Elgin, & McMurtrey, 1981; Tucker, Vanpraet, Sharman, & Van Ittersum, 1985), and have proven useful for estimating the annual and semi-annual primary productivity of vegetation on land (Gosse et al., 1986; Prince, 1991; Prince & Goward, 1995; Tucker & Sellers, 1986). The AVHRR data were collected from April 1992 through March 1993 and both the vegetation map and NDVI data sets have a common 1-km spatial resolution.

We used the Carnegie Ames Stanford Approach terrestrial carbon model to estimate NPP. The CASA model characterizes the fixation and release of carbon based on a spatially and temporally resolved prediction of NPP in a steady state (Potter et al., 1993). NPP is estimated on a monthly time scale as the amount of APAR modulated by a light use efficiency (LUE) factor.

In this study, we use a LUE factor of 0.4 g C MJ^{-1} . IPAR is determined by the product of the total incident solar radiation and the fraction of the incoming PAR intercepted by the green fraction of the vegetation (FPAR) derived from the AVHRR data (Sellers, 1985; Sellers, Randal, & Collatz, 1996). The light efficiency factor is controlled by environmental stresses for temperature and water (Kumar & Monteith, 1981; Monteith, 1977). The allocation of carbon to woods, leaves, and roots as well as the turnover times is determined by vegetation type from the vegetation classification map defining 12 classes of vegetation cover (Hansen et al., 2000). In addition to boundary conditions such as vegetation classification and its associated monthly biophysical fields derived from NDVI data, CASA also requires monthly fields of temperature and precipitation (Shea, 1986), solar radiation (Bishop & Rossow, 1991), and soil texture (Zobler, 1986). The climate drivers, temperature, precipitation, and solar radiation were re-sampled from the $1^{\circ} \times 1^{\circ}$ resolution to 1×1 km grid, by assigning the $1^{\circ} \times 1^{\circ}$ value to all 1×1 km pixels that fall in to the $1^{\circ} \times 1^{\circ}$ grid. This way, we ensure that spatial variations (at the 1-km scale) in the model response are dominated by land surface heterogeneity implicit in the satellite data. NPP results from the CASA model are well documented. In a model intercomparison study including 17 global models of terrestrial biogeochemistry, the annual NPP from CASA was 48.9 pg C (pg, 10¹⁵ g) compared to 54.9 pg C representing the annual average value from the 17 participating models (Cramer et al., 1999). Furthermore, estimates of cropland NPP from CASA compares well with field estimates that are based on harvest data (Lobell et al., 2002). In this paper, our estimates of NPP are expressed as elemental carbon, e.g., grams C per unit area.

3. Discussion and results

Monthly NPP values were calculated over the course of a year for all land cover types and summed to provide a map of total annual NPP for the United States at 1-km spatial resolution (Fig. 1b). The NPP is the product of the CASA model driven by 1992–1993 AVHRR data and current climate, and can be considered a "post-urban" representation of the net primary productivity of the land surface.

3.1. The "post-urban" condition

We compared monthly rates of NPP and annual total carbon production for urban, peri-urban, and non-urban lands over the entire United States. The classification into urban, peri-urban, and non-urban region is obtained by overlaying the DMSP urban map on the NPP maps. Here, we present results showing average NPP urban signatures for four regions that span much of the climatic variation of the continental United States (Table 1). The selection of the regions is roughly based on climatic differences ranging from typical continental climate with strong seasonality in the northern mid-west to a tropical climate in the southeast. While the regions are coarse in their delineation, differences in the urban influenced NPP signal are sufficiently expressed for comparison. The southeast region is limited to about 30° north so that only tropical climate influence is considered. The southwest region is representative of areas where vegetation was introduced with urbanization in a naturally rainfall-limited environment. The scale of this study prevents a detailed analysis of the factors contributing to the differences between NPP signatures in the different urban classes. However, in general, we suggest that NPP signatures are principally influenced by a combination of factors: (1) variation in the fractional vegetation cover; (2)



Fig. 1. (a) Urbanization map generated from nighttime satellite images from the Defense Meteorological Satellite's Operational Linescan System (DMSP/OLS) collected from October 1994 to March 1995. Red (urban), yellow (peri-urban), black (non-urban). (b) Simulated total annual NPP for the U.S. at 1×1 km horizontal resolution.

the regional prevailing climate; (3) the degree to which the urban ecosystem has been altered relative to the nearby nonurban areas, including fertilization, irrigation, and the introduction of non-native species; and (4) seasonal patterns of photosynthetic activity that are in line with the urban heat island hypothesis. Regional analyses implicate regional

Table 1

Seasonal variation of NPP (gm^{-2}) for urban, peri-urban and non-urban and

	Region I Southwest (25–37.5N, 122–97.5W)		Region II Midwest (37.5–50N, 105–97.5W)			Region III Northeast (37.5–50N, 97.5–60W)			Region IV Southeast (25–30N, 97.5–65W)			
	Urban	Peri-urban	Non-urban	Urban	Peri-urban	Non-urban	Urban	Peri-urban	Non-urban	Urban	Peri-urban	Non-urban
January	6.39	4.96	3.46	0.00	0.00	0.00	0.23	0.17	0.16	16.43	16.08	16.65
February	8.44	6.95	4.92	0.55	0.28	0.16	0.65	0.45	0.41	24.95	24.67	25.92
March	15.53	14.30	10.24	1.83	1.94	1.53	2.28	1.78	1.65	35.76	38.79	40.80
April	27.89	29.07	22.66	12.79	14.23	11.61	14.72	13.69	13.86	47.89	58.10	58.72
May	25.83	27.09	23.10	28.03	32.24	30.04	49.28	48.94	52.53	49.57	61.05	64.09
June	29.84	32.31	29.61	49.41	53.10	50.85	78.10	88.32	99.05	45.14	62.69	66.53
July	19.08	21.93	19.76	47.95	63.22	55.86	82.01	105.83	117.42	40.73	55.25	56.52
August	14.91	17.42	15.37	31.52	44.62	39.26	79.45	98.93	106.20	32.89	42.11	43.71
September	15.81	17.72	16.23	26.90	33.22	27.82	65.94	75.59	79.78	29.05	36.82	37.53
October	12.14	13.15	11.99	9.75	10.38	8.44	28.02	26.08	25.43	28.25	32.90	33.34
November	9.09	8.13	6.93	1.84	1.62	1.31	3.64	3.12	2.80	27.45	28.91	29.15
December	6.87	4.45	3.67	0.22	0.23	0.13	0.96	0.64	0.54	22.86	21.87	23.19

climate and local urban-induced climate variations as the primary drivers defining the urban NPP signal in the US (Figs. 2–5). Evidence of urban heating differences between the urban and non-urban categories used in this study were observed by Hansen et al. (2001) in an examination of temperature bias in the long-term climate record for the US. In this study, differences between urban and non-urban NPP rates are not always significant in the statistical sense (Figs. 2–5) especially in winter times for the strongly seasonal regions; however, the seasonal dynamic of the phenology suggests an early greening inside urban areas.

In Region I, which covers most of the southwestern arid and semi-arid US, over 70% of the urbanized areas were formerly in agricultural use as cropland (Table 2). In this region, where the natural prevailing conditions do not favor high productivity, urban and peri-urban areas have significantly higher rates of NPP than non-urban areas (Fig. 2a). Urban NPP is increased relative to the surrounding landscape most likely through resource augmentation (irrigation and fertilization) and the replacement of native plant species with faster growing exotics. Urban NPP is at a maximum during



Fig. 2. Seasonal dynamics of the impact of urbanization on NPP for the arid southwest (Region I). (a) Monthly mean NPP rates for urban (diamonds), peri-urban (squares) and non-urban (triangles) areas. (b) NPP difference showing the loss (negative) or gain (positive) in NPP rates (gm^{-2}) resulting from urbanization (urban–non-urban). Bars represent ± 1 standard deviation.



Fig. 3. Same as Fig. 2, except for the midwest (Region II).

the spring as planted vegetation becomes active then falls off during summer months to levels slightly below that of the non-urban lands. The summertime decrease of urban NPP is believed to result from reduced FPAR due to a combination of decreased fractional vegetation cover and a stronger heat stress in the urban area. On an annual basis, urbanized areas



Fig. 4. Same as Fig. 2, except for the northeast (Region III).



Fig. 5. Same as Fig. 2, except for the southeast (Region IV).

in Region I show a gain in NPP of about 25 gm^{-2} over their non-urban counterparts (Fig. 2b and Table 3).

In regions with higher rainfall (Regions II–IV), urbanization has a generally negative effect on primary production, especially during the peak growing season. In these cases, human sponsored resource augmentation in the urban areas does not convey a significant advantage over the natural prevailing conditions found in the surrounding nonurban landscape.

In regions with strong seasonality (Regions II and III), we noted a climate-dependent asymmetry in the seasonal response of NPP to urbanization where the NPP of both urban and peri-urban areas is greater than that of the non-urban lands from fall to spring. Although differences between urban and non-urban NPP are not outside the spread of the spatial variability, this asymmetry suggests an extended growing season in urban areas. The effect is more evident in cold regions where low temperatures, a more variable photoperiod, and a mix of deciduous and evergreen vegetation contribute to the seasonal cycle of photosynthetic production (Figs. 3 and 4). This effect is observed in many northern US cities, where urbanization has taken place in

Table 2

Structure of vegetation classes (%) in urbanized areas as defined by the DMSP-derived urban map

Vegetation type	Region I Southwest	Region II Midwest	Region III Northeast	Region IV Southeast
Forest	1	0	75	13
Wood/grass	23	0	13	39
Grass	2	0	2	7
Crop	74	100	11	41

Table 3

Annual NPP difference (g^{-2}) between urban and non-urban areas (urbannon-urban) for the selected regions

NPP (g/m ²)	Region I Southwest	Region II Midwest	Region III Northeast	Region IV Southeast
January	2.93	0	0.07	-0.22
February	3.52	0.40	0.24	-0.96
March	5.29	0.30	0.62	-5.04
April	5.23	1.18	0.86	-10.84
May	2.73	-2.01	- 3.25	-14.53
June	0.23	-1.44	-20.95	-21.39
July	-0.68	-7.90	-35.41	-15.79
August	-0.46	-7.74	-26.75	-10.81
September	-0.42	-0.91	-13.85	-8.48
October	0.15	1.31	2.58	- 5.09
November	2.16	0.53	0.84	-1.69
December	3.20	0.08	0.42	-0.32
Gain	25.44	3.80	5.63	0
Loss	-1.56	-20.01	-100.21	-95.15
Annual sum	23.88	- 16.20	- 94.58	- 95.15

Note that NPP gains occur in resource-limited regions and in cold regions with strong seasonality.

mostly forested areas (Table 2), and is more evident during spring than in the fall where the photoperiod exerts a strong influence on deciduous species and the rate of the decline in NPP of the urban, peri-urban, and non-urban areas is similar. In Region III for example, which includes many of the largest northern US cities, urban areas show a gain in NPP of about 6 gm⁻² between October and April compared to non-urban areas and a loss of 100 gm⁻² between May and September for an overall annual loss of about 95 gm⁻² (Table 3). We observed that the relative winter gain in NPP is greater in northern (colder) cities and spans a longer period. This asymmetry diminishes progressively from north to south and disappears completely in the southeastern region (Fig. 5a,b), further suggesting that the early greening of urban and peri-urban areas in the northern part of the country may be associated with urban heating. Despite the complex nature of urban land cover, it is highly likely that urban heating is driving the high winter-time rates of NPP in the urban and peri-urban areas. This is supported by the fact that the climate drivers used to compute NPP were extracted from a $1^{\circ} \times 1^{\circ}$ database and do not have sufficient spatial resolution to resolve differences in temperature between the urban classes on our 1×1 km urban map. Therefore, the differences in simulated NPP between urban, peri-urban, and non-urban areas are a direct result of the observed FPAR rather than a response to climate forcing in the model. Physiologically, warmer microclimates induced by an urban heat island would induce an earlier spring bud-burst of the vegetation within urban areas and inhibit its photosynthetic capacity during summer time.

3.2. "Pre-urban" assessment

To assess the net overall mid-1990s impact of urbanization on primary production in the United States, we simulated the monthly NPP fields of the landscape in a PREurban condition. The PRE-urban simulation estimates the productivity of the landscape that would exist in the absence of urbanization under current climate conditions. The PREurban NPP was generated by replacing the current (POSTurban) NPP values of urban and peri-urban areas with an average POST-urban NPP value calculated for non-urban lands within a 100-km radius of the urban cell for each month of the year. This way only grid cells in a relatively close geographic proximity with approximately the same climate and soil characteristics are selected in the simulation of the PRE-urban NPP fields. The land use status of nonurban lands was not altered and, as such, the simulated PREurban conditions do not preclude agriculture.

This study assumes that non-urban lands represent the best proxy to what the nearby urban and peri-urban lands once were before they were transformed. In other words, the lands now in urban and peri-urban use probably had at least the same annual NPP as the non-urban lands have now. This approach has been used in previous studies examining soil types and fertility ratings in and around urban areas and holds well as long as the distance between the three classes is constrained (Imhoff et al., 1997a; Nizeyaimana et al., 2001).

Differences between the POST- and PRE-urban scenarios were generated to evaluate the overall impact of urbanization on NPP in the US. The total annual difference between the two scenarios shows that the eastern part of the US has undergone important NPP losses over large areas (Fig. 6). Losses occur in the western US mostly along the coast, in and around large urban centers, with values as high as 700 gm⁻². The simulated results also show areas where urbanization resulted in an NPP increase. In general, these gains occur in low-density periurban areas associated with resource augmentation and ecosystem alteration due to human activity making them more productive in the POST-urban era.

The effective loss of NPP due to urbanization was estimated as the area weighted sum of the difference between the PRE-urban and POST-urban NPP fields over the course of a year. The conversion of land to urban use in the US has resulted in an annual reduction of 4.15×10^{-2} Pg of photosynthetically fixed carbon or approximately 1.6% of the total PRE-urban annual NPP input. These findings are in agreement with those of DeFries et al. (1999) where it was estimated that, compared to a simulated natural landscape, human disturbance of the land cover has resulted in a global decrease of 5% in NPP with large regional variations. Over the US they estimated an overall NPP gain of about 1.8% due to the conversion of land to agricultural use. Comparing these estimates with our results suggests that the increase in the photosynthetic carbon sink resulting from agricultural expansion in the US is roughly offset by the reduction in NPP due to urbanization. This is striking considering that the land converted to agriculture now occupies approximately 29% of the area in the US, whereas urbanized land occupies only 3%.

While the overall reduction of the photosynthetic carbon sink due to urbanization seems small relative to the total continental annual carbon input through NPP, its overall effect on the biological system may have larger consequences. Net primary production forms the basis of the food chain as photosynthesis converts solar energy to



Fig. 6. Difference in NPP showing the total annual reduction (negative) or gain (positive) in the rates of NPP (gm⁻²) (POST-urban-PRE-urban).

biologically available chemical energy. Using a relationship to convert NPP measured in terms of carbon to mass of dry organic matter (OM) (Whittaker & Likens, 1973), the reduction in OM production in one year in the US due to urbanization is slightly more than 0.091 Pg, or over 91 million metric tons of dry vegetation. To estimate the reduction in terms of biologically available energy, we use widely accepted values (Whittaker, Likens, & Lieth, 1975) to convert OM to energy and evaluate the annual reduction of energy input to the US biological system due to urbanization at 3.9×10^{14} kcal.

The significance of these numbers may be brought into perspective if we use human daily caloric needs as one means of grasping the magnitude of the reduced energy input to the biological system as a whole. While all the products of photosynthesis are obviously not fit for direct human consumption, they are used as food energy by some part of the biological system. In 1993, the year that most closely coincides with the data sets used, the Food and Agricultural Organization (FAO) estimated that the global average caloric consumption of one human being is 2368.8 kcal/day (FAO, 1999). Using these values, the annual loss to the biological system resulting from urbanization, in the US alone, is energetically comparable to the requirement of 448 million human beings.

As discussed above, while the total plant organic matter expressed as NPP is relevant to the food web, it is not equivalent to actual human food. To examine the impact of urbanization on human food production, we made a separate set of calculations exclusively for land areas converted to urban use that were formerly in agriculture. The difference between the PRE-urban and POST-urban total annual NPP for areas classified as cropland, rangeland, and pasture was used to define the amount of OM lost to each class directly as a result of urbanization. The quantity of organic matter from these areas was input to a submodel treating both the direct production of vegetal food and the production of meat through livestock (Fig. 7).

Organic matter originating from cropland was divided into two components: harvested grain and residue using a weighted average of residue to grain ratio multipliers derived for a suite of common food crops from Smil (1984). A loss factor (34%) was applied to both grain and residue to account for spoilage and loss due to transportation and storage (FAO, 1999; Vitousek et al., 1986). The grain remaining after spoilage was further divided between a direct contribution to vegetal human food calories and a proportion going to livestock based on an average percentage of grain used for feed in the US (CAST, 1999). The crop residue remaining after spoilage was diverted entirely to livestock.

The livestock calculations convert organic matter from vegetation to meat mass. Grain OM was converted to meat mass using an efficiency factor (35%) (CAST, 1999) and an efficiency factor of 6.8% was used for the residue (Vitousek et al., 1986). The OM from pasture and rangelands was also

Fig. 7. Flow diagram showing the different processes involved in the estimation of the human equivalent caloric intake from the NPP lost to urbanization in agricultural lands.

entered into the livestock model. The amount of OM lost from rangelands and pasture was calculated from the total reduction in NPP of those lands resulting from urbanization. The total amount of OM from rangelands and pasture that was considered available for livestock was calculated using a grazing efficiency factor from Galt (2000) then further reduced by the 6.8% biological efficiency multiplier for the conversion of plant OM to meat mass. The mass of meat resulting from all of the various contributions was then converted to kilocalories using an average value of 2.2 kcal/ g (wet weight) of meat (CAST, 1999). The 2.2 kcal/g value compares well with other sources for an average caloric value of different meats (FAO, 1999). Added together, the annual loss of NPP from agricultural lands due to urbanization, translates to 1.43×10^{13} kcal of human food enough to fulfill the caloric requirements of nearly 16.5 million people per year.

4. Conclusions

Most of the urbanization in the United States has taken place on the lands with higher rates of NPP. The overall effect of urbanization is to lower carbon fixation in areas that are not resource limited but because of the seasonal nature of the impact, urbanization actually provides a gain of NPP during winter months in cold regions followed by a pronounced loss during summer. The gain in winter NPP is a result of a localized "urban warming," which is extending the growing season around urban areas. The early onset of



NPP in northern urban areas is significant but not enough to offset the loss during the growing season. This seasonal component of the carbon flux in urban areas diminishes with latitude and completely disappears in warmer climates where the loss of NPP is constant throughout the year.

The estimated overall annual reduction of NPP due to urban land transformation in the US relative to total preurban input is 1.6%. This reduced sink capacity is large enough to offset the NPP gain generated by agricultural development since the pre-agricultural era.

In terms of biologically available energy, the total landscape-wide reduction in NPP input is comparable to the annual food energy requirements of a large human population. In terms of actual human food, the reduction of NPP from agricultural lands equates to food products capable of satisfying the caloric needs of 16.5 million people or about 6% of the US population.

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