

HUMAN APPROPRIATION OF THE PRODUCTS OF PHOTOSYNTHESIS

by Peter Vitousek, Paul R. Ehrlich, Anne H. Ehrlich and Pamela Matson (1986)

Originally published in BioScience, (Vol. 36, No. 6, June 1986), copyright 1986 by BioScience. Reprinted by permission of the author and BioScience.

Homo sapiens is only one of perhaps 5-30 million animal species on Earth (e.g., Erwin 1982), yet it controls a disproportionate share of the planet's resources. Evidence of human influence is everywhere: land-use patterns are readily visible from space, and the concentrations of carbon dioxide, methane, nitrous oxide, and other trace gases in the atmosphere are increasing as a consequence of human activities. Human beings are mobilizing a wide array of minerals at rates that rival or exceed geological rates.

We examined human impact on the biosphere by calculating the fraction of net primary production (NPP) that humans have appropriated. NPP is the amount of energy left after subtracting the respiration of primary producers (mostly plants) from the total amount of energy (mostly solar) that is fixed biologically. NPP provides the basis for maintenance, growth, and reproduction of all heterotrophs (consumers and decomposers); it is the total food resource on Earth. We are interested in human use of this resource both for what it implies for other species, which must use the leftovers, and for what it could imply about limits to the number of people the earth can support.

Throughout this analysis, we treat NPP as the process responsible for input of organic material and calculate human uses as output. In most cropland, input and use (harvesting) occur in the same year. In a given area of forest or other ecosystems dominated by perennials, however, human-caused output can temporarily exceed NPP input (in the year a forest is harvested, for example). If the spatial scale is large enough, we can nevertheless calculate the fraction of forest NPP used by humans as the amount of organic material humans harvest or destroy divided by the total NPP of forests worldwide.

We calculated human influences in three ways. Our low estimate is simply the amount of NPP people use directly--as food, fuel, fiber, or timber. Our intermediate estimate includes all the productivity of lands devoted entirely to human activities (such as the NPP of croplands, as opposed to the portion of crops actually eaten). We also include here the energy human activity consumes, such as in setting fires to clear land. Our high estimate further includes productive capacity lost as a result of converting open land to cities and forests to pastures or because of desertification or overuse (overgrazing, excessive erosion). The high estimate seems a reasonable statement of human impact on the biosphere.

The substantial international effort that has gone into understanding human effects on the global carbon cycle greatly contributed to our calculations. Fossil fuel combustion is currently the primary cause of rising carbon dioxide levels in the atmosphere, although the importance of land clearing and forest regrowth as a source or sink of carbon dioxide is still being debated (Bolin 1977, Broecker et al. 1979, Houghton et al. 1983). Efforts to resolve this issue have produced massive reviews and compilations of data on global NPP, organic matter storage, land use, and land conversion rates (Ajtay et al. 1979, Armentano and Loucks 1984, Houghton et al. 1983, Olson et al. 1983). In addition to these

sources, we used the Food and Agriculture Organization's (FAO) summaries of agriculture and forestry (FAO 1982, 1983, 1984).

For our calculations, we use a petagram (Pg) of organic matter, equivalent to 10¹⁵ grams or 10⁹ metric tons, as our basic unit of measure. Where our sources express results in terms of carbon, we have converted to organic matter by multiplying by 2.2 (see Olson et al. 1983); where they use kilocalories, we have converted to dry organic matter by dividing by 5. We have also rounded all our estimates and generally accepted intermediate or conservative (rather than extreme) estimates from the literature.

Global primary production

Several ecologists have attempted to calculate NPP on a global scale by classifying the earth's land surface into biomes or other functional units and then using a few detailed measurements of above and below-ground productivity within each biome (Ajtay et al. 1979, Lieth and Whittaker 1975, Whittaker and Likens 1973). We use the calculations of Ajtay et al. (1979), which yield a biomass of 1244 Pg and an annual NPP of 132.1 Pg (Table 1), as the basis for our discussion because they classify land use in detail. Their overall values for terrestrial productivity are nearly identical to those of Olson et al. (1983), but the former's estimate for forest biomass may be high. Successive revisions of forest biomass information have yielded decreasing estimates (Brown and Lugo 1984, Olson et al. 1983). Additionally, all the summaries may underestimate the magnitude of belowground NPP. For NPP in marine and freshwater ecosystems, we use De Vooy's (1979) estimate of 92.4 Pg (Table 1). The estimate for marine systems may be low because the production of extremely small phytoplankton may have been systematically excluded by the widely used carbon-14 method (Li et al. 1983).

The low calculation

Our low calculation simply estimates how much organic material is used directly by people or domestic animals (Table 2).

Human consumption of plants.

We assumed a current human population of 5.0 billion people and an average caloric intake of 2500 kcal/person/day (FAO 1980). These assumptions yield an annual consumption of 0.91 Pg of organic material. Approximately 17% of the calories people consume (and 33% of the protein) derive from animal products (FAO 1983), so we calculate that humans directly consume 0.76 Pg of vegetable material.

Alternatively, we can calculate the global production of human food. The annual grain harvest in the early and mid-1980s has been about 1.7 Pg (FAO 1983, USDA 1984), about two-thirds of which (1.1 Pg) is intended for direct human consumption and about one-third for livestock feed. The water content of harvested grain averages about 20% (Spedding et al. 1981), so the annual amount of dry material produced for human consumption is about 0.85 Pg. People also eat nongrain materials, which account for roughly an additional 0.3 Pg in dry material (FAO 1982). Overall, this gives about 1.15 Pg of plant material harvested annually, compared with 0.76 Pg for direct human consumption. Thus, about 0.39 Pg (34%) of the human food harvest from plants appears to be wasted or lost to pests or postharvest spoilage. This estimate is high but not out of line with other estimates (e.g.,

FAO 1984). We have not included this lost material in our estimate of the NPP used directly by humans.

Consumption by livestock

Estimates of how much food livestock consumes annually vary substantially. Wheeler et al. (1981) reported that in the late 1970s the world's livestock consumed 8.71×10^{15} kcal, or 1.74 Pg, of usable dry organic material per year, 75% derived from pasture, 17% from grain, and 8.5% from other agricultural products. FAO (1983) estimated that about 0.5 Pg (in dry weight) of grain and roughly 0.15 of other agricultural products annually were fed to livestock worldwide in the early 1980s. If the fraction of livestock food derived from grain is slightly less than 17% (Wheeler et al. 1981), the overall consumption of dry organic material by livestock would amount to 2.8 Pg. Pimentel extended his calculation for livestock consumption in the United States (Pimentel et al. 1980) to estimate that 3.2 Pg of forage and grain is fed annually to livestock in developed countries and 1.8 Pg in developing countries, for a total of 5 Pg worldwide.'

We cannot explain the discrepancies among these figures; we use a low estimate of 2.2 Pg of dry organic material to represent livestock consumption of plants. This rate yields an efficiency of 6.8% for conversion of plant materials into human food by livestock (the quantity of animal products humans consume divided by the plant biomass livestock consumes, or Forests).

Excellent information is available on the volume of wood harvested for construction and fiber, but less exists on firewood harvesting, especially in the tropics. Armentano and Ralston's summary (1980) makes it possible to calculate that in the early 1970s 1.65×10^9 m³ of wood for construction and fiber was harvested annually in the north temperate zone (including China), assuming that wood harvest per unit of forest area in eastern Europe outside the Soviet Union is similar to that in western Europe. Assuming (with Armentano and Ralston) an average density of 0.6 g/cm³, this corresponds to 0.99 Pg of organic material. Houghton et al. (1983) estimate 1.0 Pg for all temperate and boreal forests. Wood harvests in tropical areas add another 0.2-0.3 Pg of so-called industrial wood (FAO 1984, Seiler and Crutzen 1980).

Firewood harvests, mostly in developing countries, were estimated at 0.6 Pg/year by Hampicke (1979). Myers (1984), in contrast, estimated 1.2-2.4 Pg, but some of these figures represent wet weight. Seiler and Crutzen (1980) estimate that 1.0-1.2 Pg of fuelwood is used; the FAO (1984) estimate is 0.9-1.0 Pg, and Armentano and Loucks (1984) use 0.9-1.5 Pg. Hampicke's figure seems low, given the pervasiveness of wood as a fuel and the inefficiency of most woodburning stoves, so we use 1.0 Pg in our calculations. Altogether, we estimate that humans use 2.2 Pg of wood each year.

Aquatic ecosystems.

The total annual fish catch is approximately 0.075 Pg wet weight (FAO 1983, 1984), which converts to a dry weight of 0.013-0.024 (Royce 1972); we use 0.02 Pg. If we assume that the average fish caught fed on the second trophic level above primary producers, this harvest could represent the yield from approximately 2 Pg, or 2.2%, of marine production.

Overall.

We estimate that humans use approximately 7.2 Pg of organic material directly each year—about three percent of the biosphere's total annual NPP.

The intermediate calculation

Our intermediate computation includes the NPP co-opted by humans. By co-opted we mean material that human beings use directly or that is used in human-dominated ecosystems by communities of organisms different from those in corresponding natural ecosystems. This estimate also includes organic material that is killed (or dead organic material that is burned) by human beings during land clearing or conversion. Where these activities lead to net changes in land use, they represent a reduction in future production as well as appropriation of NPP. In this section, we consider only the appropriation of organic material and land; we consider losses of productivity in the next section.

Cropland

Ajtay et al. (1979) estimate the NPP of the world's croplands at 15 Pg/year; several other estimates are similar. Olson et al. (1983), however, calculate 26.6 Pg/yr in croplands and towns. This seems high, so we use Ajtay et al.'s more conservative estimate. We consider all cropland NPP as co-opted by humans because it all occurs in human-controlled ecosystems.

Pastureland.

In this calculation, we include all the NPP of pastures that have been converted from other ecosystem types, mostly forests, to human-controlled grazing ecosystems. Ajtay et al. estimate that this amounts to 233,000 km²/year, but this appears excessive; Seiler and Crutzen (1980) calculate that 60,000 km² of forest are now being converted to grazing land annually, mostly in Latin America, and Houghton et al. (1983) report similar results.

Most evidence suggests that at most 2 million km² have been converted in the past 30 years. Substantial areas of human-created savanna exist in Africa (J 'Rosswell 1980) and elsewhere in seasonally dry tropical areas, however, and many temperate grazing lands have been established by clearing forest (e.g., Huenneke 1986). An overall estimate of 7 million km² of forest permanently converted to grazing during human history seems reasonable. If the average productivity of this derived grazing land is the same as that of woodlands, grasslands, and savanna (Table 1), then the NPP on derived grazing land amounts to 9.8 Pg per year, or 18.8% of the total annual NPP in all grazing lands.

We must also take into account the energy consumed by livestock on natural grazing land. Of the estimated 2.2 Pg of NPP eaten by livestock, 1.5 Pg come from natural and derived grazing lands (Wheeler et al. 1981). We assume that grazing is more intensive on derived pastures and that half the forage livestock consumes is obtained from such pastures. This leaves about 0.8 Pg from natural grazing land (Table 3).

In this calculation, we also account for the biomass killed or consumed by anthropogenic fires on natural grazing land. Seiler and Crutzen (1980) estimate that 6 million km² of savanna and grassland is burned annually, mostly in human-caused fires, and that the above ground biomass in the herb-grass layer of the burned areas is between 1.8 and 2.9 Pg. This material is almost wholly consumed in fires (75%), and the remainder is killed

back to ground level. (In this case, we include only above ground biomass; belowground biomass in grasslands largely survives fires and regenerates above ground tissues.)

We assume that burning, like grazing, happens more often on derived than on natural grazing lands and that fires on derived pastures account for half the area and biomass burned each year. Fires on natural grazing lands, then, consume 0.9-1.5 Pg of organic material annually; we use an estimate of 1.0 Pg (Table 3).

Overall, we calculate that human beings co-opt 11.6 Pg of NPP on grazing lands: the total NPP (9.8 Pg) from derived pastures, 0.8 Pg consumed by livestock on natural grazing land, and 1.0 Pg in fires on natural grazing land. This represents 22.6 % of the total annual NPP in woodlands, grasslands, and savannas (Tables 1 and 3).

Forest use and conversion.

In addition to the organic material people use directly, we now include the forest biomass killed during harvesting but not used, the biomass killed or burned in shifting cultivation or by more permanent land conversion, and the NPP of plantation forests.

Forest harvesting destroys nonmerchantable portions of forest biomass while the valuable stemwood is extracted. Armentano and Loucks (1984) estimate that the overall ratio of total forest biomass to the merchantable fraction is 1.96; Johnson and Sharpe (1983) measured a ratio of 2.7 in temperate deciduous forests, which can be adjusted to 2.3 by excluding forest detritus. We use 2.1, applying this figure to harvests of industrial wood only. (The ratio for firewood is probably considerably smaller.) Accordingly, we calculate that in harvested forests, 1.3 Pg of forest biomass is destroyed but not used each year.

Forest clearing and associated fires consume or destroy large amounts of biomass and, in the process, transfer organic carbon to the atmosphere as CO₂. Considerable effort has gone into estimating this net carbon flux (loss in cleared land minus the accumulation in regrowing vegetation elsewhere). We are more interested in estimating the gross loss of biomass caused by clearing land because that gross loss reflects current human appropriation of photosynthetic products. If present cutting rates in the tropics continue, the organic matter now accumulating in regrowing forests--plus much of the remaining intact forests--will be appropriated by humans in the future.

Wong (1978) estimates that 6 Pg of organic material is consumed each year in fires associated with shifting cultivation and another 3 Pg in fires during permanent forest clearing. Seiler and Crutzen (1980) calculate that similar amounts of material are destroyed (3.1-9.1 Pg by shifting cultivation, mostly in secondary forests, and 2.0-3.4 Pg in more permanent clearing for cropland or pasture), but point out that less than half this material is actually burned.

Whether the material is consumed in fires or decomposes in cultivators' plots or cattle pastures rather than in forests, it represents human co-option of photosynthetic products. We use estimates of 6.1 Pg for shifting cultivation and 2.7 Pg for forest land conversion. Some of this material becomes firewood and hence has already been counted. Seiler and Crutzen (1980) estimate that 30% of the total firewood demand, or 0.3 Pg, is met by land clearing and shifting cultivation, so the net addition to coopted NPP is 8.5 Pg.

Ajtay et al. (1979) estimate that tree plantations produce 2.6 Pg of organic material per year. We regard tree NPP as functionally equivalent to that of cropland and count it as appropriated by Homo sapiens. Harvested products and waste during harvesting of tree plantations have already been counted; we estimate these fluxes at 1 Pg, assuming that 25% of the wood humans use comes from tree plantations (which represent only 4.8% of total forest area). Plantation forests therefore represent a net addition of 1.6 Pg to the NPP humans co-opt each year (Table 3).

The total amount of NPP directly used or co-opted annually on forest lands is estimated to be 13.6 Pg, some 27.9% of global forest NPP. Of this, 2.2 Pg is used directly for construction, fuel, or fiber; 1.3 Pg is "wasted" during harvesting; 8.5 Pg is destroyed in land clearing; and 1.6 Pg is produced in human dominated plantation forests. The loss from land clearing is the largest, and efforts like that of Melillo et al, (1985) to reconcile disparate definitions and estimates of rates of land clearing are useful.

Other areas.

Productivity in areas occupied by people--residential lawns and gardens, urban parks, golf courses, etc.--amounts to some 0.4 Pg/year (Ajtay et al. 1979). Human impact on alpine and true desert areas can be locally devastating but is unlikely to affect global NPP substantially since these areas are both relatively unproductive and little used. Desertification, on the other hand, is important on a global scale; we will consider it in our high estimate below. Human Impact on marine ecosystems remains unchanged.

Overall.

By these calculations, we estimate that humans co-opt 42.6 Pg of NPP each year. This amounts to 19.0% ($42.6/224.5$) of total net primary production--30.7% on land and 2.2% in the seas. If we accept Olson et al.'s (1983) higher estimate of cropland NPP, the amount co-opted rises to 54.2 Pg, which represents 37.8% of the then somewhat higher total terrestrial NPP of 143.7 Pg.

The high estimate

This computation includes both the NPP humans have co-opted and potential NPP lost as a consequence of human activities. Many effects on NPP must be considered, including the possible roles of acid deposition and oxidant air pollution in forest decline, the significance of soil erosion in decreasing crop productivity, and reduced estuarine productivity due to sedimentation and toxic pollution. These can be countered by possible enhanced productivity from nitrogen deposition in forests, cultural eutrophication of lakes, or the rising carbon dioxide concentration in the atmosphere.

Our discussion is confined to four relatively well-defined changes in land use that can cause declines in NPP: replacement of natural ecosystems with agricultural systems, the permanent conversion of forests to pastures, desertification, and conversion of natural systems to areas of human habitation (Table 4).

Cropland.

We believe that average NPP in agricultural systems is lower than in the natural systems they replace, largely because most plants in agricultural systems are annuals (Mitchell 1984). Longer-lived or perennial crops, multiple cropping, nutrient subsidies, and especially irrigation can offset or reverse this difference in some settings, but traditional agriculture almost always produces less than natural systems. Ajtay et al. (1979) and others estimate that average agricultural productivity worldwide is below that of natural systems (Table 1). If we assume that the productivity of land now under crops would have been similar to averages for savanna-grassland or forest (depending on a site's original vegetation), we can estimate that the 16 million km² of cropland would have had an NPP of 24 Pg under natural vegetation. Potential global NPP therefore has been diminished by 9 Pg as a consequence of converting land to agriculture. This calculation may be conservative since the best (most productive) land is preferentially converted to agriculture (Mooney and Gulmon 1983).

In contrast, Olson et al. (1983) assume that average agricultural NPP exceeds that of natural ecosystems. If we use their estimates, converting land to agriculture does not decrease NPP--but the amount of potential NPP co-opted by humans increases.

Forest conversion to pasture.

As estimated in the previous section, approximately 7 million km² of forest land has been converted to more or less permanent pasture. Assuming that this land would be as productive as average forest land had it not been converted, we calculate that the conversion represents another 1.4 Pg of NPP lost because of human activities (Ajtay et al. 1979).

Desertification

Mabbutt (1984) estimated that 35 million km² of land--75% of the total dry land area in his classification--is at least moderately desertified. Desertification is severe (defined as at least a 25% decline in productivity) on 15 million km². Assuming that natural NPP on these severely affected lands was average for dry savanna and that productivity has declined by 25%, desertification has reduced global NPP by 4.5 Pg.

Areas occupied by people.

Approximately 2 million km² of land is classified as human occupied (under cities, highways, etc.); most of it would otherwise be relatively productive. Assuming an average productivity equivalent to that in natural forests, 3 Pg of NPP is foregone in this way. Since 0.4 Pg in these areas has already been counted as co-opted (Table 3), we remove a net 2.6 Pg.

Overall.

These land-use changes contribute 17.5 Pg of organic matter to the total humans affect each year, yielding a final sum of 58.1 Pg on land. The losses raise the calculated potential NPP of terrestrial ecosystems to 149.6 Pg (132.1 + 17.5 here). Thus, humans now appropriate nearly 40% ($58.1 / 149.6 \text{ Pg} = 38.8\%$) of potential terrestrial productivity, or 25% $160.1 / (149.8 + 92.4) \text{ Pg} = 24.8\%$ of the potential global terrestrial and aquatic NPP. If we use Olson et al.'s base and leave out losses of NPP from converting land to cropland, estimated human appropriation of NPP on land rises to 62.7 Pg, or about 41%

($62.7 / 152.4 = 41.4\%$) of potential terrestrial NPP. Furthermore, humans also affect much of the other 60% of terrestrial NPP, often heavily.

Discussion

Estimates of any heterogeneous process on a global scale are certain to be based on inadequate data and hence to contain errors, and our calculations are no exception. Since all our estimates are based on international efforts designed to evaluate the status of food and agriculture and to understand human-caused alteration in the global carbon cycle, we anticipate they will be refined as these efforts continue. Nonetheless, we believe that our calculations accurately reflect the magnitude of human appropriation of the products of photosynthesis, and we believe some reasonable conclusions can be drawn from these estimates.

First, human use of marine productivity is relatively small. Although even this low level may not be sustainable (CEQ and Department of State 1980), it is unlikely to prove broadly catastrophic for oceanic ecosystems. Human influence on the lowest trophic levels in the oceans (outside severely polluted areas) is minimal, and human exploitation of marine resources therefore seems insufficient by itself to alter on a large scale any but the target populations and those of other species interacting closely with target species.

On land the situation appears very different. We estimate that organic material equivalent to about 40% of the present net primary production in terrestrial ecosystems is being co-opted by human beings each year. People use this material directly or indirectly, it flows to different consumers and decomposers than it otherwise would, or it is lost because of human-caused changes in land use. People and associated organisms use this organic material largely, but not entirely, at human direction, and the vast majority of other species must subsist on the remainder. An equivalent concentration of resources into one species and its satellites has probably not occurred since land plants first diversified.

The co-option, diversion, and destruction of these terrestrial resources clearly contributes to human caused extinctions of species and genetically distinct populations extinctions that could cause a greater reduction in organic diversity than occurred at the Cretaceous-Tertiary boundary 65 million years ago. This decimation of biotic resources will foreclose numerous options for humanity because of the loss of potentially useful species and the genetic impoverishment of others that may survive (Ehrlich and Ehrlich 1981, Ehrlich and Mooney 1983).

The information presented here cannot be used directly to calculate Earth's longterm carrying capacity for human beings because, among other things, carrying capacity depends on both the affluence of the population being supported and the technologies supporting it (Ehrlich et al. 1977). But our results do indicate that with current patterns of exploitation, distribution, and consumption, a substantially larger human population--half again its present size or more--could not be supported without co-opting well over half of terrestrial NPP. Demographic projections based on today's human population structures and growth rates point to at least that large an increase within a few decades (Demeny 1984, Frejka 1981) and a considerable expansion beyond that. Observers who believe that limits to growth are so distant as to be of no consequence for today's decision makers (Simon and Kahn 1984) appear unaware of these biological realities.

Acknowledgments

We are grateful to the numerous people who have done the massive and mostly thankless job of compiling the productivity and use information on which this analysis is based. We also thank Bruce Peterson (Ecosystems Center, Woods Hole); John Harte and John Holdren (University of California, Berkeley); Laura Huenneke, Sharon Long, Harold McGee, and Harold Mooney (Stanford); John Pastor (Oak Ridge National Laboratory); David Pimentel (Cornell); Tomas Schlichter (University of Buenos Aires); and an anonymous reviewer for reading and commenting on the manuscript. This work was supported in part by a grant from the National Aeronautics and Space Administration through the Ecosystem Science and Technology Branch, Ames Research Center, to PMV and one from the Koret Foundation of San Francisco to PRE and AHE. This paper is a contribution from the Center for Conservation Biology, Stanford University.

References

- Ajtay, G.L., P. Ketner, and P. Duvigneaud. 1979. Terrestrial primary production and phytomass. Pages 129-182 in B. Bolin, E.T. Degens, S. Kempe, P. Ketner, eds. *The Global Carbon Cycle*. John Wiley & Sons, New York.
- Armentano, T.V., and O.L. Loucks. 1984. Assessment of temporal dynamics of selected terrestrial carbon pools. U.S. Dept. of Energy Rep. DOE/ER/60104-3. Butler University, Indianapolis, IN.
- Armentano, T.V., and C.W. Ralston. 1980. The role of temperate zone forests in the global carbon cycle. *Can. J. For. Res.* 10: 53-60.
- Bolin, B. 1977. Changes of land biota and their importance for the carbon cycle. *Science* 196: 613-615.
- Broecker, W.S., T. Takahashi, H.J. Simpson, and T.H. Peng. 1979. Fate of fossil fuel carbon dioxide and the global carbon budget. *Science* 206: 409-418.
- Brown, S., and A. E. Lugo. 1984. Biomass of tropical forests: a new estimate based on forest volumes. *Science* 223: 1290-1293.
- Council on Environmental Quality (CEQ) and Department of State. 1980. *The Global 2000 Report to the President*, vol. 2. US Government Printing Office, Washington, DC.
- Demeny, P. 1984. A perspective on long-term population growth. *Popul. Dev. Rev.* 10: 103-126.
- De Vooy, C.G.N. 1979. Primary production in aquatic systems. Pages 259-292 in B. Bolin, E.T. Degens, S. Kempe, P. Ketner, eds. *The Global Carbon Cycle*. John Wiley & Sons, New York.
- Ehrlich, P.R., and A.H. Ehrlich. 1981. *Extinction*. Random House, New York.
- Ehrlich, P.R., A.H. Ehrlich, and J.P. Holdren. 1977. *Ecoscience: Population, Resources, Environment*. W.H. Freeman, San Francisco.
- Ehrlich, P.R., and H.A. Mooney. 1983. Extinction, substitution, and ecosystem services. *BioScience* 33: 248-254.
- Erwin, T.L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* 36: 74-75.
- Food and Agriculture Organization (FAO). 1980. *Food Balance Sheets, 1975-1977 Average, and Per Caput Food Supplies*. Rome, Italy.
1982. *1981 FAO Production Yearbook*. Rome, Italy.
1983. *The State of Food and Agriculture, 1982*. Rome, Italy.
1984. *The World Food Report, 1984*. Rome, Italy.
- Frejka, T. 1981. Long-term prospects for world population growth. *Popul. Dev. Rev.* 7: 489-511.
- Hampicke, U. 1979. Net transfer of carbon between the land biota and the atmosphere, induced by man. Pages 219-236 in B. Bolin, E. T. Degens, S. Kempe, P. Ketner, eds. *The Global Carbon Cycle*, John Wiley & Sons, New York.
- Houghton, R.A., J.E. Hobbie, J.M. Melillo, B. Moore, B.J. Peterson, G.R. Shaver, and G.M. Woodwell, 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: a net release of CO₂ to the atmosphere. *Ecol. Monogr.* 53: 235-262.
- Huenneke, L.F. 1986. Distribution and regional patterns of Californian grasslands. In H.A. Mooney and L.F. Huenneke, eds. *Structure and Function of Californian Grasslands*. Dr. W. Junk, Dordrecht, Netherlands, in press.
- Johnson, W.C., and D. M. Sharpe. 1983. The ratio of total to merchantable forest biomass and its application to the global carbon budget. *Can. J. For. Res.* 13: 372-383.

- Li, W.K.W., D.V. Subba Rao, W.G. Harrison, J.C. Smith, J.J. Cullen, B. Irwin, and T. Platt. 1983. Autotrophic plankton in the tropical ocean. *Science* 219: 292-295.
- Lieth, H., and R.H. Whittaker, eds. 1975. *Primary Productivity of the Biosphere*. Springer-Verlag, New York.
- Mabbutt, J.A. 1984. A new global assessment of the status and trends of desertification. *Environ. Conserv.* 11: 103-113.
- Melillo, J.M., C.A. Palm, R.A. Houghton, G.M. Woodwell, and N. Myers. 1985. A comparison of two recent estimates of disturbance in tropical forests. *Environ. Conserv.* 12: 37-40.
- Mitchell, R. 1984. The ecological basis for comparative primary production. Pages 13-53 in R. Lowrance, B.R. Stinner, and G.J. House, eds. *Agricultural Ecosystems: Unifying Concepts*. John Wiley & Sons, New York.
- Mooney, H.A., and S.L. Gulmon. 1983. The determinants of plant productivity-natural versus manmodified communities. Pages 146-158 in H.A. Mooney and M. Godron eds. *Disturbance and Ecosystems: Components of Response*. Springer Verlag, Berlin.
- Myers, N. 1984. *The Primary Source*. W.W. Norton, New York.
- Olson, J.S., J.A. Watts, and L.J. Allison. 1983. *Carbon in Live Vegetation of Major World Ecosystems*. ORNL-5862. Oak Ridge National Laboratory, Environmental Science Division. Oak Ridge, TN.
- Pimentel, D., P.A. Oltenacu, M.C. Nesheim, J. Krummel, M.S. Allen, and S. Chick. 1980. The potential for grass-fed livestock: resource constraints. *Science* 207: 843-848.
- Rosswall, T. ed. 1980. *Nitrogen Cycling in West African Ecosystems*. Royal Swedish Academy of Sciences. Stockholm, Sweden.
- Royce, W.F. 1972. *Introduction to Fisheries Sciences*. Academic Press, New York.
- Seiler, W., and P.J. Crutzen. 1980. Estimates of gross and net fluxes of carbon between the biosphere and the atmosphere from biomass burning. *Clim. Change* 2: 207-247.
- Simon, J.L., and H. Kahn. 1984. *The Resourceful Earth* Blackwell Scientific Publ., New York.
- Spedding, C. R. W., J. M. Walsingham, and A.M. Hoxey. 1981. *Biological Efficiency in agriculture*. Academic Press, New York.
- United States Department of Agriculture (USDA). 1984. *World Agriculture: Outlook and Situation Report*. WAS-38. USDA Economic Research Service, Washington, DC.
- Wheeler, R.O., G.L. Cramer, K.B. Young, and E. Ospina. 1981. *The world livestock product, feedstuff, and food grain system*. Winrock International Technical Rep., Morrilton, Arkansas.
- Whittaker, R.H., and G.E. Likens. 1973. Carbon in the biota. Pages 281-302 in G.M. Woodwell and E.V. Pecan, eds. *Carbon and the Biosphere*. National Technical Information Service, Springfield, VA.
- Wong, C.S. 1978. Atmospheric input of carbon dioxide from burning wood. *Science* 200: 197200.