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Productivity of Forests of the United States and Its Relation to Soil and Site Factors and Management Practices: A Review

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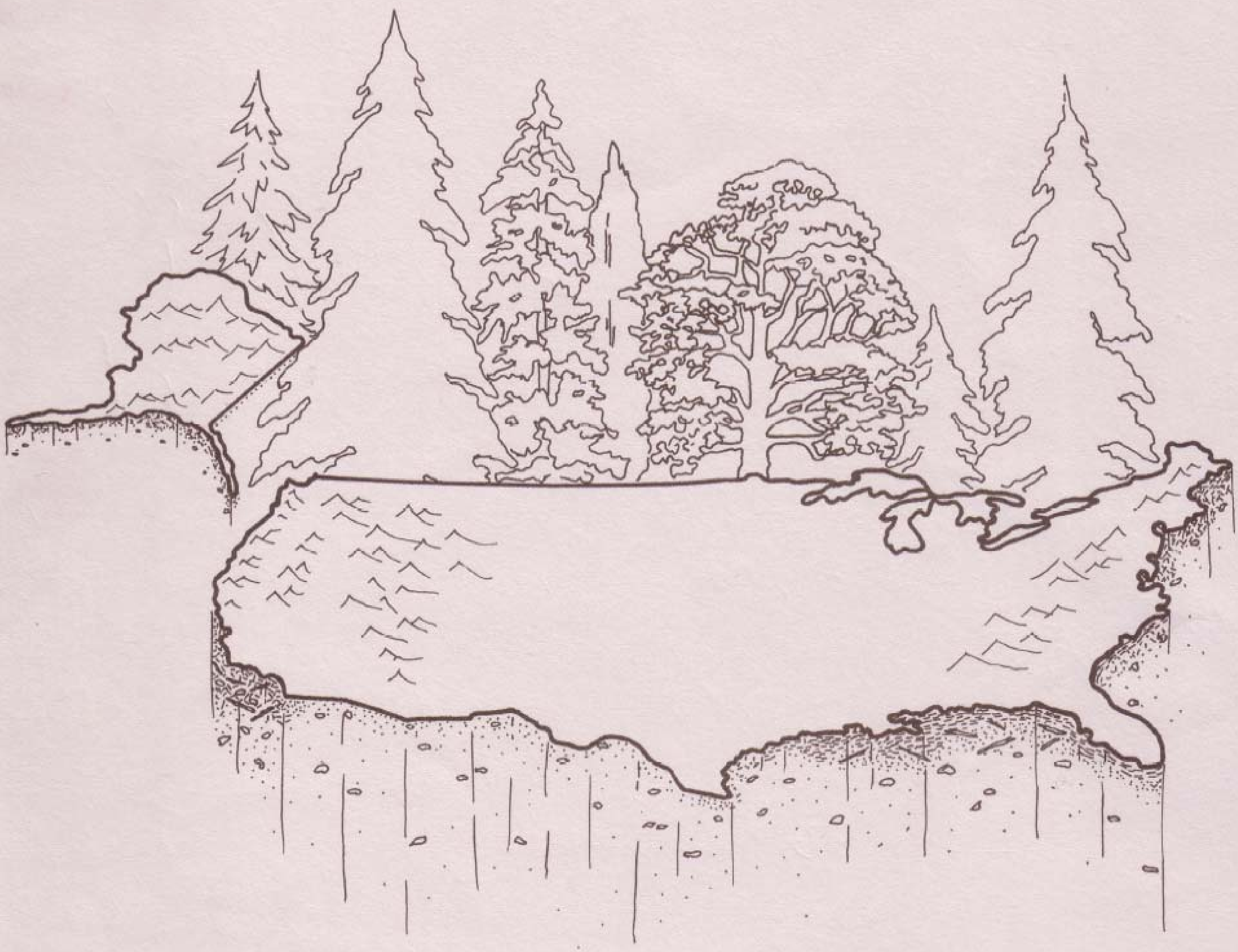

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Abstract

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Data on net primary biological productivity of United States forests are summarized by geographic region. Site factors influencing productivity are reviewed.

This paper is a review of existing literature in the productivity of various forest regions of the United States, the influence of site factors on forest productivity, and the impact of various forest-management practices on site productivity.

Keywords: Site productivity, management (forest), productivity (biological).

Contents

Introduction

A primary responsibility of managers of forestland is to maintain its productive capacity. To do this, managers of specific forest areas need access to information to (1) determine the productivity of the land and (2) relate the effects of land-management practices to forest productivity. Various State, private, and Federal forestry research programs provide this background information. Given the large forested areas of the United States and the limited forestry research budgets, research results generally lag behind the needs of managers. Coupled with this lag is a certain inertia in adopting research-based technology. One way to minimize this technological lag is for researchers to periodically review and synthesize research progress, and this paper is such an effort. The objective of the work reported here was to evaluate and synthesize published data on productivity of major forest regions of the United States and assess what is known about management impacts on the productivity. .

Forest productivity has always been a major concern of land managers, and much research has been directed toward assessment of forest productivity. The wide variety of yield tables and yield simulator models available to the forester is evidence of this. Considerable research has also been done on the impacts of management activities on forest growth and development. Several problems arise, however, when the available literature is synthesized. The main difficulty is the lack of a consistent definition of forest productivity, which is a result of the natural bias of foresters toward wood production. Unfortunately, wood production is fairly low on a tree's list of production priorities; growth of roots, foliage, and reproductive structures all are higher. Wood production is probably not the best indicator of site production potential, and the problem in assessing productivity is further compounded by using volume as a measure of productivity. Comparisons of productivity based on volume suffer from regional differences in measuring volume, a range of merchantability limits, and even site-to-site differences in the specific gravity of wood.

Net Primary Productivity: Definition and Measurement

Definition of Productivity

For this study we have adopted the ecologist's measure of productivity, "net primary productivity"-the total amount of plant material produced by a forest per unit area per year. This measure is far from ideal for management purposes; it does not express forest productivity in terms of products. But it does permit comparisons among regions, and information can be obtained on factors influencing productivity by observing how trees allocate growth on various sites.

Gross primary productivity (GPP) is the total amount of organic matter (simple carbohydrates) fixed through photosynthesis by green plants per unit of area per unit of time (usually a year). Net primary productivity (NPP) is expressed as:

$$NPP = GPP - R_a ,$$

where Ra is autotrophic (green plant) respiration. NPP has long been recognized as the only complete measure of ecosystem dry matter production (Whittaker 1962), and references to production or productivity throughout this paper refer to NPP.

NPP may be expressed either in calories as the amount of energy required to fix a given amount of carbon, or as the mass of organic matter produced. Both are expressed based on a unit area per year. On the average, 1 gram of carbon is equivalent to about 2.2 grams of organic matter or about 9.35 kelvin calories (Whittaker 1975). This equivalence partially depends on the plant material; the figures used here are average values. This equivalence is an important reminder that NPP represents storage of the Sun's energy as plant tissue.

The equation defining NPP is not particularly useful to the land manager because GPP and Ra cannot be measured accurately in terrestrial ecosystems with present technology. NPP can, however, be expressed as the sum of its components in the following and equivalent form:

$$\mathrm{NPP} = \Delta B + D + \mathrm{G} \,,$$

where ΔB is the increase in standing biomass, D is production of detritus and the turnover of annual plants or plant parts, and G is the biomass lost to grazing during a given interval (normally 1 year). These components of NPP can be measured or estimated in several ways, which will be discussed in the section, "Methods of Productivity Assessments." The values to the right of the equal sign in the above equation represent categories that can, for the most part, be measured with an acceptable degree of accuracy with current technology.

The component that most concerns forest managers is biomass increment (ΔB), which accounts for the annual increase in dry weight and volume of wood, bark, foliage, and roots. Biomass increment occurs most rapidly in young stands; in overmature stands, it can be zero to a negative quantity (Grier and Logan 1977). Forests are managed for their biomass increment, which correlates with volume increment. The typical pattern of biomass accumulation for forests as a function of stand age is shown in figure 1. Note the rapid stabilization of leaf biomass with no net annual increment occurring after canopy closure. Biomass of branches and stems increases rapidly at first; then, increment declines with age. In theory, branch and stem biomass will eventually reach a zero increment "steady state," or equilibrium, where increment is balanced by mortality. In fact, this is unlikely to occur because of the high probability of human or natural disturbance. With allowances made for different stand structures and growth rates, the patterns shown for species as widely different as pin cherry *(Prunus pensylvanica* L. f.) in New Hampshire (Marks and Bormann 1972) and Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) in Washington (Turner and Long 1975) are similiar.

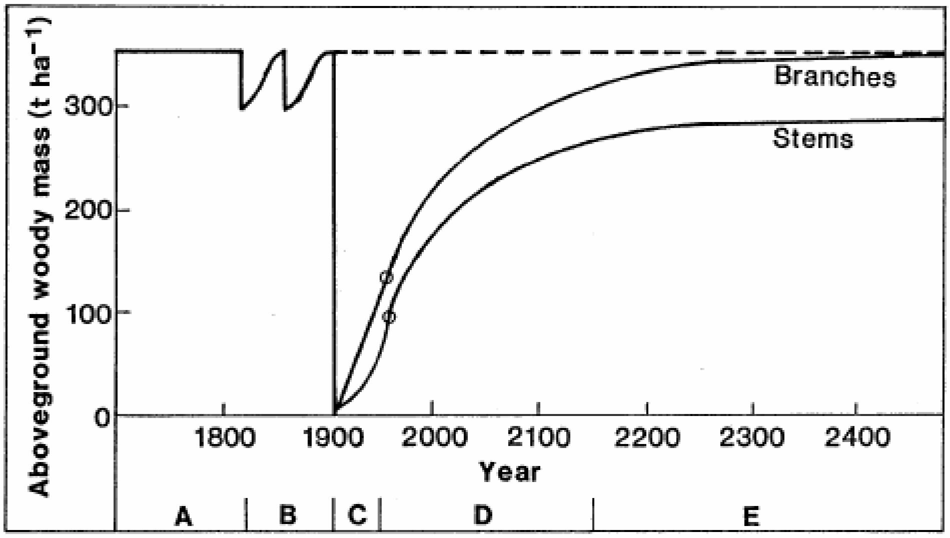

Figure 1—Patterns of leaf, branch, and stem biomass accumulation in a typical hardwood forest at Hubbard Brook, New Hampshire. Biomass fluctuations before 1900 represent logging by settlers. The rate of woody biomass accumulation begins to decline about the same time leaf biomass reaches a steady state. In theory, when total biomass reaches a steady state, the stand has reached the climax; in fact, climax stands are rare today because of both natural and human disturbances. (Data shown are primarily from Whittaker and others 1974). On the x-axis, A is presettlement forests; B, partial cutting during the late 19th century; C, reestablishment of vegetation after clearcutting in 1900; D, period of rapid biomass accumulation; and E, reduced biomass accumulation approaching steady-state biomass.

Another major component of NPP is termed "detritus production." This component incorporates litterfall, mortality, and turnover of the herbaceous layer, fine roots, and mycorrhizae. The term "turnover" is used to describe the production of plant parts that develop, mature, and die in one growing season. In forests, detritus production varies with stand age. Production of detritus above the ground is relatively small in young stands. Reported values range from about 15 percent to about 25 percent of annual net production in immature stands. Turner and Long (1975) and Fujimori and others (1976) show detritus to be about 20 percent of NPP in actively growing young to mature Douglas-fir stands. But during periods of high competitive mortality, even relatively young stands (30 to 60 years old) may have up to 60 percent of NPP in detrital production (Grier and others 1981). In stands older than 60 years, detritus is the major component of NPP. Net production in several old-growth (450-year-old) Douglas-fir stands was entirely detritus (Grier and Logan 1977). In spite of this, net aboveground production of these old-growth forests was only about 20 percent below that of young stands on comparable sites (Cole and others 1968, Fujimori and others 1976, Turner and Long 1975).

NPP by forests, therefore, declines relatively little with increasing age after some sort of equilibrium is reached. This equilibrium level is almost always below the maximum productivity achieved by the stand. As the stand matures, production shifts from biomass to detritus. The decline in biomass increment is commonly interpreted as a large decrease in productivity, but productivity may decrease only slightly.

The final term in the net production equation is "grazing." This is often the most difficult term to estimate or measure, but it should not be ignored. Under extreme conditions, grazing not only becomes an important term in estimating net production, but can also reduce future productivity and cause considerable mortality of the grazed species. Herbivores generally consume the more succulent leaves of forage plants and not the less palatable woody growth. Grazing is, therefore, use of material that would otherwise become detritus. For some grasslands, grazing may account for most of the production in the current year and, hence, most of the net production from the area. In forests, grazing generally accounts for only a small portion of the net production. Grazing is often ignored in measurements of forest productivity but may sometimes represent a fairly large portion of production. Insect outbreaks are an example of forest grazing that may significantly affect estimates of net production.

In all ecosystems, production occurs both above and below the soil surface. Although a considerable body of information is available pertaining to net aboveground production, data on net belowground production are exceedingly sparse (Vogt and others 1986), especially as part of a productivity study of an entire ecosystem. Estimates indicate that between 30 and 70 percent of total net productivity of forests occurs below the soil surface (Grier and others 1981, Harris and others 1973, Keyes and Grier 1981).

If belowground productivity were a nearly constant proportion of total site productivity, it could be considered as a constant, fixed cost when productivity of wild land ecosystems is assessed. But recent studies indicate that the proportion of net production allocated to belowground structures increases as site quality decreases (Keyes and Grier 1981) and increases with increasing stand age (Grier and others 1981). The ratio of belowground to aboveground NPP is also drastically different among different types of vegetation and different species.

Figure 2 shows some theoretical patterns of (A) mortality, (B) litterfall , (C) leaf area, and (D) aboveground NPP. Production below the ground is not included in these graphs because data are insufficient at this time. In all three examples of succession, the graph begins with secondary succession after some type of disturbance, such as clearcutting or fire. These are only three of the many patterns possible, but they should give some idea of how NPP and its components change through stand development and succession on a site. The first case might represent an even-aged stand of a fire-adapted species; for example, lodgepole pine *(Pinus contorta* Dougl. ex Loud.), which grows rapidly at first, then begins to stagnate, and is eventually wiped out by fire and the cycle starts again. The second example is typical of many all-aged mixed stands, both coniferous and deciduous, where species replacement is a gradual process and NPP fluctuates around some mean value for long periods. The third example reflects a lag between successional stages. This occurs when an early successional stand begins to fall apart but before later successional species have fully occupied the site.

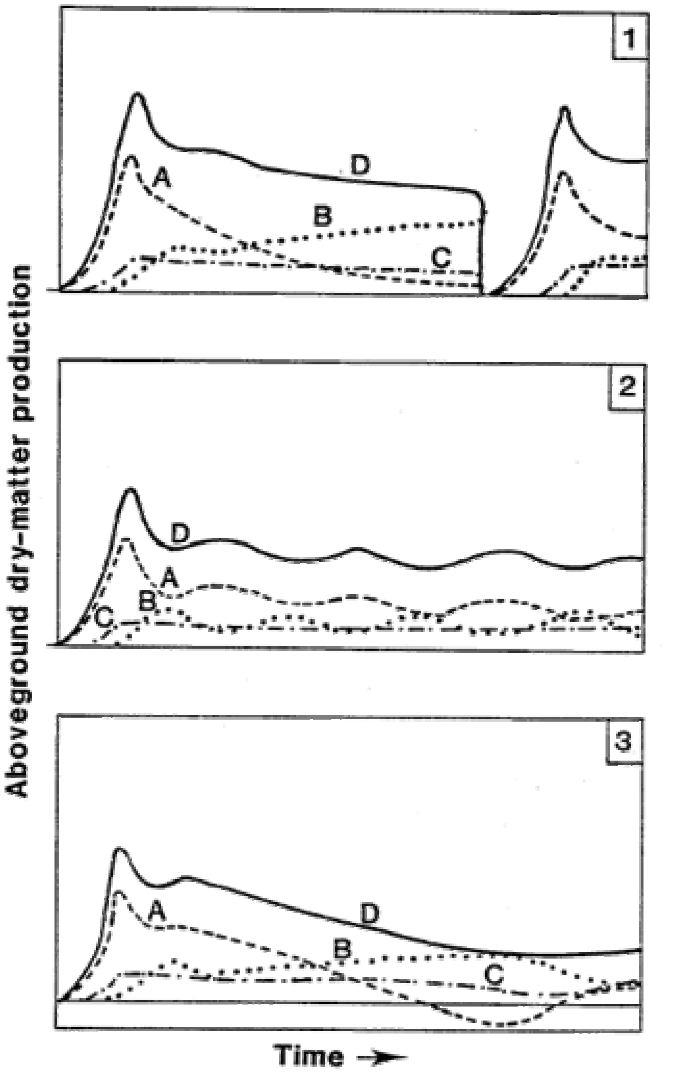

Figure 2—Three generalized patterns of stand development during secondary succession. Panel 1 represents repeated stands of a short - lived, intolerant, fire-adapted species. Panel 2 represents development of all-aged, mixed-species stands. Panel 3 represents a slow transition between pioneer species and succeeding species. The lines represent (A) mortality, (B) litterfall, (C) leaf area, and (D) net primary productivity .

Methods of Productivity Assessment

Forest ecosystems have a large and complex structure that is difficult to measure; as a consequence, a variety of methods of differing efficiency and reliability are used to estimate NPP. Whittaker and Woodwell (1969), Newbould (1967), and others have extensively reviewed these methods. We will not compare the methods in detail, but the different techniques will be summarized, along with their inherent strengths and weaknesses. The technique selected to estimate NPP for a particular study may, unfortunately, influence the estimate obtained.

Five approaches to measuring NPP will be discussed: (1) gas-exchange techniques, (2) relation to community photosynthetic indices, (3) relation to climatic and environmental parameters, (4) harvest techniques, and (5) dimension analysis (Art and Marks 1971). The particular characteristics of the ecosystem being measured and the goals of the researcher will often dictate the method of NPP assessment used.

Gas-exchange techniques—Forest productivity can be approached through the analysis of gas exchange of individual trees and the forest as a whole by measuring the difference between fluxes of carbon dioxide (CO2) as fixed by photosynthesis and as released by plant respiration. Field leaf arid plant cuvettes (chambers) for measuring gas exchange have been developed to accommodate a variety of experimental purposes (for example, Schulze and Koch 1971). Field measurements of gas exchange for the purpose of estimating NPP use the defining equation, $NPP = GPP - R_a$.

The large size of forest dominants and the complexity of forest communities make monitoring net assimilation of carbon dioxide at the community level difficult and expensive. Measuring respiration losses of branches, bark, stems, and roots (Botkin and others 1970) demands extensive labor and technical support and has been done successfully at the ecosystem level in only two instances: in Brookhaven, New York (Woodwell and Whittaker 1968), and Oak Ridge, Tennessee (Reichle and others 1973).

The micrometeorological approach is an alternative to growth-chamber analysis in different canopy strata of the forest (Odum and Jordan 1970). Whole-community gas exchange is measured by daytime depletion and nighttime accumulation of carbon dioxide in the forest atmosphere. Daytime depletion is taken as an estimate of photosynthetic assimilation, or GPP, and nighttime accumulation is used as an estimate of respiration. Local temperature inversions can be used to measure nighttime accumulation of carbon dioxide (Art and Marks 1971). This approach has very specific site requirements that are rarely found.

Soil respiration has also been used as an index to primary production (Kucera and Kirkham 1971, Lieth and Ouellette 1962). The actual sources of carbon dioxide diffusing from the soil are difficult to define.

Gas-exchange methods may be appealing in their conceptual simplicity and because they represent a direct approach to estimating NPP "' but they are rarely used: they are expensive, require sophisticated equipment, and do not provide the growth information needed by forest managers.

Photosynthetic indices—Certain short cuts to estimating productivity through photosynthetic indices are explored and reviewed by Art and Marks (1971). Some appropriate indices (besides dry weight of current leaves and twigs) are annual leaf litterfall , leaf-area index, chlorophyll content per unit of ground area, and light extinction by foliage (Whittaker 1966). As an example, leaf litterfall seems to be a relatively constant 20 percent of NPP in young Douglas-fir stands after canopy closure.[1] For deciduous stands, litterfall may be closer to 40 or 50 percent of NPP and near 100 percent of NPP in grasslands (Bray and Dudkiewicz 1963, Ovington and others 1963). Measurement of litterfall might provide a reasonable index of NPP in some stands.

Leaf-area index (average leaf surface area per unit area of ground surface) and amount of clorophyll per unit area are measures of the "photosynthetic apparatus" of the community. As such, they may be strongly related (Medina and Lieth 1964) or weakly related (Bray 1960, Lieth 1973) to NPP. Unfortunately, these indices correlate poorly with NPP, and further research is needed to determine their utility.

Environmental data —Net primary production has been estimated from measurements of environmental data (Lieth and Box 1972). In this approach, net productivity of a given stand is assumed to be controlled and correlated with environmental factors acting to limit plant growth. Because stand age, composition, and structure are ignored, these correlations provide an estimate of theoretical productivity for the site and not necessarily for the stand currently occupying that site. For comparisons of site productivity potential, correlations between productivity and environment may be the best approach to site classification.

Environmental variables have been used to predict primary productivity in a variety of ecosystems (Sharpe 1975). For forests, the most common variables are moisture availability and temperature; other variables are sunlight intensity, nutrient availability, and seasonal changes in climatic factors (Sharpe 1975).

Figure 3 gives an example of correlations between NPP and temperature and precipitation on a global scale. Estimates of evapotranspiration, which incorporate both precipitation and temperature, have also been used to predict NPP; for example, Rosenzweig (1968) developed logarithmic relations between NPP of climax vegetation and actual evapotranspiration (fig. 4). On a global scale, Lieth and Box (1972) used models based on climatic data and actual evapotranspiration and produced comparable but slightly higher values than Rosenzweig. Models of this type are generally good only on global or continental scales because they are not sensitive to local variations in soil properties, microclimate, topography, and site history.

Models using local environmental data certainly have potential, but as yet little has been done because NPP has not been measured for enough stands and sites in any one locality to provide a data base large enough for local predictive modeling. Different environmental factors will obviously be important in different forest types. Correlations of net productivity with environmental factors on a limited set of climax communities can be strong; for instance, Whittaker's (1966) study of the relation of NPP to elevation in Smokey Mountain National Park. When similar models are applied to early successional communities, the correlations are weaker because these models cannot account for variations in NPP caused by stand structure or developmental stage.

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[1] Grier, C.C. Unpublished data on file, Northern Arizona University, School of Forestry, Flagstaff, Arizona.

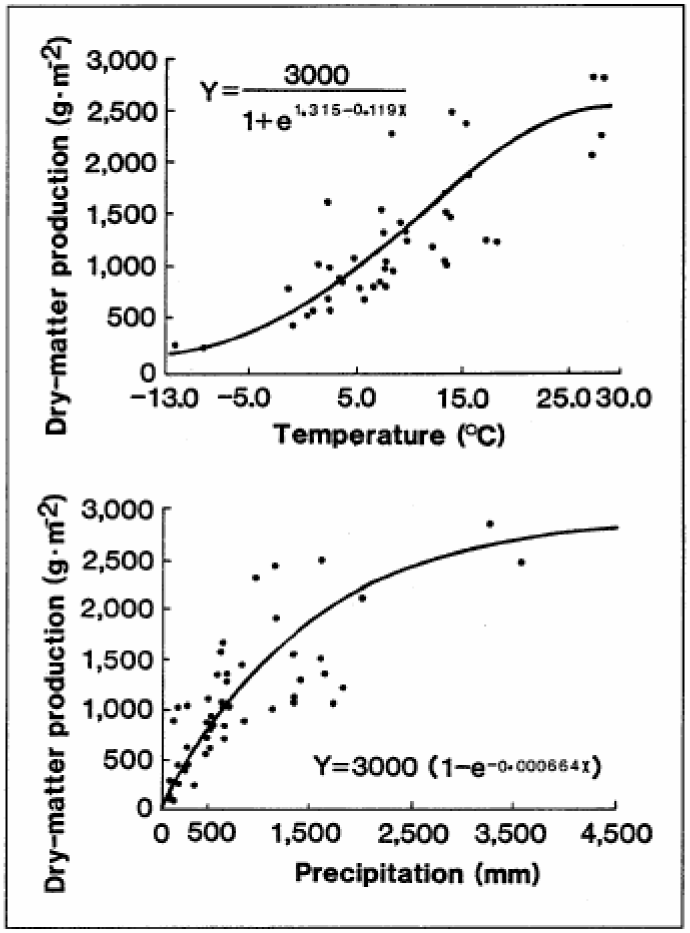

Figure 3—Estimates of aboveground NPP in relation to mean annual temperature and mean annual precipitation (Ueth 1973).

Harvest techniques— The most direct approach to N PP assessment for some communities or portions of communities (such as herbaceous understory) is through harvesting of aboveground plant parts during the growing season (Satoo 1966, 1970; Zavitkovski 1976). For annuals or communities of annual plants, biomass can be almost equivalent to NPP, which makes harvest necessary only once at peak biomass accumulation for each species. In more diverse communities, such as the understory of a deciduous woodland, several harvests may be needed to accurately assess NPP of species maturing at different times during the growing season (Woodwell and Whittaker 1968). In many forest communities, the contribution of the understory vegetation is small (from 1 to 15 percent) relative to total ecosystem productivity and is frequently ignored for that reason. Several researchers (for example, Zavitkovski and Newton 1968). have pointed out, however, the ecological importance of the understory and the need for accuracy in measuring it. Where understory contribution to NPP is measured, the harvest method is generally used.

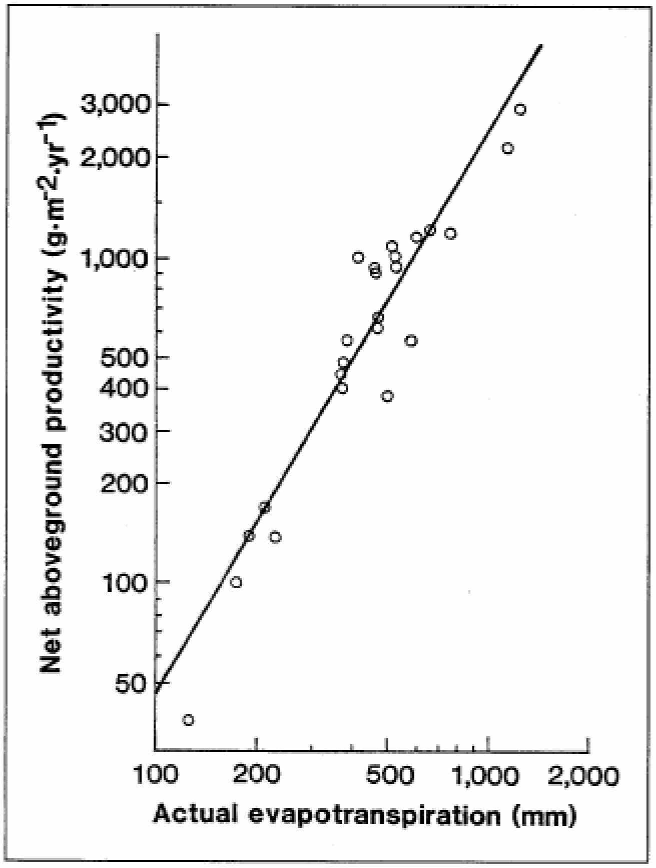

Figure 4— Estimate of aboveground NPP in relation to actual evaporation (from Rosenzweig 1968). Figure has been redrawn from original to provide arithmetic values for x- and y-axes. (Note: Axes are logarithmic).

One problem with the harvest method is that the mortality of green plants before and after peak growth is not generally accounted for. Unless current-year detrital production is accounted for, NPP will be underestimated. For communities with many species, many collections must be made to catch each species at peak biomass. The growth of the current year must be easily identified to use the harvest method on shrubs and other perennial plants. For some species this can be a problem. Esti mates of grazing must also be incorporated, and these may be difficult to obtain.

The harvest method will probably continue to be the most popular method for assessing production of most grass-, herb-, or shrub-dominated communites or community components. This method is best suited to homogeneous cultivated plants, some early successional ecosystems, and certain types of forest understory vegetation (Wiegert and Evans 1964).

Dimension analysis-The majority of forest NPP studies are based on direct measurements of sizes and weights of plants and plant parts (Newbould 1967, Woodwell and Whittaker 1968). Three ways to synthesize such measurements into productivity estimates are (1) mean-tree, (2) productivity ratios, and (3) regression analysis.

1. Mean-tree: As the term implies, the mean-tree approach applies measures of size and growth rates of the average tree in a stand to all individuals. It is most successfully applied to even-aged plantations where trees are similar in size and form (Ovington 1956). Madgwick (1971) found mean-tree estimates of dry weight production in an old-field stand of Virginia pine *(Pinus virginiana* Mill.) equivalent to those based on regression methods. The degree of accuracy decreases with increasing size variability within the stand (Ovington and others 1968, Satoo 1968).

   The stratified-tree technique is a variant of this method. Stands are stratified by diameter size classes, each of which is represented by a tree of mean dimensions for the particular stratum.

2. Productivity ratios: Another estimation method correlates forest stand character - istics with NPP to develop numerical ratios. These ratios are used to estimate NPP of other ecosystem components. In practice, this requires clipping current twigs of shrubs and tree seedlings and aboveground herbaceous growth, determining individual dry-weight productivity ratios, and applying these ratios to stand NPP (Burger 1940, Whittaker 1966).

   Productivity of larger trees cannot be easily determined by clipping, however. They are measured through estimated volume increment, defined as one-half the mean annual wood increment times plant height (Lieth and Whittaker 1975). Because wood growth itself is incorporated in the definition, estimated volume increment expresses productivity in a way that measuring diameter, basal area, and stem volume do not.

   Because growth rates change with tree age and size (Whittaker 1962), productivity estimates based on clipping weights and estimated volume increment are not always consistent. Environmental factors also influence productivity ratios within a single species; for example, the ratio of foliage productivity to estimated volume increment increases with less favorable site conditions (Whittaker 1962). Despite these shifts with age and environment, productivity ratios are much less variable than plant measurements themselves. Thus,_ they can be applied to mixed-aged forests where the mean-tree approach would not work (Whittaker 1966). Ratios of this sort tend to be quite specific to the area and species for which they were derived and should not be used out of their environmental context.

3. Regression analysis:. Regression equations describing growth (weight and volume) in response to changing proportions (for example, diameter at breast height [d.b.h.] and height) are termed "allometric" equations and have been used to estimate biomass and productivity in a variety of forest types. The great majority of forest productivity studies in the past 20 years use this method (Baskerville 1965, Grier and Logan, 191"1, Ovington and Madgwick 1959, Reiners 1972).

Regression analysis is conducted on harvested plants spanning the range of sizes that occur in the stand. The sample trees are felled and measured so that biomass and productivity can be related (as dependent variables) to diameter (or other easily measured independent variables) by using regression equations (Art and Marks 1971). Fujimori and others (1976), for example, use regression techniques to calculate annual increases in biomass of stems and branches for several community types. They estimate annual foliage production by analyzing relations between leaf production (measured with litterfall traps) and stem diameter. Increases in shrub biomass are obtained by analyzing the relation between stem production and stem diameter (at soil surface) times stem length. Net biomass increment is obtained by subtracting mortality losses during the year. In other studies (for example, Grier 1976), regression equations are used to obtain biomass estimates at the beginning and end of an interval; biomass increment is the difference between the two. The other components of NPP are estimated by using other techniques.

The field work required to develop regression equations with good predictive ability can be extremely tedious and time consuming. Analysis requires access to computers because of the large amount of data. Once the regressions are developed, however, estimates of biomass and productivity can be obtained easily and quickly. One problem with this sort of analysis is that it does not account for changes in growth rates and growth forms caused by changes in age, site, or management (Grier and others 1984). For this reason, regression equations developed for one type of forest stand may be applicable only to other forest stands on the same type of site and with basically the same age and growth structure. The larger the data base used to develop the regressions, the broader their application. There is a tradeoff, though, between generality of use and error of estimate for a particular stand.

The most intensive and detailed application of the regression approach is the system of dimension analysis of woody plants developed at the Brookhaven National Laboratory, Long Island, New York (Whittaker and Woodwell 1967, 1968, 1969). This approach is based on the principle that the forms of woody plants in a wide size range follow the same general design and can be related allometrically. Complex characteristics of plants can, therefore, be easily related to measured features. This method provides a satisfactory way to estimate productivity of woody plant tissue because it is based on measurements of plant parts that indicate growth per unit of time (for example, wood rings and bud scale scars).

Problems in NPP Assessment

One reason NPP has been so actively studied is that it provides a way to compare ecosystems differing floristically, historically, and structurally. The same things that make NPP a useful measure also contribute, however, to confusion in interpreting differences in production rates between ecosystems. Generalized trends of NPP over time for a given site are still not well known. Until productivity has been determined for many sites, and through time and successional stages on the same sites, comparisons will be largely a matter of academic interest and of little direct use to the manager.

Several problems are associated with comparing ecosystem dynamics by using NPP. One problem is a lack of consistency in measuring techniques and another is in estimating various components of NPP. Individual researchers have pointed out weak points in their own studies, and several reviews of measuring problems in depth are available (Ovington 1963, Sharpe 1975). Because of difficulties with measuring certain components of NPP, not all published estimates of NPP include all components. The components most commonly ignored are fine roots, coarse roots, grazing loss, and the contribution of forest understory to production.

Grazing by herbivores, one of the three major components in the NPP equations, has only rarely been quantified (Crow 1978, Woodwell and Whittaker 1968). A number of studies have considered grazing by phytophagous insects as insignificant; however, several studies have shown that it can account for between 1 and 8 percent annual NPP (Franklin 1970, Mattson and Addy 1975). Under outbreak conditions, insects have been observed to consume all of the annual foliage production of a stand (Mattson and Addy 1975). Disregarding other plant parts that are difficult to collect and quantify, such as reproductive structures, augments underestimation of community NPP.

An inconsistency occurs with the inclusion of mortality as a component of NPP. In many forests, especially in mature stands, mortality is a highly significant portion of biomass and productivity. For example, -in some old-growth Douglas-fir stands, 70 percent of total NPP (5 to 7 $t \cdot ha^{-1} \cdot yr^{-1}$) was accounted for as mortality (Grier and Logan 1977). Even in relatively young stands undergoing high rates of competitive mortality, the mortality component of NPP may be as high as 40 or 50 percent.[2] Researchers who completely ignore mortality may be grossly underestimating NPP (Bradbury and Hofstra 1976).

A major problem in comparisons of NPP is that it is a rate and, as such, changes with stand development, age, successional stage, and climatic variability. NPP studies are generally constrained by time and money, and most stands can be intensively analyzed for only one or two growing seasons. Extrapolating results and conclusions from an atypical year is a risk. One way to avoid this problem is to average growth increment over a long time, but this may result in a different problem. Averaging growth over 5 to 10 years ignores the growth dynamics of the trees because constant radial increment is assumed (Day and Monk 1977, Whittaker and Niering 1975), which is more of a problem in a young, developing stand than in a mature stand.

An estimate of NPP for one interval in the development of a stand will give a rate that mayor may not represent the rates that could be expected in either past or future intervals. To imply that one site is more productive than another based on one measurment of NPP on each site is tentative at best. If both are climax stands, the data may be somewhat valid; but if the stands are in earlier successional stages and actual NPP is being compared, then the comparison may not be meaningful.

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[2] Grier, C.C. Unpublished data on file, Northern Arizona University, School of Forestry, Flagstaff, Arizona.

The problem of integrating phenology into NPP assessment is recognized by Ovington (1963) and by Leith (1974). The effects of seasonality on sampling hardwoods is well known, but comparable data on evergreen species are scarce. Madgwick (1968) shows that the sampling date can considerably affect the biomass and productivity estimate by altering the weight of seasonally variable ecosystem components such as flowers, lower branches, and cones.

Because reliable and accurate NPP data are so difficult to obtain, the results of previous studies are often extrapolated to other areas (Hanley 1976). Regressions of growth rates on easily measured tree variables are available for many species (Sollins and Anderson 1971). The overapplication of equations calculated for a specific forest and region to communities with different site qualities and climates may result in a large margin of error.

Given the problems associated with measuring and interpreting NPP, one might well wonder about the value of using NPP. The answer is that currently no other unit of measurement is available that is as universally applicable. Site comparisons of NPP for management purposes are not a reality. Further research should clarify our understanding of NPP and lead to better predictive capabilities.

NPP Estimates of Forest Sites In the United States

Table 1 lists net productivity rates for a variety of deciduous and coniferous forest stands. The stands listed in the table that have the lowest NPP estimates tend to be either very young «10 years), very old (450 years), or what is generally considered noncommercial forest *(Picea mariana* (Mill.) B.S.P. in Alaska, *Populus tremuloides* Michx. in Michigan, *Quercus* spp. in Arizona, and *Pinus rigida* Mill. in New York). The stands showing the highest NPP rates are generally young (10 to 30 years) or growing under very favorable conditions, or both.

The inconsistencies in measured variables and the differences in the degree of precision in producing these estimates make further comparisons difficult. Although the exclusion of one component, or more, of NPP does not necessarily have a significant impact on the final estimate, large underestimations are possible. Understory vegetation, for example, may not be important for some coniferous stands where little light reaches the forest floor, but in other stands the shrub and herbaceous layers may make up a large portion of NPP.

There is little correlation between standing biomass and NPP (Table 1). The association would probably be stronger if biomass of climax stands were correlated with potential NPP.

Table 1—Estimates of net primary productivity in various forest regions and forest types of North America[a]

Forest type and associated species	Location	Age	Components measured[b] Rts	US	Wlf	Mrt	Grz	Biomass	NPP	Source
		years						t/ha	$t^{-1} \cdot ha^{-1} \cdot yr^{-1}$	
		HARDWOOD FORESTS								
Acer saccharum Marsh. *Aesculus octandra* Marsh. *Halesia carolina* L.	Tennessee Smokey Mountains	Mature	•	•	•	•	•	500	15.3	Whittaker 1966
Aesculus octandra Marsh. *Tilia heterophylla* Vent. *Prunus serotina* Ehrh.	Tennessee Smokey Mountains	222		•	•	•	•	500 578	11.3 13.1	Whittaker 1966
Alnus incana (L). Moench	Alaska	20	•	•			•	43	10.8	Van Cleve and others 1971
Alnus rubra Bong.	Washington	31-37	•				•	185	26.3	Turner and others 1976
Alnus rubra Bong.	Oregon Coast Range	5-20 30-50	• •	• •			• •	7-14 184-208	15-22.2 7-11.2	Zavitkovski 1976
Alnus rugosa (DuRoi) K. Spreng. *Fraxinus nigra* Marsh. *Populus balsamifera* L.	Michigan	?	•		•	•	•	30-52	4.6-5.4	Parker and Schneider 1975
Fagus grandifolia Ehrh. *Acer saccharum* Marsh. *Betula lutea* Michx. f.	New Hampshire Hubbard Brook	83-124	•					98-159 121-189	9.7-13.1 11.1-15.4	Whittaker and others 1974
Fagus grandifolia Ehrh. *Acer saccharum* Marsh.	Tennessee Smokey Mountains	84	•	•	•	•	•	131	7.6	Whittaker 1966
Liriodendron tulipifera L. *Acer rubrum* L. *Robinia pseudoacacia* L.	Tennessee Smokey Mountains	29	•	•	•	•	•	221	24	Whittaker 1966
Liriodendron tulipifera L. *Quercus* spp. *Pinus echinata* Mill. *Carya tomentosa* Nutt.	Tennessee	40-48						133	7.6	Sollins and others 1973
Populus tremuloides Michx.	New Mexico	80	•	•				154	4.1	Gosz 1980
Populus tremuloides Michx.	Arizona	34	•		•	•	•	125	10.5	Whittaker and Niering 1975
Populus tremuloides Michx. *Populus grandidentata* Michx. *Acer rubrum* L. *Quercus rubra* L.	Michigan	20-70	•	•		•	•	14-103	2-3.9	Cooper 1980
Populus tremuloides Michx. *Acer saccharum* Marsh. *Populus grandidenetaeta* Michx.	Wisconsin	39-63		•	•	•	•	174 194	10.3 11.5	Pastor and Bockheim 1981
Populus tremuloides Michx. *Acer rubrum* L. *Betula papyrifera* Marsh. *Acer saccharum* Marsh.	Wisconsin	50	•		?	?	•	93-120	7.6-8.7	Crow 1978
Quercus alba L. *Quercus velutina* Lam. *Prunus seroteina* Ehrh.	Wisconsin	130		•			•	264 330	13.7 20.3	DeAngelis and others 1981
Quercus alba L. *Quercus* spp.	Missouri	35-92	•	•		•	•	98	6.8	Rochow 1974
Quercus coccinea Muenchh. *Quercus alba* L. *Pinus rigida* Mill. *Quercus velutina* Lam.	New York Brookhaven	43					•	64 100	10.7 14.1	Whittaker and Woodwell 1968
Quercus ellipsoidalis E.J. Hill *Acer rubrum* L.	Minnesota	45-50	•	•		•	•	124	9.8	Reiners 1972

See footnotes at end of table.

Table 1—Estimates of net primary productivity in various forest regions and forest types of North America[a] (continued)

Forest type and associated species	Location	Age	Components measured[b]					Biomass	NPP	Source
			Rts	US	Wlf	Mrt	Grz			
		years						t/ha	$t^{-1} \cdot ha^{-1} \cdot yr^{-1}$	
Quercus oblongifolia Torr. *Quercus emoryi* Torr.	Arizona	117	•		•	•	•	11	1.2	Whittaker and Niering 1975
		CONIFEROUS FORESTS								
Abies amabilis (Dougl.) Forbes *Tsuga heterophylla* (Raf.) Sarg. *Abies procera* Rehd.	Washington	23					•	52 77	6.1 17.9	Grier and others 1981
Tsuga mertensiana (Bong.) Carr.		180					•	446 583	4.5 16.7	
Abies procera Rehd. *Pseudotsuga menziesii* (Mirb.) Franco *Abies amabilis* (Dougl.) Forbes	Oregon	100-130	•	•	•	•	•	880	12.9	Fujimori and others 1976
Abies fraseri (Pursh) Poir. *Picea rubens* Sarg.	Tennessee Smokey Mountains	Mature	•	•	•	•	•	200-310	4.7-14	Whittaker 1966
Abies lasiocarpa (Hook.) Nutt. *Pseudotsuga menziesii* (Mirb.) Franco *Pinus strobus* L.	Arizona	106	•		•	•	•	357	8.6	Whittaker and Niering 1975
Picea mariana (Mill.) B.S.P.	Alaska	130	•	•		•	•	118	2.1	DeAngelis and others 1981
Pinus banksiana Lamb. *Populus tremuloides* Michx. *Betula papyrifera* Marsh.	Minnesota	1-5	•			•	•	0.6-11	0.7-7.7	Ohmann and Grigal 1979
Pinus echinata Mill. *Liriodendron tulipifera* L.	Tennessee	30	•	•			•	122	11.4	Harris and others 1973
Pinus monticola Dougl. *Larix occidentalis* Nutt. *Thuja plicata* Donn *Tsuga heterophylla* (Raf.) Sarg. *Pseudotsuga menziesii* (Mirb.) Franco *Abies grandis* (Dougl.) Lindl.	Idaho	100-250		•	•		•	265-330	4.7-10	Hanley 1976
Quercus prinus L. *Quercus borealis* Michx. *Acer rubrum* L.	Tennessee Smokey Mountains	Mature	•	•	•	•	•	420	18.2	Whittaker 1963, 1966
Quercus prinus L. *Carya* spp. *Quercus* spp.	Tennessee	30-80	•	•			•	138	11.2	Harris and others 1973
Quercus prinus L. *Acer rubrum* L. *Quercus coccinea* Muenchh.	North Carolina	60-200	•			•	•	140	9.7	Day and Monk 1977
Quercus stellata Wangenh. *Quercus marilandica* Muenchh.	Oklahoma	80				•	•	181 220	12.9 15.2	Johnson and Risser 1974
Taxodium distichum (L.) Rich. *Nyssa sylvatica* Marsh.	Georgia	?	•			•	•	301	7.6	Schlesinger 1978
Taxodium distichum (L). Rich. *Nyssa sylvatica* Marsh.	Louisiana	50-95	•	•		•	•	400	11.2	Conner and Day 1976
Pinus monticola Dougl.	Idaho	103		•	•		•	415-675 488-794	11.4-17.6 13.1-20	Hanley 1976
Pinus ponderosa Laws.	Arizona	150	•		•	•	•	162-250	4.9-5.7	Whittaker and Niering 1975
Pinus rigida Mill.	New York	20-40 60-80	• •	• •	• •	• •	• •	9-11 61-88	1.2-1.5 7.4-8.7	Olsvig-Whittaker 1980

See footnotes at end of table.

Table 1—Estimates of net primary productivity in various forest regions and forest types of North America[a] (continued)

Forest type and associated species	Location	Age	Components measured[b]					Biomass	NPP	Source
			Rts	US	Wlf	Mrt	Grz			
		years						t/ha	$t^{-1} \cdot ha^{-1} \cdot yr^{-1}$	
Pinus strobus L.	North Carolina	8-12		•		•	•	43	13.5	Swank and Schreuder 1973
Pinus taeda L.	Mississippi	10	•	•	•	•	•	56	12	Demott 1979
Pinus taeda L.	North Carolina	8-12		•		•	•	16-91 19-108	12-20.3 13.7-13.2	Nemeth 1973
Pinus virginiana Mill.	Virginia	17	•	•	•	•	•	76	15.3	Madgwick 1968
Pseudotsuga menziesii (Mirb.) Franco	Washington	36		•			•	172	13.8 203	Dice 1970 17.5
Pseudotsuga menziesii (Mirb.) Franco	Washington poor site	40		•	•		•	249 306	7.3 15.4	Keyes and Grier 1981
	Washington good site	40		•	•		•	468 556	13.7 17.8	Keyes and Grier 1981
Pseudotsuga menziesii (Mirb.) Franco	Oregon	150	•	•	•	•	•	865	10.5	Gholz 1982
Pseudotsuga menziesii (Mirb.) Franco *Acer macrophyllum* Pursh	Oregon	90-110	•	•	•	•	•	661	12.7	Fujimori and others 1976
Pseudotsuga menziesii (Mirb.) Franco *Tsuga heterophylla* (Raf.) Sarg. *Thuja plicata* Donn	Oregon	450					•	667 811	8.3 11.1	Grier and Logan 1977
Pseudotsuga menziesii (Mirb.) Franco *Tsuga heterophylla* (Raf.) Sarg. *Thuja plicata* Donn	Oregon	450				•	•	560 683	2.1 4.8	Grier and Logan 1977
Pseudotsuga menziesii (Mirb.) Franco	Washington	22	•				•	139	10.8	Turner and Long 1975
		42	•				•	209	9.9	
		73	•				•	307	5.7	
Thuja occidentalis L. *Betula papyrifera* Marsh.	Minnesota	70-100	•	•		•	•	159	11.4	Reiners 1972
Tsuga canadensis (L.) Carr.	Tennessee Smokey Mountains	?	•		•	•	•	510	10.2	Whittaker 1966
Tsuga heterophylla (Raf.) Sarg.	Oregon	26		•				193 231	32.2 37.7	Fujimori 1971
Tsuga heterophylla (Raf.) Sarg.	Oregon	121						1062	22.8	Grier 1976

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[a] Values reported in this table were compiled from results of the studies indicated. Virtually all values are derived from some form of dimension analysis. Where understory contributions to NPP are reported, values were obtained by harvest. Except where noted, values are for aboveground NPP only.

[b] Rts = roots; US = understory vegetation; Wlf = woody litterfall; Mrt = tree mortality; and Grz = grazing.

Factors Affecting Net Primary Productivity

Net primary productivity, defined in the previous section, is a measure of forest productivity that integrates environmental site conditions, vegetation, and stage of vegetation development. Because NPP can be determined for any ecosystem, regardless of structure or developmental stage, it can be used to compare ecosystems as different as coniferous forests and tidal marshes. Depending on the development and structure of vegetation present on a given site, NPP may fluctuate over time between rates near zero and some site-specific maximum.

It is common to speak of the potential productivity of a particular site when evaluating forest lands, or to classify sites according to their productive capacity. Because NPP is the measure of productive capacity of a fully occupied site, NPP can possibly be used to determine site quality. But because NPP increases rapidly with development of young stands, NPP is not a realistic or practical index of site quality. Actual NPP on a site may be low even on productive sites shortly after disturbance. For this reason, the only meaningful measures of productivity for site comparison and evaluation may be the potential maximum net productivity rates possible for a given site.

Although maximum or potential NPP rates may be useful for site comparisons, they are not necessarily something to manage for. They are really only a conceptual framework to base discussions of site quality on and have yet to be determined for more than a few sites. Managers of a given site, therefore, need not strive toward maintaining short-term productivity maximums but instead should strive to preserve or possibly enhance the potential for long-term productivity.

Environmental factors affecting potential productivity of a site can be separated into two general groups: extrinsic factors and intrinsic factors. Extrinsic factors provide the framework ecosystems develop on and are most influential in determining long-term regional productivity potentials. Included are climate, topography, and geology. Although all three can change or fluctuate over time, these factors are not influenced by the presence or absence of vegetation.

Intrinsic factors are affected by ecosystem processes and are subject to modification by forest management. Examples of intrinsic factors are certain soil physical, chemical, and biological properties and microclimate. Intrinsic site factors generally do not affect long-term productivity potentials when viewed in terms of geologic time; but within the timeframe of forest management, they may raise or lower these potentials significantly. Because of the inherent complexity of natural systems, some site factors—for instance, some soil characteristics—cannot be called either entirely extrinsic or entirely intrinsic. But these two categories do provide a reasonable framework for the discussion of the factors controlling potential NPP rates at a given site.

Extrinsic Factors

Extrinsic factors define the physical environment of a site and appear to set upper limits on potential productivity. The primary factors affecting plant growth are moisture, nutrients, temperature, and light. On a broad scale, these are controlled by extrinsic factors. Productivity potential tends to be low whenever one or more of these factors are limiting. Productivity potential is low in tundra environments as a result of temperature limitations and low in desert ecosystems as a result of moisture limitations. Of the three extrinsic site factors, climate appears to exert an overriding effect on the regional expression of vegetation types. Climate has direct influence on moisture, temperature, and light regimes, and indirect influence on nutrient availability.

Climatic data has long been used as a basis for delineating major global vegetation formations (Holdridge 1947, Thornthwaite 1931, Walter 1973). Climatic regimes also form the basis for the concept of the climatic climax as described by Clements (1936). Predictions of regional NPP on a global scale that use one or more climatic variables have been reasonably accurate. Climatic variables correlating well with measures of NPP include mean annual temperature, average annual precipitation, actual evapotranspiration, and length of the growing season (Lieth and Box 1972, Rosenzweig 1968). Correlations of NPP with climatic data are generally only valid on global and continental scales and tend to break down over smaller geographic areas.

Regional predictions of NPP must include other variables besides just climate. The other two extrinsic site factors, topography and geology, can have very definite influences on the productivity of a site. The geology of an area interacting with climate over long periods of time creates general drainage patterns, landforms, and types of soil parent material. The soil parent material will affect the nutrient status and other physical and chemical properties of the soil important for plant growth.

Topography is basically the result of the geologic and climatic history of a region. Topographic position can have profound effects on microclimate and soil conditions in hilly or mountainous terrain. South-facing slopes are often significantly warmer and drier than are north-facing slopes and, hence, may have lower productivity potential in dry regions or higher productivity in cold regions. Ridgetops may have generally colder climates, shallower soils, and lower productivity than do lower elevation sites in the same region. In desert regions, the reverse may be true, with greater productivity possible at the higher elevations owing to greater precipitation. Even in relatively flat terrain, low-lying areas subject to periodic flooding or restricted drainage, such as river floodplains, swamps, marshes, and bogs, may have much higher or lower productivity potential than do surrounding upland sites. Several studies have shown gradients in net productivity associated with elevational or topographic gradients (fig. 5) (Westman and Whittaker 1975, Whittaker 1963, Whittaker and Niering 1975).

Separating individual effects of climate, geology, and topography on vegetation development and potential productivity is nearly impossible because all three interact in shaping the general physical environment of an area. Because measuring the actual physical environment of a site is extremely difficult, most forest site classifications use vegetation as an integrative descriptor of site. Some work has been done to develop predictive models for potential productivity based on site index and continuous forest-inventory data (O'Neill and DeAngelis 1981, Sharpe 1975). Other models incorporate physical characteristics of the site with vegetation characteristics (Czarnowski 1964). Existing systems of forest site classification, such as the habitat type system (Daubenmire and Daubenmire 1968), currently being used throughout the Western States, may provide a framework for estimating productivity potential. All these predictive models incorporate both extrinsic and intrinsic site factors.

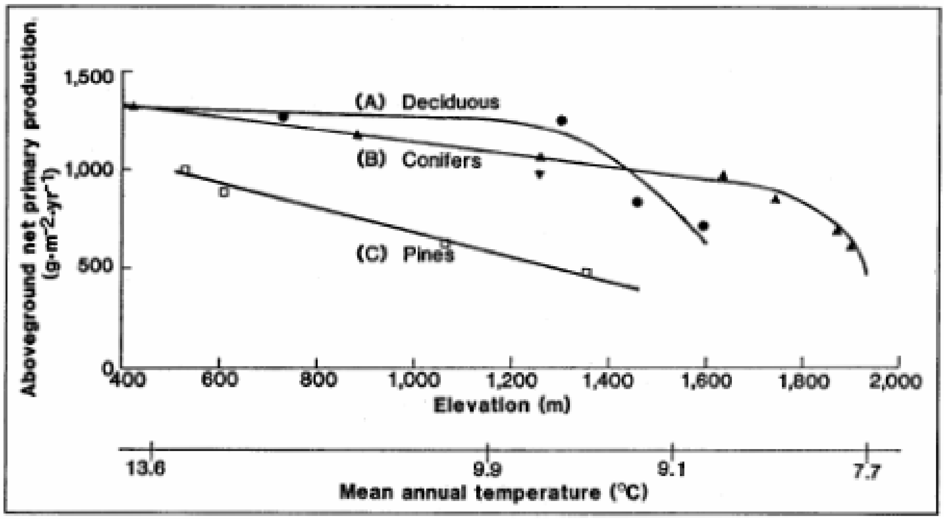

Figure 5—Aboveground NPP estimates along an elevational gradient in the Great Smokey Mountains, Tennessee: (A) broad-leaved deciduous forests in moist environments; (B) evergreen coniferous forests of moist environments; and (C) pine forests of dry environments (Whittaker 1975).

Intrinsic Factors

Intrinsic site factors represent characteristics of site that can affect the productivity of the site, are influenced by ecosystem processes, and are controllable (or at least semicontrollable) by management. The most important intrinsic factors are those dealing with soil properties because they can affect potential productivity. Soil parent materials are formed from past geological activities and climate, but many of the soil-forming processes are influenced by vegetation development and disturbances such as fire and erosion. The soil properties affecting productivity potential are the same ones affecting plant growth in general. Soil moisture-holding capacity, soil nutrient status, and soil porosity or aeration are the factors that correlate best with site productivity (Carmean 1975, Ralston 1964). They are considered intrinsic because they are affected by ecosystem processes and are subject to modification by human activity.

Moisture availability for plant growth is a function of precipitation and runoff and of the soil's moisture-holding capacity. The soil water-storage capacity is especially important in regions with definite drought periods during the active growing season. Soil physical properties influencing water-holding capacity include texture, structure, depth, and organic matter content of the various soil horizons. These variables can be altered by either natural processes or human activities. Activities decreasing soil moisture-holding capacity generally lower the productivity potential of upland sites.

Soil nutritional status is controlled by a large number of extrinsic and intrinsic site factors, including geology or parent material, climate, topography, time, fire history, land-use history, and past and present vegetation. Nutrients essential for plant growth come from weathering of soil minerals, from atmospheric fallout, from precipitation, and through the decomposition of organic materials. Fixing of nitrogen by symbiotic organisms can also account for significant inputs of nitrogen. Atmospheric fallout, precipitation, and mineral weathering usually provide nutrients at fairly low but steady rates. Precipitation inputs of nitrogen, phosphorus, calcium, magnesium, and potassium are typically in the range of 1 to 8 kilograms per hectare per year (Cole and others 1968, Henderson and others 1978); however, in areas of high atmospheric pollution, such as the Northeastern United States, inputs of nitrogen and sulfur from acid precipitation and atmospheric fallout may be measurably greater (Whittaker and others 1979). Release of nutrients through weathering of primary minerals is highly dependent on climate and soil parent material. In dry climates, soil parent materials tend to weather slowly and release rates are low. In warm, wet climates, weathering is accelerated and nutrient release is more rapid when minerals readily yielding nutrients are present in the parent material in adequate quantities.

Biological inputs of nitrogen through atmospheric fixation can be important in some ecosystems. Plant communities with significant components of either snowbrush *(Ceanothus velutinus* Dougl.), red alder *(Alnus rubra* Bong.), or other species supporting nitrogen-fixing symbionts can fix as much as 30 to 200 kilograms of nitrogen per hectare per year (Davey and Wollum 1979). Additional inputs of nitrogen may come from nonsymbiotic nitrogen-fixing organisms associated with the decay of wood or from free-living, blue-green algae (Jones and others 1974).

Initial stages of vegetation succession on a site tend to exploit the mineral resources of the soil and incorporate nutrients into plant tissue much faster than they can be replaced by decomposition and weathering. Thus, soils with large nutrient capitals will initially be more productive than will those with lower nutrient capitals if nutrient status is a growth-limiting factor. In later stages of succession, dependence on mineral soil as a source of nutrients decreases and reliance on nutrient cycling pathways increases. The greater reliance on nutrient cycling in older stands may be partially explained by the depletion of nutrients in the mineral soil during the early stages of stand development. Switzer and others (1968) show that young southern pine stands initially obtain 100 percent of their nutrients from the mineral soil. In contrast over 80 percent of the annual nutrient requirement of a stand that had reached canopy closure is accounted for by recycling of nutrients returned to the soil in litterfall and canopy leaching (Jorgensen and others 1975).

Nutrient-cycling patterns seem to be very similar for a wide range of forest communities. External nutrient cycling is the process whereby nutrients returned to the soil in litterfall or canopy leaching are mineralized by decomposing organisms and are then 'reabsorbed by the vegetation. Internal nutrient cycling is the redistribution of minerals from one part of the plant to another. Recent studies indicate that nutrient redistribution within conifers is greater on nutrient-poor sites than on nutrient-rich sites (Turner 1975) and that internal cycling appears to increase with age (Sollins and others 1980). Soil fertility, therefore, takes on slightly different meanings depending on the stage of vegetation development on the site. Early growth of forest stands may be limited by the existing nutrient capital of the soil. Later growth may depend more on the rates of mineralization in the organic horizons of the soil. The fertility of a site is the factor most easily altered through management. It is also one of the most difficult factors to quantify.

Soil aeration is the third soil factor affecting forest productivity and is subject to change through management. Soil aeration is the process of gas exchange between soil and atmosphere and is necessary to provide oxygen to the roots and the aerobic soil organisms and to remove carbon dioxide produced by root and microbial respiration. Gas exchange in the soil is a function of porosity and moisture content of the soil. Insufficient soil aeration can result from either high soil densities or poor drainage.

Medium- to fine-textured soils with high bulk densities have low porosity and are dominated by very fine pores. This results in high resistance to the transfer of oxygen and water to the rooting zone. Forest soil bulk densities range from less than 0.8 g/cm^3 to more than 1.6 g/cm3 (Brady 1974). Gravelly soils may have high bulk densities without being poorly aerated. Compacted soils with a high proportion of silt and clay exhibit the poorest aeration. Smith and Wollard (1969) report limitations of forest productivity on poorly aerated soils. Reductions in soil porosity often result from soil compaction brought on by management practices. Restricted soil permeability can cause reduced infiltration of precipitation and snowmelt and surface erosion. Compaction of lower horizons can result in perched water tables, anaerobic conditions, and gleization. Soils saturated with water tend to be poorly aerated because available pore space is occupied by water, and gas diffusion through water is slow. If saturated conditions are sustained over long periods, anaerobic conditions occur and forest growth may be impaired. This reduction in growth may be due to a lack of oxygen to the roots, which restricts metabolism and thus nutrient and water uptake. Trees may actually suffer drought stress in saturated soils because lack of oxygen to the roots inhibits uptake of water. Insufficient aeration also prevents penetration by deep roots and thereby reduces the availability of plant nutrients (Leyton and Rousseau 1958). If anaerobic conditions continue for long periods, major changes in soil chemical and physical properties are likely.

Conclusions from the foregoing discussion are that the most productive forest soils have high moisture-holding capacity, good fertility, adequate aeration, and unimpeded drainage. These soil characteristics represent some of the most important intrinsic site factors because they can raise or lower the productivity potential of the site. Any management practice producing a deterioration of any of these factors will likely reduce site productivity. The time required for the site to recover from disturbance is a function of the degree of disturbance and the resilience of the soil (Klock 1983).

Other intrinsic factors will control the actual NPP of a particular site; the most important is vegetation succession and development. Peak productivity for a forest successional sequence generally occurs in the early seral to midseral stages, which are dominated by fast-growing, shade-intolerant tree species. Peak productivity for a forest stand occurs at about the same time as canopy closure. Stands having high initial densities reach peak productivity before stands that are understocked. Some stands may show a second peak in productivity after a period of competitive mortality and stand adjustment, but this has yet to be substantiated. Very old stands or successional stages may have low apparent productivity; however, what happens to NPP as stands age is still being studied. Aging patterns across all forest types are probably not consistent: different species or forest types reach maximum productivity at different times (O'Neill and DeAngelis 1981). Figure 6 shows the general patterns of NPP and the components of NPP for second-growth Douglas-fir forests in the Pacific Northwest.

Climatic variability is also extremely important in determining yearly productivity rates. Very dry years will show lower rates of productivity than might normally be expected, and wetter years may result in higher productivity. Changes in microctimatic conditions, such as shade, humidity, and soil temperature, can also alter productivity. These changes may be hard to quantify. Changes in microclimatic conditions often result from changes in stand structure that will affect productivity more than will the resulting changes in microclimate.

Natural disturbances, such as fire, windthrow, insect outbreaks, and disease will affect the actual productivity of the site by changing the vegetation structure, composition, developmental state or growth rate, or the microclimatic conditions on the site. Management practices change NPP in the same ways. Thinning, fertilizing, prescribed burning, and harvesting all can alter the actual net productivity rates in the same manner.

The actual NPP for a particular year or interval therefore depends on the species present, the age and structure of the stand, and the disturbance history of the site. NPP will also fluctuate yearly because of climatic variability. Potential productivity, on the other hand, is set by the physical environment of the site, but may be different for different species on the same site. It does not change unless the physical environment is altered substantially.

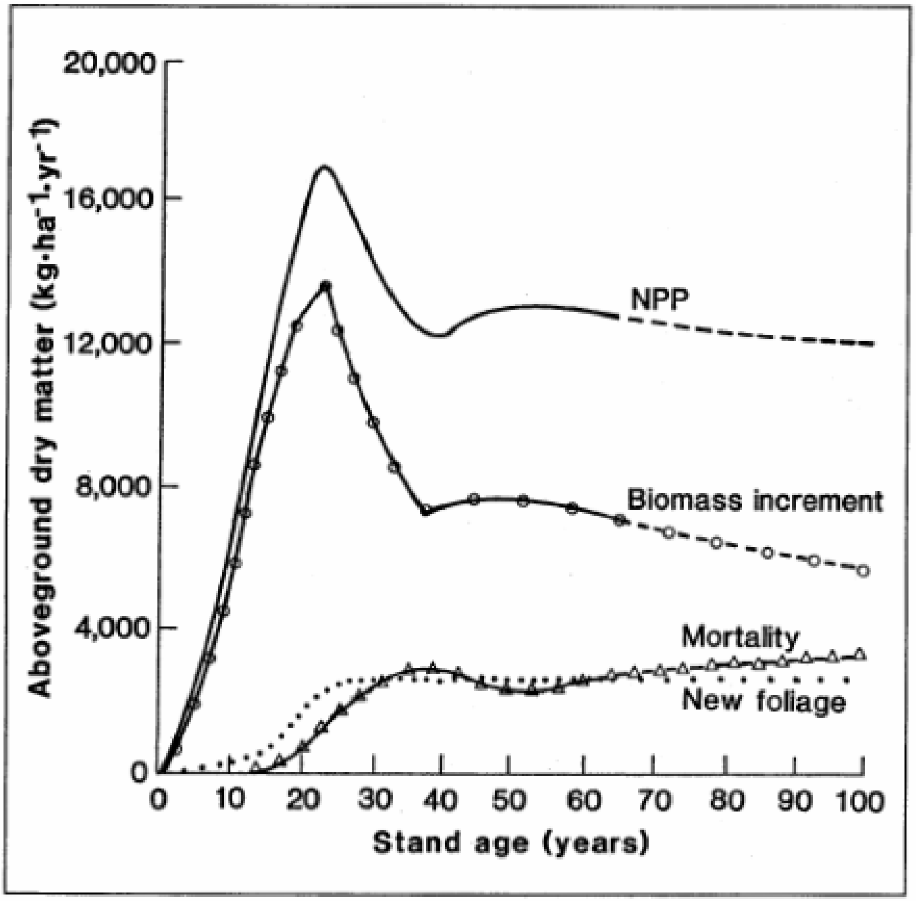

Figure 6—General patterns of NPP and the components of NPP for the first 100 years of Douglas-fir stand development in the Pacific Northwest. Curves are for aboveground production only and are derived from data for about 75 second-growth stands aged 15 to 65 years.

Effects of Management Activities on Net Primary Production

Almost all management activities will produce changes in actual productivity rates. Those affecting the potential productivity of the site concern the land manager most. It would be convenient if management practices could be categorized according to their impact on potential productivity, but this is not possible. An action causing a long-term decrease in potential productivity on one site could actually enhance potential productivity on another site. In general, practices causing one or more of the primary factors influencing plant growth (moisture, nutrients, temperature, and light) to become limiting or more severely limiting on a site for a prolonged period will result in a decrease in potential NPP. Conversely, practices acting to remove limitations or reduce the severity of a limitation will enhance potential NPP.

In this section, we will give examples of management practices that can alter the potential productivity of the site by changing the physical, chemical, or biological characteristics of the soil. The examples represent a cross section of the kinds of practices that can change potential productivity of the site. Most of these examples are specific to a particular forest type in a particular region. Criteria for selecting a practice for a given site must be guided by the particular characteristics of that site and by research results from similar sites.

Effects of Management Activities on Soil Physical Properties

Soil physical properties are susceptible to change induced by a variety of forest-management practices. The physical property most commonly affected is soil structure, which is partially responsible for determining soil moisture-holding capacity and soil aeration. The original soil texture, structure, and mineralogy determines to a large extent the response of the soil to various practices. Also important are the severity of disturbance, the frequency of disturbance, and the moisture content of the soil at the time of disturbance.

Soil compaction is a problem commonly associated with a variety of harvesting and site preparation techniques (Cromack and others 1979, Stone and others 1979, Switzer and others 1979). Compaction, can reduce aeration and impede water movement through the soil and can produce long-term impacts on plant growth and development (Daddow and Warrington 1983). If trees growing on the site cannot adapt to the compacted soil and recovery is slow, the potential site productivity can be reduced (Cromack and others 1979). Observed recovery rates for soils that have been compacted range from 8 to 40 years with surface soil horizons recovering sooner than deeper horizons (Thorud and Frissell1976).

Soil moisture conditions at the time of disturbance have a large influence on the degree of compaction that will occur on a particular soil. Bulk-density increases on dry soils are confined to the soil surface. The same soils when wet will compact to greater depths and generally remain compacted longer (Switzer and others 1979). In the Coast Ranges of Oregon and Washington, logging continues through the wet winter months when soils are often at field capacity. Under these conditions, compaction of some soils can be severe arid can result in landslides and erosion steep slopes (Ketcheson and Froehlich 1978).

Management practices most commonly associated with compaction are tractors, rubber-tired skidders, or other heavy equipment being used for logging, yarding, slash piling, and other site-preparation work. Switzer and others (1979) found that changes in bulk density can occur with less than three passes of logging equipment. Tractor yarding can cause compaction of more than 30 percent of harvested areas in the Pacific Northwest (Cromack and others 1979). Soil compaction can often be minimized by timing logging to coincide with periods of low soil moisture or by keeping use of heavy equipment to a minimum on soils susceptible to compaction. Winter logging on snow can prevent soil disturbance in areas that have winter snowpacks but remain accessible.

As soil compaction increases, root penetration is impeded until plant growth is reduced. The "growth-limiting" bulk density of a soil is defined as the threshold where root growth essentially stops and a reduction in plant growth occurs (Daddow and Warrington 1983). Soils of different textures will be affected to different degrees by compaction because of the average pore size and mechanical resistance. The "growth-limiting" bulk density will be higher for soils with a high percentage of macropores than for soils of finer texture. Generally, as soils become more compacted, the bulk densities become greater, pore space is reduced, infiltration is reduced, and the moisture-holding capacity of the soil is reduced. This compaction can result in greater surface runoff and erosion on sloping ground and accumulations of standing water in depressions on flatter ground. Conditions unfavorable for plant growth can result from poor aeration, reduced moisture availability, and inability of roots to penetrate the soil.

Studies on the impact of soil compaction on tree growth have been conducted throughout the United States. In a study on medium- to fine-textured soils in the Coastal Plain of North Carolina, height growth of 7-year-old loblolly pine *(Pinus taeda* L) was negatively correlated to micropore space in the surface soil (Terry 1978). New shoot growth of 4-month-old loblolly pine planted on a well-used skid road measured 5 inches (12.7 cm), while seedlings in the same soil just off the road had shoots measuring 18 inches (45.7 cm) (Maki 1976). Switzer and others (1979) reported 30 to 70 percent reductions in early height growth of loblolly pine on heavily trafficked and eroded areas. Youngberg (1959) reports a 43-percent reduction in seedling height growth in the Pacific Northwest on primary skid trails relative to uncompacted areas. Significant reductions in the growth of ponderosa pine *(Pinus ponderosa* Dougl. ex Laws.) and Douglas-fir are attributed to increased soil bulk densities created by harvesting operations with 57-percent reductions in height growth recorded for 8-year-old Douglas-fir trees growing in the compacted area (Froehlich 1973). Growth reductions of this nature may persist for several years.

Another problem similar to compaction that can occur on exposed soils is the crusting of the surface soil. Rain falling on exposed mineral soil can break up soil aggregates and disperse fine particles, which causes surface soil pores to become clogged (Ruark and others 1982). This clogging of the surface can lead to reductions in aeration and infiltration and increases in runoff and erosion.

Managers are often faced with the problem of providing a mineral-soil seedbed for regeneration without causing damage to soil physical properties. The problem has no easy solution, and often tradeoffs must be made. Because changes in soil physical properties can be long lasting and can reduce the potential productivity of the site for long periods, care should be taken to keep mineral soil disturbances to a minimum.

Site preparation techniques that can have major impacts on soil physical properties include terracing, mechanical scalping, root raking, and some forms of slash piling. Whenever the integrity of the soil profile is deeply disturbed or surface horizons are removed, the potential exists for productivity losses. Terracing is an example of an extreme management practice that can completely alter the integrity of the soil profile and the physical properties of the soil. This type of drastic site preparation should be undertaken only as a last resort. All these practices have been effective, however, under certain conditions and can be carried out without causing losses to productivity potential.

Prescribed burning can occasionally result in alterations to soil physical properties. These changes can be either detrimental or beneficial to site quality depending on fire severity and effects of the fire on soil properties, such as moisture retention, organic matter, and erodability. Changes in soil physical properties will generally be greater with fires of high intensity. One distinct benefit of prescribed burning may be a reduction in the susceptibility of the stand to severe wildfires, which could have worse effects.

A major consequence of burning is the reduction or elimination of the surface organic layers of the soil. Often, the majority of the forest floor is removed. As a result, the absorption and retention of water in the surface soil can be significantly reduced (Pritchett 1979a). Dyrness and others (1957) found that severe burning in the Pacific Northwest lowers total soil aggregation; they attribute this to the removal of colloidal organic matter by fire. They report that after severe fires, the ability of the surface layers of the soil to retain moisture when exposed to heat is significantly reduced and conclude that the presence of the surface litter is very important in moderating water loss from the soil system. Because the organic layers of the soil usually have high moisture-holding capacity, the decrease in soil organic matter as a result of fire can reduce the moisture-holding capacity of the soil and increase the susceptibility of the site to erosion (Dyrness and others 1957, Pritchett 1979a).

Ash produced in the combustion of organic material is very finely textured and when deposited on the surface of the soil reduces macropore space and can reduce the permeability of the soil to water by forming a surface crust (Woodmansee and Wallach 1978). In extreme cases, surface or subsurface soil layers will become hydrophobic. These hydrophobic layers can increase the probability of overland flow and erosion and can cause soil horizons below the hydrophobic layer to become droughty (DeBano and others 1979). Fire increases water repellence in sandy soils for up to 5 years after a burn (Dyrness 1976).

A blackened surface horizon will absorb greater amounts of incident solar radiation and, hence, cause higher soil temperature and greater water evaporation from the soil. Moisture stress resulting from high evaporation rates on blackened soils can cause seedling mortality in mixed-conifer forests in southwestern Oregon (Hallin 1968). Increased soil temperatures associated with burned soils can also limit seedling establishment. On the other hand, adding charcoal to some coarsely-textured soils may improve their moisture-holding capacity (Tryon 1948).

Light to moderate burns usually have little effect on the physical properties of the mineral soil; however, intense fires can cause the breakdown of soil aggregates and the fusion of clay particles into sand-like aggregates in the top several centimeters of the mineral soil (Dyrness and others 1957). Erosion caused by reduced infiltration can further alter soil physical properties by removing finely textured particles and altering the soil structure. These changes may take hundreds of years to reverse and can reduce the potential productivity of the site substantially. These drastic results are uncommon and should not overshadow the many beneficial effects of burning.

Other management activities can also cause erosion and mass movement of soils. One primary activity associated with accelerated surface erosion and mass erosion is road building (McColl and Grigal1979, Megahan 1972). Dyrness (1967) reports that although logging roads occupied only 2 percent of the area studied, they contributed up to 72 percent of the mass erosion after a storm. Between 3.7 and 9.4 percent of the land surface in heavily logged watersheds in the Klamath River basin of Oregon is currently or was recently subject to some form of erosion (Coates and Collins 1981). This percentage probably represents an extreme, but it serves to illustrate how large a proportion of the landscape can suffer lowered potential productivity as a result of erosional processes associated with logging.

Compaction, erosion, and changes associated with intense burning are the primary contributors to changes in soil physical properties that result in reductions in potential productivity.

Effects of Management Activities on Soil Chemical Properties

The potential productivity of a site can be raised or lowered by management activities causing a permanent or long-term increase or decrease in the availability of nutrients essential for plant growth. Productivity can also be lowered by actions raising the concentration of some chemical element to concentrations toxic to plant growth. The nutrient balance and chemical status of a soil is dynamic rather than static. Nutrients are constantly being added to soil through weathering, atmospheric fallout, and decomposition. Nutrients are also continually being removed from soil by vegetation and by leaching to groundwater. The availability of any nutrient in the soil depends not only on the total amount in the soil but also on a whole complex of factors including soil moisture and temperature, concentrations of other nutrients, soil pH, and microbial activity.

Most mature forest ecosystems conserve nutrients present at, or below, growth-limiting amounts. For this reason, most forests have relatively low rates of nutrient losses caused by leaching. Nutrients such as nitrogen and phosphorus often show a net accumulation over time. Because the chemistry of the soil is controlled by many interrelated and often fluctuating factors, almost any management activity can bring about soil chemical changes. Often these changes are short lived and have little impact on site quality. Occasionally, the changes cause increases or decreases in actual productivity that will last for several years. Rarely, a chemical change can result in permanent site degradation or in decreases in potential productivity that last longer than the length of a rotation. The types of soil chemical changes and the magnitude and duration of these changes determine whether or not potential productivity will change and, if so, for how long.

Nutrient Losses Associated With Harvesting

Any time organic matter is removed from a site, a net loss of nutrients from that site also occurs. In timber harvesting or thinning, nutrient losses tend to be proportional to the volume removed. The proportion of the total site nutrients tied up in trees differs for different forest types and also for different sites within the same general forest type. On the average, temperate coniferous forest sites may have only 10 to 15 percent of total nitrogen and phosphorus and 30 to 40 percent of total potassium stored in trees (Pritchett 1979b). Tropical forest sites often have a much greater proportion of total site nutrients stored in trees: up to 30 percent of the total nitrogen and 80 to 90 percent of the total phosphorus and potassium (Pritchett 1979b). The proportion of site nutrients present in trees also varies with the age of the stand and the development of a pronounced humus layer (Tamm 1980). The greater the proportion of total site nutrients present in the trees, the greater the potential for site degradation through harvesting.

In conventional harvesting, where only the bole or stemwood is removed, nutrient losses tend to be low. Conventional harvesting of an old-growth Douglas-fir forest in the Cascade Range in Oregon removed 65 percent of the total site biomass but only 12 percent of the total site nitrogen (Cromack and others 1979). Stemwood and bark of most temperate forest trees account for about 65 to 85 percent of the total biomass but only 25 to 50 percent of the total nitrogen in the trees (Marion 1979, Morrison and Foster 1979). Concentrations of other nutrients occur in the stem in about the same proportion as nitrogen. Nutrient losses from stem removal, averaged over the length of the rotation, tend to be less than 1 $kg \cdot ha^{-1} \cdot yr^{-1}$ for phosphorus and sulfur, up to 10 $kg \cdot ha^{-1} \cdot yr^{-1}$ for nitrogen and potassium, and between 5 and 15 $kg \cdot ha^{-1} \cdot yr^{-1}$ for calcium (Pritchett 1979b). Natural inputs of nutrients will often compensate for losses of this magnitude, resulting in no loss of long-term productivity potential. On nutrient poor sites having a high percentage of total nutrients stored in the trees, productivity potentials could be lowered. Some reductions in potential productivity can be offset by lengthening the next rotation or by fertilizing the site (Wells and Jorgenson 1979).

Harvest practices removing more than just stemwood also remove a greater proportion of the site nutrients. Whole-tree harvests can increase average nitrogen-removal rates in some temperate coniferous forests by 100 percent and in some temperate broadleaf forests by as much as 215 percent (Marion 1979). The actual increase in nutrient losses brought on by whole-tree harvesting varies greatly with species, age, and site productivity, but harvest methods removing more than just the stem result in substantially greater nutrient losses (Morrison and Foster 1979). The absolute amounts removed are less important than the time required for the site to replace the lost nutrients. Kimmins (1977) refers to this as the return to an "ecological condition that existed prior to rotation." The recuperation time after whole-tree harvest of a jack pine *(Pinus banksiana* Lamb.) stand in Ontario was estimated at 39 years (Morrison and Foster 1979). Weetman and Webber (1972) conclude that on well-drained soils with a high cation-exchange capacity, a whole-tree harvest of spruce stands every 50 years would not result in long-term productivity losses. Other species on different sites could have recovery rates very different from these.

Nutrient losses associated with removing organic matter from a site are affected not only by the magnitude of removal but also by the frequency of removal. If rotation lengths are shorter than the time required for a site to naturally replace nutrients lost in harvest, then productivity losses will occur. Poor sites may require fairly long rotations to prevent productivity losses. Better sites would initially be able to recover faster and support more frequent harvests. Intensive, short-rotation plantations are similar to agricultural crops and, as such, will probably require fertilizing and other practices associated with intensive agriculture to maintain productivity (Hansen and Baker 1979). Repeated light cuts, such as commercial thinnings and selection harvests, tend to remove more nutrients from a site over time than a single cut at the end of a rotation (Patric and Smith 1975). Thinnings capture biomass that would otherwise return nutrients to the soil through mortality and natural decomposition. In general, any activity that increases the yield from a site will also increase the nutrient losses from that site. Switzer and others (1979) report a generalized trend for southern pine forests where each 1-percent increase in yield produces a 3-percent increase in nutrient losses.

Nutrient Losses After Harvesting

The nutrient status of a forest site can be markedly altered by forest harvesting. One change is the removal of nutrients in the harvested timber; other changes are related to harvesting effects on nutrient cycling. Bormann and Likens (1979) refer to the period after timber harvesting as a "reorganization phase" of stand development, during which hydrologic, energetic, and biogeochemical processes may fluctuate drastically. In undisturbed stands, these processes tend to be, relatively constant and predictable. Changes occurring during this period include reduction or removal of competition for light, nutrients, and moisture by the trees; changes in the microclimate; and deposition of large quantities 'of organic matter that otherwise would be deposited slowly over time. The measured ecosystem responses to these changes include increases in streamwater discharge, increases in nutrient concentrations in leachates moving out of the soil, and increases in the rate of forest-floor-decomposition (Bormann and Likens 1979, Covington 1981, Kimmins and Feller 1979). Nutrient losses through leaching are often substantial and can result in either short- or long-term site degradation. Short-term improvements in nutrient availability may also occur from the breakdown of organic matter in the forest floor or in the slash left on the site.

Reductions in transpiration tend to increase soil moisture. Loss of the canopy also results in higher soil temperatures that, when combined with increased soil moistures, seem to create conditions favorable for increased rates of decomposition, mineralization, and nitrification on many forest sites. Nitrification produces mobile nitrate anions that may pair with soil cations such as calcium, potassium, and magnesium. Because uptake of nutrients is greatly reduced after harvest, the result may be a loss of nutrients by leaching. Nitrification may be the primary driving force in observed nutrient losses after harvesting (Wells and Jorgensen 1979), or it may explain only part of the measured loss in cations (Kimmins and Feller 1976). Other anions such as the bicarbonate anion, a byproduct of decomposition, may also contribute to losses from cation leaching (McColl and Grigal 1979).

The amounts of nutrients lost to leaching differ considerably depending on forest types, site characteristics, environmental conditions, and postharvest conditions. Vitousek and Melillo (1979) present a compilation of recorded nitrate losses after clearcutting. Some sites show almost no increase in nitrate leaving the site in streamwater or by deep leaching; others show nitrate after harvesting to be 20 times that found in uncut stands. In general, nitrate losses are apparently greater for deciduous than for coniferous forests. For coniferous forests in the Pacific Northwest, nitrate losses after clearcutting are generally 2 to 10 times those of pre harvest amounts (Cole and Gessel 1965, Kimmins and Feller 1976, Sollins and McCorison 1981). Losses of other nutrients by leaching are usually less than nitrate losses but differ considerably depending on the site and the ion mobility. Nutrients released through decomposition and mineralization may simply move from the organic horizons to the mineral horizons without any appreciable losses. Even on sites where losses by leaching are high, these losses can still be considered low relative to the losses attributable to timber removal (Sollins and McCorison 1981).

If revegetation of the site is rapid, the accelerated leaching losses usually last for only a few years. Even with immediate revegetation of the site, however, a lag of at least one year occurs in which more nutrients are mobilized than can be taken up by the vegetation (Bormann and Likens 1979). The nutrients released through decomposition of the forest floor and increased nitrification can enhance the growth of regeneration on the site. On some sites, such as boreal forests where decomposition is very slow beneath the forest canopy, exposure of the forest floor is necessary for maintaining adequate nutrient supplies (Patrie and Smith 1975, Viro 1974). If slash is left on the site, it may act as a nutrient sink and release nutrients slowly as the new stand matures (Covington 1981). Slash can also act to immobilize nitrogen by increasing the ratio of carbon to nitrogen. Immobilized nitrogen is not immediately available for plant growth but can act as an important pathway for preventing leaching losses of nitrogen.

Effects of Burning on Soil Chemistry

Site preparation can also alter soil chemical properties and, hence, site productivity. Slash burning is a common site preparation method that can affect soil chemical properties tremendously. A great deal of controversy is often associated with using fire because of the wide variety of effects, some of which are definitely detrimental to site quality and some of which are beneficial.

Fire speeds up decomposition; organic matter that would normally take several years to decompose is converted to ash, and carbon, nitrogen and other elements are released as gases. The volatilization of nitrogen during burning can cause significant losses of total site nitrogen.. The amount of nitrogen volatilized depends on the intensity of the burn and the characteristics of the fuel. At extreme temperatures, all nitrogen in the fuels will be volatilized (Boyer and Dell 1980). Intense wildfires on some sites can result in nitrogen volatilization losses totaling 60 percent of the site nitrogen (Grier 1975). Prescribed burning will generally remove a much smaller percentage of the site total. Kimmins and Feller (1976) estimated nitrogen volatilization losses from slash burning after old-growth harvest at 530 kg/ha. Losses of nitrogen after second-growth harvests seem to be considerably smaller—about 150 to 300 kg/ha (Grier 1972). Slash burning would probably be ill advised on sites with very low total nitrogen reserves. On other sites, volatilization losses may be insignificant.

Some elements are also lost as particulates in smoke during burning, but much more than half of the original biomass supply of mineral elements other than nitrogen remain on the site as ash (Woodmansee and Wallach 1978). These nutrients are in a relatively soluble form and are, thus, more or less available for plant uptake. Their solubility, however, also increases the chance for losses from surface runoff and leaching. Temporarily increased concentrations of cations in streamwater after burning are common (DeByle and Packer 1972, Kimmins and Feller 1976). Heavy rains immediately after burning can result in substantial nutrient losses. Wind erosion after burning can also cause nutrient losses.

Many researchers report an increase in pH after burning (Boyer and Dell 1980, Nisley 1978, Woodmansee and Wallach 1978). The increase in soil pH is usually short lived in areas of high precipitation, but in areas of low precipitation, elevated soil pH may last for several years. Increase in soil pH can increase nitrification and enhance availability of other nutrients. It can also have effects on soil microbial populations.

As long as nutrients in the ash are not immediately lost through erosion or leaching, they become available for plant growth and may increase productivity temporarily. In boreal forests in Scandinavia where nutrients tend to become immobilized in the forest floor, burning can improve the plant-available nutrient status of the site for 10 years or more (Viro 1974). After burning of a ponderosa pine site, availability of potassium, phosphorus, calcium, magnesium, sulfur, and nitrogen increased (Nisley 1978). Flushes in growth after burning are common in many areas of the world and are generally attributed to increased solubility and hence, availability of cations and to increased rates of nitrification on some sites. This period of increased nutrient availability may last only a few months or may persist for several years. Increases in nutrient availability may occur even if substantial loss of total site nutrients occurs. Burning can also reduce the cation-exchange capacity of the soil for at least a year from the loss of organic exchange sites (DeBano and others 1979). This loss could be important on sites where the exchange capacity of the soil is almost entirely in the organic horizons.

Burning will almost always result in some loss of nutrients, especially nitrogen, through volatilization or leaching. Other avenues for nutrient losses from burning can be minimized by avoiding severe fires and conditions leading to accelerated erosion. Prescribed burning should be avoided on sites having very shallow, nutrient-poor soils, on very steep slopes where the erosion potential is great, and on some other sites where nutrient losses may severely reduce productivity potential. Prescribed burning is a powerful silvicultural tool that usually has less impact on a site than do alternative means of accomplishing the same goals. Burning on most sites has little effect on potential productivity and on many sites will bring about a temporary increase in site productivity.

Soil Chemical Changes Caused by Fertilization

Where forest growth is limited by availability of one or more nutrients, fertilization may increase productivity, at least temporarily. Tree growth responses have been observed after a variety of chemical and organic fertilizers were applied. Nitrogen is the nutrient most frequently applied to forest stands, but phosphorus and potassium are common in some areas. Additions of micronutrients have also produced marked increases in growth on sites that had deficiencies. Several physical and biological site factors control the ability of an ecosystem to circulate and supply growth-limiting mineral nutrients added through fertilization. These factors in large part determine the magnitude and duration of growth response. Factors influencing fertilizer response include soil physical, chemical, and biological properties, climatic conditions, species, age of stand, stocking, form and amount of fertilizer applied, and season of application. If available moisture or some other factor is the primary growth-limiting factor on the site, then fertilizing may have little effect. Even if nutrients are known to be limiting, a growth response does not always occur. Many unknowns still limit our understanding of nutrient cycling pathways and the long-term impacts of fertilizing on site quality and potential productivity.

Additions of elements such as phosphorus, potassium, magnesium, and some of the micronutrients occasionally produce relatively long-lasting growth responses if conditions are such that these nutrients are efficiently cycled in the ecosystem (Ballard 1979). Applying nitrogen usually does not raise the potential productivity of the site and can generally be considered a crop treatment rather than a site treatment (Miller 1981). The observed growth response to nitrogen fertilizers usually lasts between 5 and 10 years (Ballard 1979, Brix 1983, Davey 1968, Peterson 1982, Weetman and others 1980). After this period, growth is usually at or near that of controls. The main effect of nitrogen fertilizer is to shorten the rotation. Long-term impacts on potential productivity are difficult to assess and probably not common.

The amount of applied nitrogen actually taken up by the trees is estimated to be 10 to 50 percent (Ballard 1979, Cole 1979, Davey 1968, Otchere Boateng 1979). Nitrogen not taken up by the trees may be stored, lost, or immobilized in a variety of ways. Substantial amounts of nitrogen added as urea can be hydrolized to ammonium, which can then replace cations on exchange sites (Cole 1979). Losses can occur through leaching if nitrification converts added nitrogen to nitrate ions. Gaseous losses can occur either through denitrification, the reduction of nitrate to gaseous N, or through volatilization of ammonia compounds. Although losses from leaching and gaseous losses may be substantial under certain conditions, the difference between nitrogen amounts applied as fertilizer and nitrogen amounts taken up by the trees is often the result of immobilization. Immobilization is greatest with urea fertilizer, especially at low dosages (Overrein 1971). With low dosages, a growth response in the trees may not occur because the added nitrogen is rapidly immobilized by the soil microbial population (Davey 1968). A short-term reduction in growth may occur if the applied dosage is insufficient to meet requirements of the soil microbes (Miller and others 1976).

Additions of nitrogen to the soil can cause loss of cations, which could cause nutrient imbalances or reductions in soil fertility. Cole (1979) reported significant losses of potassium, calcium, and magnesium after fertilization with urea without any leaching of nitrate. When increased nitrification occurs from increased soil pH and an abundant source of ammonium, it can lead to cation loss through leaching. On nitrogen deficient sites, however, populations of nitrifiers tend to be low, and a delay is associated with the buildup of nitrifying bacteria before increased nitrification can occur (Johnson 1979). A buildup of nitrifying bacteria can be beneficial on sites normally having low rates of nitrification. Weetman and others (1980) report higher nitrification rates persisted 15 years after black spruce *(Picea mariana* (Mill.) B.S.P.) sites in Canada were fertilized.

Fertilizing can have still other effects on the site. Balanced fertilizing can be beneficial in reducing insect and disease susceptibility; however, fertilizing with nitrogen alone can occasionally increase the susceptibility of the stand to insect or disease attack (Ballard 1979). Nitrogen fertilizing can also reduce cold and drought hardiness (Ballard 1979). One of the greatest dangers is the possibility of creating nutrient imbalances (Davey 1968). Additions of nutrient elements to the soil should be undertaken with some knowledge of the soil because nutrient amendments can affect the availability of other elements. Site productivity can be lowered by creation of nutrient imbalances.

Improvements in the nitrogen status of the soil also can be achieved through the use of nitrogen-fixing plants. These plants have certain advantages over chemical fertilizers on severely disturbed soils or when stands are very young because the plants provide steady levels of nitrogen over time and improve the soil through additions of organic matter (DeBell and Miller 1979). One drawback to using nitrogen-fixing plants is that they often compete with the desired tree crop for other growth-limiting factors such as moisture and other nutrients.

Adding nutrients to the soil is one of the few forest-management activities that can increase potential productivity. Many questions on the fate of fertilizers after they have been applied are still unanswered; the long-term effects of fertilizers on soil chemical and biological properties are still largely unknown. Fertilizing can often cause significant increases in growth and productivity, but it can also decrease site fertility by creating nutrient imbalances or by losing other elements.

Effects of Pollutants on Soil Chemistry

Increasing attention is being paid to the effects of air pollution on forest growth. Acid rain in the Northeastern United States is thought to be affecting thousands of acres of forest land. Most of the studies on acid rain deal with the effects on the trees themselves. Tamm and Cowling (1976) suggest that growth reduction in forest trees exposed to acid rain is due to several factors including erosion of the cuticle, loss of stomatal control, necrosis of internal plant cells, alteration of leaf and root exudate processes, disturbance of normal metabolism, and interference with reproduction. Many of these conditions increase the susceptibility of the trees to other stress factors.

Very little work has been done on the long-term effects of acid rain or other air pollution on soil fertility. As Krug and Frink (1983) point out, separating effects of acid rain from normal processes of soil acidification accompanying vegetation succession and soil formation is very difficult. The primary effects of pollutants on soils seem to be changes in pH, increased availability of certain nutrients such as sulfur and nitrogen, and changes in the redox state of the soil (Zinke 1980). These changes in turn affect soil chemistry and soil microorganisms. Increased additions of nitrogen or other minerals through pollution sometimes actually enhance plant growth; on the other hand, additions of certain heavy metals through fallout from a pollution source may reach concentrations in the soil that are toxic to plant growth. Concentrations of heavy metals in the soil around smelters occasionally stop tree growth altogether (Smith 1981). Even if the source of heavy-metal pollution is eliminated, the time needed before soil containing toxic concentrations of heavy metals is again able to support normal vegetation is unknown. Much work remains on the problem of long-term productivity losses or gains associated with air pollution.

Summary

Site productivity is a function of time and a variety of factors related to soil and climate. These various site factors may be collectively lumped into two categories: extrinsic and intrinsic. Extrinsic factors are those over which the ecosystem has no marked influence and include soil parent material, topography, and regional climate. Intrinsic factors are those influenced by the presence of the ecosystem and processes occurring within it. Intrinsic site factors include a range of soil-forming processes: forest influences such as shade, increased humidity, and altered soil water regime; nutrient conservation, especially nitrogen; formation of surface and soil organic matter; and the effects of water, nutrient, and carbon cycling on site productivity.

The other important factor influencing ecosystem productivity is time, which may be considered either in the long or short term. Long-term effects of time include the processes of soil development and plant succession. Short-term effects include changes in stand development and recovery after minor disturbance. Development of a productive soil from raw material can require thousands of years. Changes in site conditions permitting climax vegetation to become established can take hundreds of years, and natural reestablishment of a forest after severe site disturbance can occupy similar intervals. But recovery of former productivity after timber harvest may take as little as 3 years (Marks and Bormann 1972).

The relation between productivity and time, extrinsic site factors, vegetation, and intrinsic site factors is complex and cannot be easily modeled. Except for time, each is a composite of a large number of factors ranging from plant species to specific combinations and seasonal patterns of precipitation and air temperature. Extrinsic factors and vegetation can be considered dependent variables mutually influencing one another and productivity.

Solar radiation, altitude, slope and aspect, precipitation, and temperature regimes are essentially the boundaries the forest manager must work within. These boundaries place upper limits on site productivity no matter what other factors are operating. Irrigation, for example, may be used to alter site water balance for small areas. But large scale modifications of the effect of regional climate are generally not economically feasible, at least not now. Land managers interested in maintaining or increase ing land productivity must focus on managing intrinsic site factors and vegetation.

Managing vegetation has been the primary focus of forest managers in the past, so considerable research has been done on site preparation, regeneration, spacing and stocking, and comparisons of even- versus uneven-aged stand management. This silvicultural research has been of considerable value; now, forests can usually be harvested and reliably regenerated with a desirable species using standardized techniques. Unfortunately, the effects of vegetation management on intrinsic site factors has received relatively little systematic attention.

Most of the research on management effects on intrinsic site factors has used the case study approach and focused on narrow, specific questions. For example, studies of the effects of clearcutting on nutrient loss from soils have been more concerned with changes in streamwater quality (Cromack and others 1979, Fredriksen 1971, Harr 1976, Kimmins and Feller 1976) than in determining the effect nutrient losses have on site productivity. Studies of slash burning have similarly focused on changes in soil properties (Tarrant 1956, Viro 1969, Wells and others 1979) and nutrient losses (Cole and others 1975) without determining whether these changes and losses have any effect on site productivity.

Studies of forest productivity, on the other hand, have lacked the systematic approach needed to relate productivity to measurable site characteristics. Certainly, normal or empirical yield tables relate the production of forest products to stand age and site index. Information of this sort is necessary for managing forests for product yield, but such information has severe limitations. Site index cannot be reliably determined on a clearcut. In species conversion operations, site index for an existing species may not represent an equivalent site index for another species. Work such as that done by Steinbrenner (1979), who developed techniques for estimating site index from measurements of various extrinsic and intrinsic site characteristics, shows a way around some of these problems. Such techniques are, however, species specific, fail to deal with the dynamic nature of forest ecosystems, and are based on observation of past rather than future productivity.

Another problem with earlier productivity studies is their focus. Most studies on forest management have been extensive in nature and have been concerned primarily with wood yield rather than total productivity. Granted, the two are often closely correlated, but not always. Most studies of net productivity have been intensive and have had primarily an ecological focus. Such studies have concentrated on ecosystems of scientific rather than management interest, such as those in the pygmy forests of coastal northern California (Westman and Whittaker 1975). The distinction between these two study emphases is important: The more extensive forest-yield studies show different volume yields from different species on the same site, and the more intensive studies of net production indicate that total productivity, within limits, may be independent of species. Forest yield studies show the production of wood for a given species on a given site at a given age. Although net productivity also varies with stand age, measurements of NPP on mature stands may indicate the potential productivity of the site.

Early attempts to use productivity information to predict forest yields were often misleading. Yields of forest products from tropical forests tend to fall well below expectations created by reports of high NPP because litterfall rather than biomass increment is the dominant component of NPP in tropical forests (Jordan 1983). Although tremendously productive from the standpoint of carbon fixation, tropical forests may produce wood at low rates. Average wood production in the tropics is apparently about equal to or slightly less than wood production in temperate zone forests (Jordan 1983). Investments in forest stands should be based not only on the potential NPP of the site but also on the ability of the site to produce the desired products.

When attempting to assess the effect of forest management on site productivity, the researcher almost immediately encounters several obstacles. One is the lack of consistent, comparable measures of productivity within or among forest regions. Another is the tendency toward the "case study" approach for determining management effects on site factors. A third obstacle is the failure of researchers to provide adequate descriptions of research site characteristics, which makes any comparisons difficult and subjective. The final obstacle is the lack of attention to the effects of management practices on site productivity. Notable exceptions to this are thinning and fertilization research.

These obstacles have produced a paradox. The literature is full of studies on the effect of a given forest practice on one or more intrinsic site factors, and literature is also reasonably well supplied with reports of growth and yield for various site qualities. But so far, this information has not been brought together.

Present research does suggest certain general trends; for example, a number of researchers report declines in volume yields from soil compaction by rubber-tired skidders (see Froehlich 1974). Thus we can generalize and say that, typically, use of rubber-tired skidders will cause reduced volume growth because of soil compaction. But several perfectly valid questions remain. What degree of compaction causes how much growth loss? At what time of the year is compaction a problem? Is compaction always a problem? Are some species less sensitive to compaction than others? And so on. Similar generalities can be made about slash burning, herbicide application, fertilizing, site preparation, road and landing construction, thinning and other forest-management practices. Similar questions can be asked of each generality.

Predicting the impact of forest management on site productivity requires information beyond the site-specific data currently available. A systems-analysis approach with clearly defined objectives may be the best way to focus on the problem and the approach best suited to providing the research direction necessary for future studies.

Research Recommendations

We believe that several questions need to be answered and several potential lines of research followed to predict management impacts on site productivity. Is productivity a site characteristic, and as such, more or less independent of species and age? One way to answer this question is to do (1) regional surveys of site productivity in essentially unmanaged stands to obtain baseline information on productivity, and (2) research on the relation between site productivity and the various extrinsic site factors. Recent research (described in the "Introduction") indicates that up to 80 percent of the variation in site productivity may be explained by simple regressions on site water balance or other extrinsic variables. This correlation approach may be a fruitful direction for new regional research.

The intrinsic site variables having major direct or indirect influence on productivity must be identified. Soil texture, aeration, nutrient status, and thermal regime seem likely candidates, but other factors such as litter decomposition rates should not be overlooked.

Finally, systematic, quantitative research into management impacts on the various intrinsic site variables is necessary and must be combined with research into the sensitivity of these factors to management and the sensitivity of productivity to changes in these variables.

The major elements of the research described should be conducted within the framework of systems analysis. The ultimate objective of such research would be a computer model that could realistically predict management impacts on productivity. This model probably would not need the detail attempted in ecosystem modeling by the United States/International Biological Program (see Reichle 1970) because the objectives would be different. A model indicating the direction of productivity after management—increased, decreased, or unchanged—would be a significant first step.

Conclusions

Knowledge about rates of NPP in forested ecosystems of the Unites States is steadily accumulating. Through the work of researchers using increasingly sophisticated techniques, data are being gathered for comparing and cross checking a range of forest ecosystems. An important next step is to synthesize and integrate these data to identify trends, limiting factors, and ecosystem characteristics influencing the magnitude of growth rates. The data must be extended to address problems such as the shifting of ecosystem dynamics through time.

Although our knowledge of the patterns and characteristics of NPP of forest sites seem small relative to the number of unknowns that still exist, some aspects of NPP are well documented.

1. NPP varies with stand development and is highest at the time of canopy closure in young, newly established stands.
2. In the early stages of stand development, NPP is largely a function of biomass increment. In later stages of development, NPP may be largely composed of detrital production.
3. NPP may decline slightly with stand age but will not approach zero until harvesting, fire, or some other disturbance removes most of the vegetation.
4. High rates of NPP do not necessarily indicate high yields of forest products. The relative proportion of detrital production to biomass increment can be an important factor here.

This regional synthesis of NPP values for forest ecosystems has pointed out areas where further information is needed. Research efforts should be directed toward several activities.

1. Gather more information on specific aspects and components of NPP that remain largely unknown; for example, production of fine roots, loss to herbivores (fungi, insects), and effects of seasons.
2. Accumulate more information on forest types that have not been intensively studied; for example, southern Rocky Mountains, northeastern coniferous forests, and deciduous forests of the Pacific Northwest.
3. When comparing existing NPP data, isolate differences to learn what specific increments of moisture, temperature, and nutrients result in specific NPP, yields, biomass, or other measure of productivity.
4. Collect more detailed data on soils and other environmental elements so NPP can be related to more permanent ecosystem parameters and eventually predictive equations can be developed.

Regional analysis and predictive modeling of NPP for forest communities are useful in assessing the ability of these communities to convert sunlight into usable energy. Data integration will provide baseline data for future comparisons of net primary productivity in ecosystems influenced by forest-management activities.

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English Equivalents

1 millimeter (mm) = 0.0394 inch

1 centimeter (cm) = 0.3937 inch

1 cubic centimeter (cm^3) = 0.0610 cubic inch

1 meter (m) = 39.37 inches or 3.2808 feet

1 square meter (m^2) = 10.7639 square feet

1 gram (g) = 0.035274 ounce (avdp.)

1 hectare (ha) = 2.471 acres

1 kilogram (kg) = 2.2046 pounds

1 metric ton (t) = 2,204.6 pounds

1 metric ton per hectare (t/ha) = 893 pounds per acre
°C = (°F - 32)/1.8

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Data on net primary biological productivity of United States forests are summarized by geographic region. Site factors influencing productivity are reviewed.

This paper is a review of existing literature in the productivity of various forest regions of the United States, the influence of site factors on forest productivity, and the impact of various forest-management practices on site productivity.

Keywords: Site productivity, management (forest), productivity (biological).

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