# 3

# Ecological Indexes as a Means of Evaluating Climate, Species Distribution, and Primary Production

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## INTRODUCTION

Much of the research conducted in the Coniferous Forest Biome program was directed toward obtaining a deep understanding of one or more ecosystems. This chapter reports on some of the efforts to obtain a broader understanding of how gradients of moisture, temperature, and light across the biome affect ecosystem structure and function.

The diversity of vegetation and environment found in the western coniferous biome (Chapter 1; Whittaker 1961; Waring 1969; Franklin and Dyrness 1973) makes land-use allocation and management difficult. Productivity, for example, is difficult to predict, because trees grow differently in cool moist sites than they do under other conditions. In addition, the number of trees per hectare on dry sites never approaches that found on more moist sites (Wikstrom and Hutchinson 1971; Maclean and Bolsinger 1973). Successful regeneration of cutover land is often difficult because of a great variety of conditions (Cleary et al. 1977).

The natural vegetation types mentioned in Chapter 2 provide a means of identifying ecosystems that behave in a similar manner following disturbance. Ecological indexing methods have now been developed that help determine why each ecosystem behaves differently; they therefore aid in choosing among management options for maximizing desired forest products. These methods involve measuring the climate at representative forest sites and evaluating the climatic data with models of the response of Douglas-fir (Waring et al. 1972). The result is a set of ecological indexes that quantify the climate at each location. This is analogous to planting an individual or clone of one species at each of several locations and measuring the response to that particular environment.

The quantification of environmental factors has helped: (1) to explain species distribution and community composition (Chapter 2; Waring 1969;

Waring et al. 1975; D. B. Zobel and G. M. Hawk, pers. comm.; (2) to explain changes in productivity along environmental gradients (Emmingham and Waring 1977; Reed and Waring 1974); and (3) to predict silvicultural problems and suggest solutions for them (Cleary et al. 1977). Perhaps the most important contribution has been the demonstration of the important link between natural vegetation classification and climate (Dyrness et al. 1974; Zobel et al. 1976).

This chapter compares widely situated coniferous ecosystems using these ecological indexing methods. Emphasis was on determining which climatic factors were responsible for changes in the structure and function of the ecosystems. Structural features were height and basal area of tree stands, while functional analysis centered on primary productivity. Ecological indexes included evaluations of temperature, soil moisture, evaporative demand, and light.

## BACKGROUND

The techniques used to compare climates with ecological indexes were the result of over ten years of research into the physiology and ecology of coniferous biome species and ecosystems. The general approach is stated in Waring et al. (1972).

The major steps involved in comparing forest ecosystems include: (1) choosing sites representative of widely occurring forest ecosystems or habitat types; (2) collecting climatic and physiological data from each ecosystem; (3) using Douglas-fir, a widespread dominant plant, as a reference species to develop models of how the physical environment affects important plant processes on a daily basis; (4) evaluating the climate with these models (that is, simulations); (5) summing up the results of the simulations for important time intervals; (6) comparing the ecological indexes with observed structural and functional characteristics of the ecosystem; and (7) using the ecological indexes in a stand growth and succession simulation (see Chapter 4).

Comparison of the environment at different locations required a standard set of plant response models. The models were based on one reference species (coastal Douglas-fir), which, although widespread, does not span the diversity of environments found within the coniferous forest biome. No species does. This technique has the advantage of providing a single set of standards but should not be interpreted as a precise estimate of what the local variety or species could do.

Ecological indexes used were: (1) temperature growth index (TGI)—effect of soil and air temperatures on Douglas-fir growth (Cleary and Waring 1969); (2) moisture stress indexes—(a) maximum predawn plant moisture deficit or xylem water potential during the summer (Waring and Cleary 1967; Waring 1969; Zobel et al. 1976), and (b) sum of deficits during the growing season (Emmingham 1974), where the growing season is the number of days between year days 121 and 288 when soil and air temperatures are above 5°C and -1°C, respectively; (3) the summation of daily simulated photosynthesis indexes—(a) potential, (b) predicted actual, and (c) the ratio of predicted to potential (Emmingham and Waring 1977; these are estimates for coastal Douglas-fir and may be quite different from actual $CO_2$ fixation by a local conifer species); and (4) transpiration indexes—(a) potential (the summation of the daily product of absolute humidity deficit and maximum leaf conductance), (b) predicted actual (using leaf conductance estimated from moisture deficits), and (c) predicted/potential ratio. This last ratio is well correlated with the maximum height of trees in a variety of coniferous forest ecosystems (Reed and Waring 1974).

The data required to evaluate temperature, light, and moisture regimes were collected by cooperators in each state (see Acknowledgments). Temperature, humidity, and moisture stress observations were taken within each forest stand. Radiation data were recorded in the open. While the temperature, humidity, and radiation data were measurements of the physical conditions taken continuously, the soil moisture condition was evaluated by measuring plant water deficits at night on established one- to two-m-tall trees at two-week intervals. Methods are described in detail in Waring and Cleary (1967), Cleary and Waring (1969), Waring (1969), Zobel et al. (1976), Emmingham and Waring (1977), and Emmingham and Lundberg (1977).

Several measures of site productivity were used because of the difficulty in assessing stands of different ages. Site index (base age 100) was used because it is a conventional measure of site quality (Carmean 1975). Despite its widespread use, however, site index has many disadvantages (Daubenmire 1976). Thus two other measures of productivity were also used: growth basal area (GBA) (F. C. Hall, pers. comm.), and the product of a constant and the height and diameter growth indexes, being a volume index. The GBA method involved estimation of the ability of dominant trees to grow in diameter given the basal area of the surrounding trees as an estimate of competition. The basal area at which trees would grow 2.54 cm in radius in 30 years ($GBA_{30}$) was chosen as an index because many of these stands were growing at or near that rate.

## STUDY AREAS

Study sites in Alaska, Arizona, Colorado, Idaho, Montana, Oregon, Utah, and Washington were selected to cover the geographic, floristic, and climatic ranges found within the coniferous forest biome. For descriptive purposes the study sites were divided into arctic and alpine forests, dry forests, and modal forest types.

In all areas the study plots were chosen to be representative of widespread ecosystems. In Oregon and Idaho the plant communities were described and named according to the dominant climax species after Dyrness et al. (1974) and Daubenmire and Daubenmire (1968). In other areas plant communities were named for the species that dominated the tree stand. In all cases the descriptive data were collected on the study plot. Floristic and physical descriptions are given in Tables 3.1 and 3.2, respectively.

**TABLE 3.1** *Floristic description of forest ecosystems studied.*

| LOCATION<br>Forest type | Major tree species [a] | Tree layer cover (%) | Major shrub species | Shrub layer cover (%) | Major ground layer plants | Ground layer cover (%) |
|---|---|---|---|---|---|---|
| ALASKA[b] | | | | | | |
| Black spruce (Arctic) | *Picea mariana*[a] | 55 | *Salix scouleriana*<br>*Vaccinium uliginosum*<br>*Vaccinium vitis-idaea* | 25 | *Geocaulon lividum*<br>*Pleurozium schreberi*<br>*Cladonia* spp. | 100 |
| White spruce (Arctic) | *Picea glauca*[a]<br>*Populus tremuloides* | 70 | *Alnus crispa*<br>*Salix alaxensis*<br>*Viburnum edule* | 20 | *Hylocomium* sp.<br>*Pleurozium* sp. | 50 |
| ARIZONA[c] | | | | | | |
| Ponderosa pine (dry) | *Pinus ponderosa*[a] | 75 | none | 0 | *Festuca arizonica*<br>*Muhlenbergia montana* | 5 |
| COLORADO[d] | | | | | | |
| Spruce fir (alpine) | *Picea engelmannii*<br>*Abies lasiocarpa*[a] | 70 | *Vaccinium scoparium*<br>*Ribes lacustre*<br>*Sambucus pubens* | 15 | *Carex geyeri*<br>*Arnica cordifolia*<br>Lichens, mosses | 75 |
| IDAHO[e] | | | | | | |
| Douglas-fir (dry) | *Pinus ponderosa*<br>*Pseudotsuga menziesii*[a] var. *glauca* | 80 | *Physocarpus malvaceus*<br>*Symphoricarpos albus*<br>*Berberis repens* | 30 | *Fragaria* spp.<br>*Festuca idahoensis*<br>*Achillea millefolium* | 5 |
| Grand fir (modal) | *Pinus ponderosa*<br>*Pseudotsuga menziesii* var. *glauca*<br>*Larix occidentalis*<br>*Pinus contorta*<br>*Abies grandis*[a] | 90 | *Berberis repens*<br>*Rosa gymnocarpa*<br>*Holodiscus discolor*<br>*Rubus parviflorus*<br>*Pachistima myrsinites* | 15 | *Calamagrostis rubescens*<br>*Linnaea borealis*<br>*Fragaria* spp.<br>*Clintonia uniflora* | 20 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Western hemlock (modal) | *Pseudotsuga menziesii*<br>var. *glauca*<br>*Larix occidentalis*<br>*Pinus monticola*<br>*Thuja plicata*<br>*Abies grandis*<br>*Tsuga heterophylla*[a] | 95 | *Rubus parviflorus*<br>*Rosa gymnocarpa*<br>*Lonicera utahensis*<br>*Spiraea betulifolia*<br>*Pachistima myrsinites* | 10 | *Linnaea borealis*<br>*Clintonia uniflora*<br>*Viola orbiculata*<br>*Adenocaulon bicolor*<br>*Smilacina stellata* | 25 |
| Lodgepole pine (modal) | *Pinus contorta*<br>*Pseudotsuga menziesii*<br>var. *glauca*<br>*Abies lasiocarpa*[a]<br>*Pinus monticola* | 60 | *Vaccinium membranaceum*<br>*Pachistima myrsinites*<br>*Sorbus sitchensis* | 10 | *Xerophyllum tenax*<br>*Spiraea betulifolia*<br>*Goodyera oblongifolia* | 40 |
| Subalpine fir (alpine) | *Tsuga heterophylla*[a]<br>*Larix occidentalis*<br>*Abies lasiocarpa*<br>*Pinus monticola* | 70 | *Menziesia ferruginea*<br>*Vaccinium membranaceum*<br>*Vaccinium scoparium* | 10 | *Xerophyllum tenax*<br>*Gaultheria humifusa*<br>*Goodyera oblongifolia* | 30 |
| OREGON[f] | | | | | | |
| Sitka spruce (modal) | *Pseudotsuga menziessi*<br>var. *menziesii*<br>*Picea sitchensis*<br>*Tsuga heterophylla*[a] | 95 | *Vaccinium parvifolium*<br>*Menziesia ferruginea* | 25 | *Polystichum munitum*<br>*Oxalis oregana*<br>*Maianthemum dilatatum*<br>*Montia sibirica*<br>*Eurhynchium oreganum* | 50 |
| Douglas-fir (dry) | *Psuedotsuga menziesii*[a]<br>var. *menziesii*<br>*Pinus lambertiana* | 50 | *Holodiscus discolor*<br>*Acer circinatum*<br>*Corylus cornuta*<br>var. *californica*<br>*Berberis nervosa* | 30 | *Whipplea modesta*<br>*Polystichum munitum*<br>*Synthyris reniformis*<br>*Linnaea borealis* | 30 |
| Western hemlock (modal) | *Pseudotsuga menziesii*<br>var. *menziesii*<br>*Tsuga heterophylla*[a] | 100 | *Rhododendron macrophyllum*<br>*Berberis nervosa*<br>*Acer circinatum* | 40 | *Linnaea borealis*<br>*Polystichum munitum*<br>*Coptis laciniata*<br>*Chimaphila umbellata* | 30 |

**TABLE 3.1** *Continued*

| LOCATION<br>Forest type | Major tree species [a] | Tree layer cover (%) | Major shrub species | Shrub layer cover (%) | Major ground layer plants | Ground layer cover (%) |
|---|---|---|---|---|---|---|
| OREGON[f] | | | | | | |
| Pacific silver fir (modal) | *Pseudotsuga menziesii*<br>var. *menziesii*<br>*Abies amabilis*[a]<br>*Tsuga heterophylla* | 100 | *Vaccinium membranaceum*<br>*Acer circinatum* | 5 | *Tiarella unifoliata*<br>*Achlys triphylla*<br>*Cornus canadensis* | 40 |
| Mountain hemlock (arctic & alpine) | *Tsuga mertensiana*[a]<br>*Abies procera*<br>*Abies amabilis*[a]<br>*Pinus monticola* | 60 | *Vaccinium membranaceum* | 5 | *Xerophyllum tenax*<br>*Pyrola secunda* | 50 |
| MONTANA[e] | | | | | | |
| Douglas-fir (modal) | *Pseudotsuga menziesii*[a]<br>var. *glauca*<br>*Pinus contorta*<br>*Larix occidentalis* | 60 | *Arctostaphylos uva-ursi*<br>*Berberis repens*<br>*Spiraea betulifolia* | 15 | *Calamagrostis rubescens*<br>*Arnica cordifolia* | 5 |
| UTAH[g] | | | | | | |
| Douglas-fir (modal) | *Psuedotsuga menziesii*[a]<br>var. *glauca*<br>*Pinus flexilis* | 80 | *Acer glabrum*<br>*Berberis repens*<br>*Lonicera utahensis* | 10 | *Clematis pseudoalpina*<br>*Arnica cordifolia*<br>*Goodyera oblongifolia* | 5 |
| Englemann spruce-subalpine fir (arctic & alpine) | *Picea engelmannii*<br>*Abies lasiocarpa*[a] | 75 | *Pachistima myrsinites*<br>*Lonicera utahensis* | 1 | *Osmorhiza chilensis*<br>*Pedicularis racemosa*<br>*Aster foliaceus* | 15 |

| | | | | | | |
|---|---|---|---|---|---|---|
| WASHINGTON[h] | | | | | | |
| Ponderosa pine-oak (dry) | *Pinus ponderosa*[a]<br>*Quercus garryana*<br>*Pseudotsuga menziesii*[a] var. *menziesii* | 50 | *Ceanothus integerrimus*<br>*Amelanchier alnifolia*<br>*Corylus cornuta* | 5 | *Apocynum androsaemifolium* var. *pumilum*<br>*Vicia americana* var. *truncata*<br>*Lupinus* sp.<br>*Arenaria macrophylla*<br>Gramineae | 10 |
| Ponderosa pine (dry) | *Pinus ponderosa*<br>*Pseudotsuga menziesii* var. *menziesii*[i] | 80 | *Purshia tridentata*<br>*Chrysothamnus viscidiflorus* | 5 | *Achillea millefolium*<br>*Viola nuttallii*<br>*Osmorhiza chilensis*<br>*Horkelia fusca*<br>Gramineae | 90 |
| Pacific silver fir (modal)— | *Abies amabilis*[a]<br>*Abies procera*<br>*Pseudotsuga menziesii* var. *menziesii*<br>*Tsuga heterophylla* | 90 | *Vaccinium membranaceum*<br>*Pachistima myrsinites*<br>*Acer circinatum* | 20 | *Berberis nervosa*<br>*Xerophyllum tenax*<br>*Chimaphila umbellata*<br>*Linnaea borealis* | 10 |
| Grand fir (modal) | *Pseudotsuga menziesii*[a] var. *menziesii*<br>*Pinus ponderosa*<br>*Abies grandis* | 95 | *Holodiscus discolor*<br>*Corylus cornuta*<br>*Rubus parviflorus*<br>*Symphoricarpos mollis* | 5 | *Berberis nervosa*<br>*Chimaphila menziesii*<br>*Pteridium aquilinum*<br>*Achlys triphylla*<br>*Trientalis latifolia* | 10 |

[a]Designates the major reproducing tree species.
[b]Viereck and Little 1975.
[c]Avery et al. 1976.
[d]J. D. Richards, personal communication.
[e]Hitchcock and Cronquist 1974.
[f]Franklin and Dyrness 1973.
[g]Henderson et al. 1976.
[h]Susan Meyer, under direction of K. L. Reed; James Long and Gordon Swartzman contributed to the study.
[i]*Pseudotsuga menziesii* was judged to be the climax species in this location although it had been excluded by repeated fires.

**TABLE 3.2** *Physical description of reference sites and tree stands.*

| LOCATION Forest type | Latitude | Longitude | Elevation (m) | Slope (°) | Aspect | Dominant Tree Means Age (yr) | Dominant Tree Means Diam (cm) | Dominant Tree Means Ht (m) | Stand basal area ($m^2$/ha) |
|---|---|---|---|---|---|---|---|---|---|
| ALASKA | | | | | | | | | |
| Black spruce | 65°10′ | 147°53′ | 490 | 0 | — | 68 | 7 | 6 | 6 |
| White spruce | 64°51′ | 148°44′ | 260 | 10 | SSW | 70 | 37 | 20 | 40 |
| ARIZONA | | | | | | | | | |
| Ponderosa pine | 35°16′ | 111°45′ | 2270 | 0 | — | 88 | 41 | 20 | 39 |
| COLORADO | | | | | | | | | |
| Engelmann spruce-subalpine fir | 37°50′ | 107°30′ | 3470 | 15 | W | 100 | 24 | 17 | 44 |
| IDAHO | | | | | | | | | |
| Douglas-fir | 48°22′ | 116°29′ | 780 | 27 | SSW | 82 | 46 | 28 | 31 |
| Grand fir | 48°22′ | 116°29′ | 730 | 9 | W | 71 | 38 | 27 | 41 |
| Western hemlock | 48°22′ | 116°29′ | 850 | 6 | NW | 100 | 40 | 32 | 40 |
| Londgepole pine | 48°21′ | 116°25′ | 1555 | 14 | WSW | 94 | 24 | 18 | 60 |
| Subalpine fir | 48°21′ | 116°25′ | 1555 | 6 | NE | 137 | 27 | 20 | 42 |
| MONTANA | | | | | | | | | |
| Douglas-fir | 46°52′ | 113°27′ | 1470 | 16 | S | 175 | 26 | 20 | 45 |
| OREGON | | | | | | | | | |
| Sitka spruce | 45°04′ | 123°57′ | 200 | 10 | W | 116 | 76 | 48 | 119 |
| Douglas-fir | 44°12′ | 122°15′ | 510 | 35 | SW | 450 | 117 | 49 | 56 |
| Western hemlock | 44°13′ | 122°14′ | 530 | 20 | NNW | 450 | 129 | 75 | 119 |
| Pacific silver fir | 44°16′ | 112°08′ | 1310 | 27 | W | 350 | 104 | 46 | 109 |
| Mountain hemlock | 44°21′ | 122°04′ | 1530 | 15 | NW | 135 | 53 | 37 | 65 |
| UTAH | | | | | | | | | |
| Douglas-fir | 41°57′ | 111°31′ | 2210 | 2 | E | 166 | 41 | 27 | 43 |
| Engelmann spruce-subalpine fir | 41°58′ | 111°25′ | 2650 | 32 | N | 237 | 67 | 32 | 58 |
| WASHINGTON | | | | | | | | | |
| Ponderosa pine-oak | 45°55′ | 121°04′ | 646 | 1 | WNW | 83 | 41 | 20 | 41 |
| Ponderosa pine | 46°00′ | 121°19′ | 572 | 0 | — | 139 | 72 | 32 | 46 |
| Pacific silver fir | 46°07′ | 121°37′ | 1009 | 19 | W | 217 | 63 | 40 | 77 |
| Grand fir | 46°00′ | 121°26′ | 750 | 1 | SE | 207 | 67 | 40 | 50 |

## Arctic and Alpine Forest Types

The most northern and severe study site was a diminutive black spruce forest north of Fairbanks, Alaska, where the permafrost layer melted to a depth of only 50 to 60 cm during the growing season (Viereck 1973). A few kilometers west of Fairbanks a white spruce forest was chosen because it, too, experienced the rigors of the central Alaskan winter but was not underlain by permafrost (Van Cleve and Zasada 1976; Zasada 1976).

In Colorado and Utah, Engelmann spruce and subalpine fir forests at high elevation were examined. The composition and basal area of the stands were similar, but the trees in Utah were over 100 years older and 20 m taller than those in Colorado.

The coolest site in northern Idaho was the subalpine fir stand, which had white pine and western larch as seral dominant tree species rather than Engelmann spruce. It was classified as an *Abies lasiocarpa/Menziesia ferruginea* habitat type (Daubenmire and Daubenmire 1968).

A mountain hemlock in the Cascade Mountains of Oregon was at the cool end of the Oregon gradient and had a rich mixture of tree species including seral noble fir, western white pine, and the shade-tolerant Pacific silver fir. This site was representative of the *Tsuga mertensiana—Abies amabilis/Xerophyllum tenax* habitat type of Dyrness et al. (1974).

## Modal Forest Types

The modal forest types were those judged to be at neither the cold—moist nor warm–dry extremes in the local area. Three forest sites in Oregon (Sitka spruce, western hemlock, and Pacific silver fir) were chosen. These forests were the tallest (48 to 75 m) and had the greatest basal area (over 100 $m^2$/ha) found in this study.

Near the Pacific Ocean a forest dominated by Sitka spruce and western hemlock was chosen because of its high productivity (Fujimori 1971). In contrast to all the other study sites, snow is rare at this location.

At the western hemlock forest site in the western Cascades of Oregon, snow is common, but persistent winter snowpack is unusual. Stands are dominated by large, old-growth Douglas-fir that average over 1 m in diameter at breast height (dbh). This site is typical of the *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa* habitat type (Dyrness et al. 1974).

At higher elevations, the Pacific silver fir forest sites of Oregon and Washington contained both Douglas-fir and noble fir as seral dominants. A heavy snowpack is common on these sites and snow often persists until the first of July.

The grand fir site in western Washington occurred in a depression and from climatic records it was evident that frost was frequent and severe. Like the grand fir site in Idaho *(Abies grandis/Pachistima myrsinites* habitat type), it had both Douglas-fir and ponderosa pine as seral dominants in the stand.

The three modal types in Idaho included the grand fir and western hemlock *(Tsuga heterophylla/Pachistima myrsinites* habitat type) sites, and a lodgepole pine stand on an *Abies lasiocarpa/Xerophyllum tenax* habitat type. The grand fir and hemlock sites were similar in elevation, but the fir type was on a more southerly aspect. Lodgepole pine was at higher elevation in a denser stand (60 versus 40 $m^2$/ha basal area) than the grand fir and hemlock. Despite the greater basal area found in this stand, tree height indicated lower site productivity.

The Douglas-fir site in northern Utah and the lodgepole pine stand in Montana were chosen to represent modal types in their areas. Both stands were at the cool end of the climatic gradient for Douglas-fir. Henderson et al. (1976) classed the Utah site as a *Pseudotsuga menziesii* (var. *glauca*)/*Berberis repens* habitat type, while the Montana site fell into the *Pseudotsuga menziesii* (var. *glauca*)/*Linnaea borealis* habitat type of Pfister et al. (1977).

### Dry Forest Types

An open ponderosa pine forest near Flagstaff, Arizona, was the most southern of the sites. It was chosen for comparison with the ponderosa pine stand in Washington. The pine communities in western Washington were in the arid rain shadow of the Cascade Mountains. The driest of the two sites was a ponderosa pine/Oregon white oak community located on rocky, shallow soils. A pure pine stand was located at a lower elevation on a deeper soil. Douglas-fir was judged capable of regenerating, but it had been excluded by repeated wildfires.

The driest of the Idaho sites was typical of the *Pseudotsuga menziesii* (var. *glauca*)/*Physocarpus malvaceus* habitat type. It was chosen for comparison with the *Pseudotsuga menziesii* (var. *menziesii*)/*Holodiscus discolor* habitat type in Oregon, which is the driest conifer-dominated type west of the Cascade Mountains of Oregon. The larger trees on this site were 49 m high and the basal area was 56 m/ha. Thus growth was relatively good compared with that on other dry sites, but considerably less than on other Oregon sites.

## COMPARISON OF ECOLOGICAL AND PRODUCTIVITY INDEXES ACROSS THE CONIFEROUS BIOME

Evaluation of the climate at a variety of western coniferous forest sites provided a means to examine functional relations responsible for differences in vegetation composition and productivity. For example, interior western hemlock, Douglas-fir, and ponderosa pine forest sites can be compared with similar forest types nearer the Pacific coast. Arctic and alpine forests also can be compared. Ecological (temperature, moisture, photosynthesis, and transpiration) and productivity indexes are shown in Table 3.3 for each site. Sites were assigned reference numbers.

## Temperature Indexes

The TGI ranged from 14 to 115 at the cold and dry extremes, while modal types in Oregon were 80 to 90 (Table 3.3). For the arctic sites (1 and 2) TGI values were less than 25, while on the alpine sites in Colorado (4), and Idaho (9), Oregon (15), and Utah (17), they averaged about 43. Warm dry sites (3, 5, 11, 18, and 19) averaged 89. The Douglas-fir type in Oregon (11) and pine/oak types in Washington (18) had TGI values over 105. Interestingly, the ponderosa pine site in Arizona (3) had a temperature index of only 70, partly because of restriction of the growing season by frost. In general the low-elevation sites in Oregon and Washington had greater temperature indexes than inland areas because they had longer growing seasons.

## Moisture Stress Indexes

Both maximum and sum-of-moisture stress measured on small trees at each site confirmed the droughty nature of the sites with Douglas-fir or ponderosa pine as dominant species (sites 3, 5, 6, 11, 16, and 18, Table 3.3). The grand fir type (6) in Idaho was included because Douglas-fir and ponderosa pine dominated the stand. The Douglas-fir/ponderosa pine site in Washington (19) had much lower stress than these dominants indicated, suggesting that repeated fires have excluded more tolerant species. Even relatively moist sites, including the spruce sites in Oregon (12) and Alaska (1 and 2) had maximum moisture deficits of –5 or –6 bars.

Moisture stress sum, which represents accumulated drought during the growing season, was greatest in ponderosa pine types of Arizona (3) and Washington (18) and the Douglas-fir site (11) in Oregon (Table 3.3). Lowest sums were in Alaska (sites 1 and 2) and the Engelmann spruce site (19) in Utah. The spruce site in Utah had a low moisture stress total because summer frosts cut the growing season off before the moisture deficit became severe.

Modal forest types in the Cascades of Washington and Oregon (sites 13, 14, 20, and 21) averaged less than –11 bars maximum moisture deficit at the peak of drought (Table 3.3). In contrast, inland modal sites (7, 8, 10, and 16) averaged around –15 bars. Although all these sites probably start the growing season with soils at field capacity, the inland sites apparently did not have as great a soil water storage capacity to meet evaporative demand.

The western hemlock forests of Oregon have many floristic similarities to those in Idaho, although inland forests were more diverse in both tree and shrub layers. Climatically, the Oregon site (13) was warmer (TGI = 90) than the Idaho site (7; TGI = 65) and more moist (–9.1 versus –15.9 maximum moisture deficit; Table 3.3). The ponderosa pine type in Washington (18) was warmer (TGI = 115 versus 70), but similar in moisture deficit to the analogous pine type in Arizona (3).

**TABLE 3.3** *Indexes to reference stand productivity and environment.*

| | | | | | | | Ecological indexes (in growing season) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Productivity indexes | | | | Moisture stress (–bars) | | Photosynthesis ($mg[CO_2]dm^{-2}$) | | | Transpiration ($mg[H_2O]cm^{-2}$) | |
| Site No. | LOCATION Forest type | Eco-class[a] | Ht[b] | Diam[c] | Vol[d] | TGI[e] | Max. | Sum. | Potential | Predicted | Ratio | Predicted | Ratio |
| | ALASKA | | | | | | | | | | | | |
| 1 | Black spruce | A | 28[f] | 25 | 10 | 14 | 6.1 | 200 | 2538 | 1076 | 0.42 | — | — |
| 2 | White spruce | A | 86[g] | 87 | 107 | 24 | 5.7 | 316 | 4870 | 2801 | 0.58 | 274 | 0.57 |
| | ARIZONA | | | | | | | | | | | | |
| 3 | Ponderosa pine | D | 83[h] | 175 | 207 | 70 | 22.2 | 1715 | 10 196 | 1296 | 0.13 | 107 | 0.11 |
| | COLORADO | | | | | | | | | | | | |
| 4 | Engelmann spruce-subalpine fir | A | 56[f] | — | — | 50 | 13.8 | 820 | 9191 | 3502 | 0.38 | 214 | 0.39 |
| | IDAHO | | | | | | | | | | | | |
| 5 | Douglas-fir | D | 98[f] | 142 | 199 | 80 | 19.5 | 1235 | 11 242 | 2842 | 0.25 | 191 | 0.25 |
| 6 | Grand fir | M | 101[f] | 171 | 247 | 64 | 21.5 | 1022 | 10 322 | 3300 | 0.32 | 215 | 0.31 |
| 7 | Western hemlock | M | 105[f] | 161 | 241 | 65 | 15.9 | 992 | 11 109 | 3725 | 0.34 | — | — |
| 8 | Lodgepole pine | M | 62[f] | 200 | 177 | 43 | 15.6 | 820 | 7540 | 2118 | 0.28 | 178 | 0.30 |
| 9 | Subalpine fir | A | 59[f] | 165 | 139 | 33 | 12.5 | 721 | 6587 | 1774 | 0.27 | 129 | 0.27 |
| | MONTANA | | | | | | | | | | | | |
| 10 | Lodgepole pine | M | 50 | 164 | 117 | 59 | 10.5 | 687 | 9687 | 5123 | 0.53 | 360 | 0.54 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | OREGON | | | | | | | | | | | | |
| 11 | Sitka spruce | M | 150[j] | 480 | 1303 | 80 | 5.0 | 402 | 13 170 | 10 296 | 0.78 | — | — |
| 12 | Douglas-fir | D | 120[j] | 210 | 360 | 106 | 25.7 | 2017 | 13 116 | 5190 | 0.40 | 460 | 0.46 |
| 13 | Western hemlock | M | 160[j] | 477 | 1070 | 90 | 9.1 | 758 | 12 936 | 8694 | 0.67 | 646 | 0.58 |
| 14 | Pacific silver fir | M | 120[j] | 413 | 708 | 60 | 8.1 | 579 | 9308 | 5697 | 0.61 | 272 | 0.51 |
| 15 | Mountain hemlock | A | 110[j] | 280 | 440 | 47 | 13.4 | 629 | 6559 | 3546 | 0.54 | 216 | 0.44 |
| | UTAH | | | | | | | | | | | | |
| 16 | Douglas-fir | M | 75[k] | 167 | 179 | 53 | 18.6 | 1230 | 8522 | 2045 | 0.24 | 247 | 0.33 |
| 17 | Engelmann spruce-subalpine fir | A | 65[k] | 290 | 269 | 41 | 13.1 | 373 | 4905 | 4882 | 0.95 | 689 | 0.95 |
| | WASHINGTON | | | | | | | | | | | | |
| 18 | Ponderosa pine-oak | D | 70[i] | 95 | 95 | 115 | 20.8 | 1840 | 13 020 | 2907 | 0.22 | 298 | 0.19 |
| 19 | Douglas-fir-ponderosa pine | D | 88[i] | 390 | 490 | 73 | 7.8 | 754 | 9615 | 3311 | 0.34 | 283 | 0.35 |
| 20 | Pacific silver fir | M | 104[j] | 186 | 276 | 60 | 11.0 | 688 | 9537 | 4705 | 0.49 | 381 | 0.52 |
| 21 | Grand fir | M | 108[j] | 441 | 680 | 69 | 7.5 | 630 | 8508 | 3791 | 0.45 | 361 | 0.43 |

[a]Each site was placed in one of the following ecological classes: A = arctic and alpine; D = dry; and M = modal type.

[b]The height/growth index is the height (in feet; 1 ft - 0.305 m) to which dominant and codominant trees grow in 100 years.

[c]The diameter/growth index is the basal area (in square feet per acre; square feet per acre times 0.2296 = square meters per hectare) of surrounding or competing trees when dominant and codominant trees grow by a radius of 0.85 mm/yr or 1 in/30 yr ($GBA_{30}$).

[d]The volume/growth index is equal to the height index times volume index times $70^{-1}$. This approximates cubic volume growth potential of the site.

[e]TGI is the temperature/growth index, which integrates the effect of air and soil temperatures on tree growth (Cleary and Waring 1969; Zobel et al. 1976).

[f]The height/growth index was estimated directly when trees were near 100 years of age (see Table 3.2).

[g]Derived from Farr 1967.

[h]Derived from Minor 1964.

[i]Derived from Meyer 1961.

[j]Derived from McArdle et al. 1961.

[k]From Henderson et al. 1976.

**Photosynthesis Indexes**

The lowest potential photosynthesis was at the Alaska black spruce permafrost site, while the highest was in the Oregon Sitka spruce zone (Table 3.3). The potential photosynthesis index was relatively high for the Arizona ponderosa pine and the warm, low-elevation sites in Idaho, Oregon, and Washington. Surprisingly, there was only about a fivefold difference between photosynthesis potentials at all the sites.

Photosynthesis simulations throughout the year for nine representative sites are shown in Figure 3.1. The upper curve is the simulated potential photosynthesis using air temperature and solar radiation. The predicted (actual) photosynthesis is the lower or heavy line, and represents the photosynthesis given moisture deficits, frost, and cold soils. The Oregon sites are characteristic of the west coast area, including Oregon and Washington. The other sites shown include the cold extremes in Alaska and Colorado, as well as the interior forests of Utah, Idaho, Arizona, and Montana.

The potential photosynthesis during the summer was between 70 and 90 $mg \cdot dm^{-2} \cdot day^{-1}$ for all sites. There was a general trend toward higher potential with decreasing latitude. The similarity between sites at such wide extremes suggests, however, that temperature and radiant energy are not the most important limiting factors during the growing season.

There were large differences in photosynthetic potential during the winter months. Interior sites were generally lower than coastal sites. At the coastal sites, the winter potential was near 40 $mg \cdot dm^{-2} \cdot day^{-1}$ (Figure 3, 1f, i) while in the arctic and more severe sites it was zero (Figure 3.1a, b, d). Although classed as an alpine site, the mountain hemlock site in Oregon showed considerable potential because of mild air temperatures (0° to 5°C) during part of the winter.

In extreme arctic Alaska and the nearly desert environment of Arizona, no more than 50 percent of the photosynthetic potential was captured during any period of the year (Figure 3.1a, g). In all other locations, nearly 100 percent of the potential for photosynthesis was captured at some time during the year. The big difference between the interior sites in Colorado, Idaho, and Montana (Figure 3.1b, e, h) was in the duration of full photosynthetic potential. In the western hemlock (Figure 3.1f) and Douglas-fir types of Oregon (Figure 3.1i), the winter and spring months appear especially important for the capture of the sun's energy. The mountain hemlock site in Oregon (Figure 3.1c) showed a soil temperature restriction during winter and spring and fairly severe reduction from drought during the growing season.

Although western hemlock sites in Idaho (Figure 3.1e) and Oregon (Figure 3.1f) have similar photosynthetic potential, moisture stress at the Idaho site reduced predicted photosynthesis to less than half that in Oregon. This helps explain higher productivity (site index 160 versus 105) of the Oregon sites. Also, wintertime photosynthetic potential was greater in Oregon (Figure 3.1f).

Comparison of Douglas-fir forests of Oregon and Idaho showed a similar trend in temperature and predicted photosynthesis (Table 3.3); however, maximum moisture deficit was greater in Oregon Douglas-fir forests (Table 3.3). Conditions for photosynthesis during winter and spring are considerably more favorable in Oregon than in the Douglas-fir forests of either Idaho or Utah.

On a growing season basis, ponderosa pine forests of Washington were considerably warmer than those in Arizona (Table 3.3). In addition, dry spring conditions in Arizona (Figure 3.1g) induced high moisture deficits reducing predicted photosynthesis to only about 13 percent of the potential. Moisture stress indexes for the growing season were similar for both sites (Table 3.3).

The lowest predicted photosynthesis indexes occurred at the geographic extremes; in Alaska black spruce and Arizona ponderosa pine sites. The highest predicted photosynthesis indexes were at the coastal location and western hemlock site in Oregon. There was a nearly tenfold difference in the index between the black spruce site in Alaska and Sitka spruce site in Oregon.

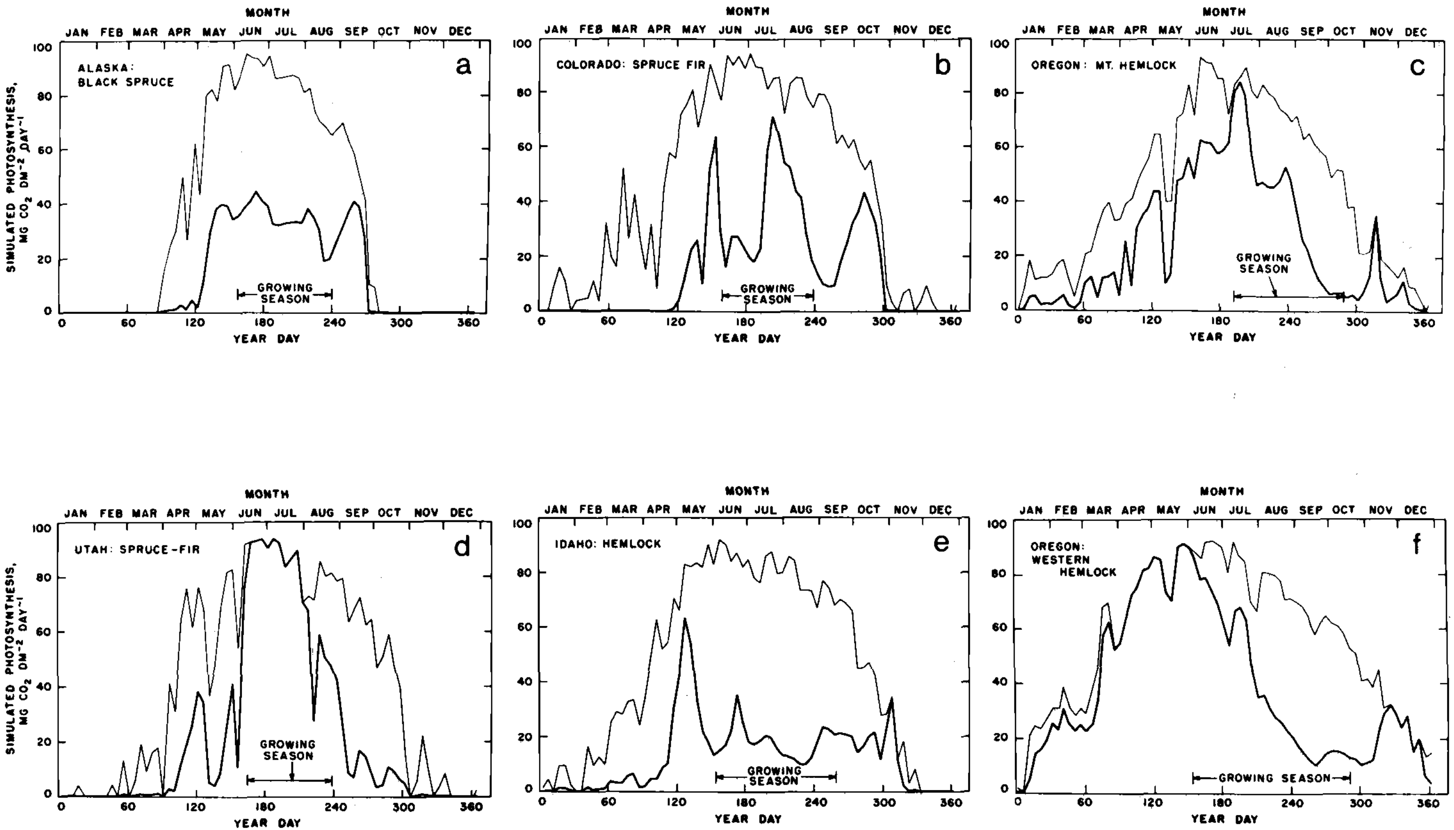
Comparison of photosynthesis ratio showed the ponderosa pine site in Arizona was at the low extreme with only 13 percent of the potential. In contrast, the spruce-fir site in Utah had 95 percent of the potential. The Sitka spruce site (12) had the highest predicted photosynthesis, but this was only 78 percent of the potential photosynthesis.

## Transpiration Indexes

Lowest predicted transpiration occurred in Arizona (3), where, although demand for water was quite high, moisture stress restricted leaf conductance (Table 3.3). Highest transpiration occurred at the western hemlock site in Oregon (13), where demand was high and supply relatively good. Humidity data were not available for the Sitka spruce site and therefore were not included in this comparison. Transpiration ratios were highly correlated with the photosynthesis ratio because both were dependent on moisture deficits and leaf conductance.

## Productivity Indexes and Relationships to Ecological Indexes

The relationship between productivity and temperature index is shown in Figure 3.2. Productivity diminished at either end of the temperature scale, indicating that cold temperatures restrict productivity and that high temperatures were generally accompanied by excessive evaporative demand and high respiration costs. The solid curve traces the maximum potential productivity.


MONTH
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
SIMULATED PHOTOSYNTHESIS, MG CO2 DM-2 DAY-1
YEAR DAY
ALASKA: BLACK SPRUCE
a
COLORADO: SPRUCE FIR
b
OREGON: MT. HEMLOCK
c
UTAH: SPRUCE-FIR
d
IDAHO: HEMLOCK
e
OREGON: WESTERN HEMLOCK
f
GROWING SEASON

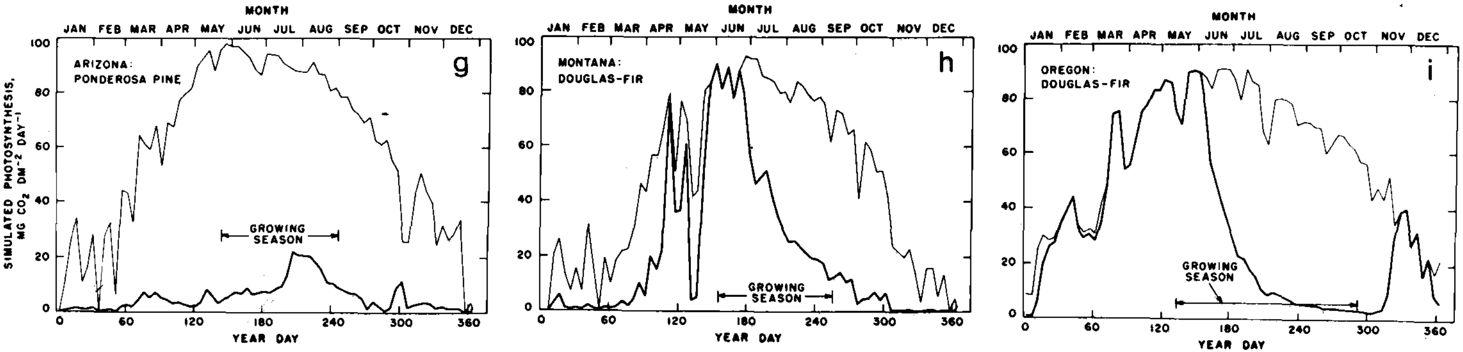



**FIGURE 3.1** *Graphs of potential (upper, thin line) and predicted (lower, thick line) photosynthesis are shown for nine representative forest ecosystems for the entire year. Note that the potential during the growing season is similar for all sites. Large differences are evident in the amount of the potential captured as predicted photosynthesis and in the dormant season potential photosynthesis. The photosynthesis indexes are equivalent to area under the curve during the growing season.*

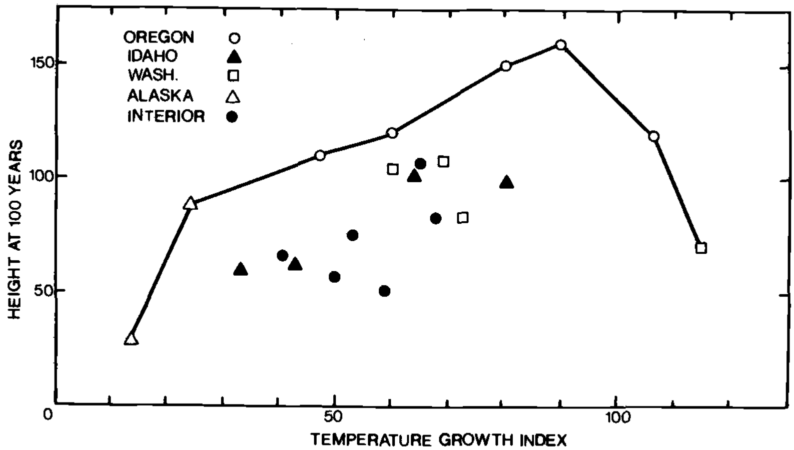



**FIGURE 3.2** *The estimated height to which trees would grow in 100 years plotted against the TGI during the growing season. The line represents the maximum possible height growth for sites across the temperature range (see Table 3.3 for units).*

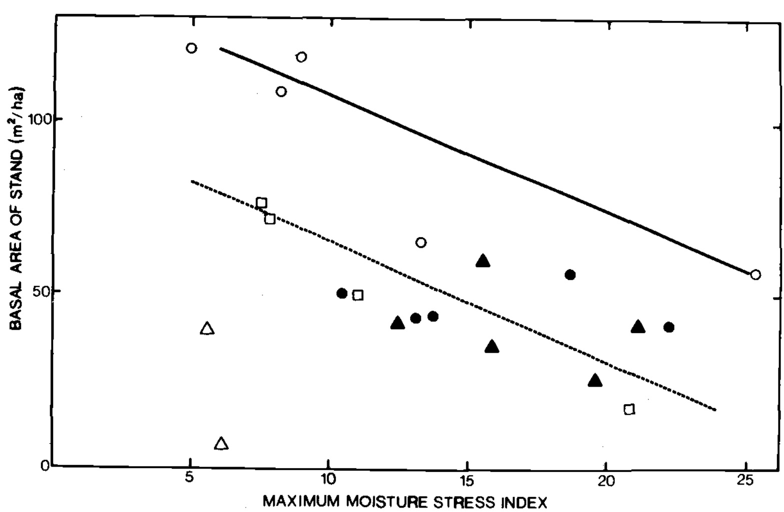



**FIGURE 3.3** *The actual basal area of stand plotted over the maximum moisture deficit measured on understory reference trees. The low-elevation Oregon sites (○) apparently had a higher capacity to accumulate basal area at any moisture stress than the sites in Washington (□), Idaho (▲), and the other interior sites (●). Even at low moisture stresses, the Alaska sites (△) had low basal areas. (Moisture stress index is in -bars.)*

In Figure 3.3 total stand basal area is plotted against maximum moisture stress index. Low moisture stresses are required for, but do not guarantee, high productivity. The solid line is an estimate of maximum basal area at moisture stress index levels in areas with a mild winter. The dotted line shows basal area in inland areas where winters are severe. The implication is that stressful conditions during the growing season may be compensated for by photosynthesis during the dormant season. Also, the maximum stress index is most useful in comparing sites in a smaller area with similar macroclimates.

The relation between volume productivity and summer photosynthesis index is shown in Figure 3.4. This is nearly a linear relationship and all indexes of productivity were better correlated with the predicted photosynthesis index than any of the other ecological indexes. Correlation coefficients ($r$) between the predicted photosynthesis and site index, $GBA_{30}$, volume index, and accumulated basal area were 0.81, 0.73, 0.86, and 0.73, respectively. Since the model used to compute the predicted photosynthesis index includes evaluation of many of the stress factors affecting primary production, this high correlation could be expected. Between 75 and 85 percent of the variation in site index, volume index, basal area growth, or total basal area was explained in multiple

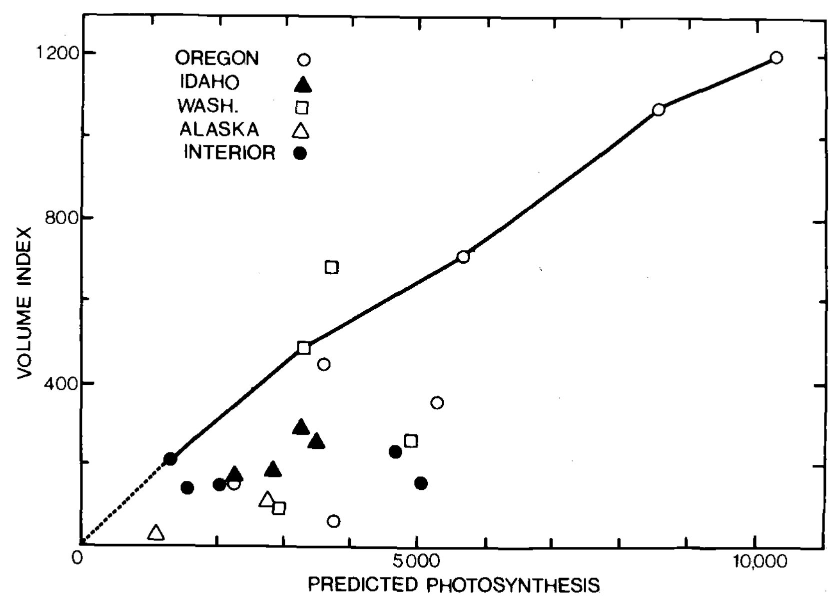



**FIGURE 3.4** *The relation between maximum volume index and predicted photosynthesis (during the growing season) was nearly linear. The fact that many of the points fell below the curve indicated that other factors such as nutrition, winter conditions, or respiration have an important bearing on productivity (see Table 3.3 for units).*

regression equations that included up to three of the indexes to environment. The most common second and third terms to enter were the maximum plant moisture stress and transpiration or photosynthesis ratio. The fact that many of the points fall below the line connecting the higher volume index values indicates there are other important factors unaccounted for in this comparison. Preliminary comparisons indicate that an *annual* predicted photosynthesis index accounts for more of these factors.

## CONCLUSIONS

Ecological indexes provide a method for evaluating stress in coniferous forest ecosystems. One stress feature that seems to be common to all coniferous forest ecosystems is drought or physiological drought. Even the moist coastal Sitka spruce ecosystem had moisture stress that lasted several weeks and reduced predicted actual photosynthesis to 78 percent of the potential for that site. At the black spruce site in Alaska, moisture stresses of -4 to -6 bars during the growing season were responsible for a 50 percent reduction in carbon fixation. This may be a case of physiological drought induced by the cool temperature in the root system.

The two- to five-times greater productivity of the modal types in western Oregon can be explained in several ways. They had less moisture stress and were warmer than the inland areas. This allowed for more photosynthesis during the summer. Mild winter conditions indicate that a significant portion of the annual carbon uptake may occur during the "dormant" period on the coastal and Cascade Mountains.

Results of the photosynthesis simulations support the hypothesis that the rise of the western mountain ranges and resultant summer drought was a primary factor in the elimination of rich hardwood forest ecosystems apparent in the fossil records (Franklin and Dyrness 1973). Evergreen trees can take advantage of the relatively favorable winter conditions when hardwoods are without leaves.

The system of ecological indexes used here provides a systematic way of quantifying the difficult-to-measure environmental differences found among coniferous forest ecosystems. It can be used to quantify test hypotheses about species distribution, ecosystem structure, or functional attributes. For example, the hypothesis that the climate in northern Idaho and western Oregon is similar because forests of western hemlock dominate the landscape was proved false; the Oregon site was both warmer and less droughty.

High correlation between the ecological indexes and productivity demonstrates the link between the ecosystem function and the indexes. The nearly linear relationship between productivity and the predicted photosynthesis index make that index the most promising for future investigation.

## LITERATURE CITED

Avery, C. C., F. R. Larson, and G. H. Schubert, 1976, Fifty-year records of virgin stand development in southwestern ponderosa pine, *U.S. Department of Agriculture Forest Service General Technical Report RM-22,* Fort Collins, Colo., 71p.

Carmean, W. H., 1975, Forest site quality evaluation in the United States, *Adv. Agron.* **27**:209–269.

Cleary, B. D., and R. H. Waring, 1969, Temperature: Collection of data and its analysis for the interpretation of plant growth and distribution, *Can. J. Bot.* **47**:167–173.

Cleary, B. D., R. D. Greaves, and R. K. Hermann, 1977, *Regenerating Oregon's Forests,* Oregon State University Extension Service, Corvallis, Oreg., 300p.

Daubenmire, R., 1976, The use of vegetation in assessing the productivity of forest lands, *Bot. Rev.* **42**:115–143.

Daubenmire, R., and J. B. Daubenmire, 1968, Forest vegetation of eastern Washington and northern Idaho, *Washington Agricultural Experimental Station Technical Bulletin 60,* Washington State University, Pullman, Wash., 104p.

Dyrness, C. T., J. F. Franklin, and W. H. Moir, 1974, A preliminary classification of forest communities in the central portion of the western Cascades in Oregon, *US/IBP Coniferous Forest Biome Bulletin 4,* University of Washington, Seattle, 123p.

Emmingham, W. H., 1974, Physiological responses of four Douglas-fir populations in three contrasting field environments, Ph.D. dissertation, Oregon State University, Corvallis, 162p.

Emmingham, W. H., and G. A. Lundburg, 1977, Climatic and physiological data summaries for the H. J. Andrews Reference Stand Network, *US/IBP Coniferous Forest Biome Internal Report 166,* University of Washington, Seattle, 109p.

Emmingham, W. H., and R. H. Waring, 1977, An index of photosynthesis for comparing forest sites in western Oregon, *Can. J. For. Res.* **7**:165–174.

Farr, W. A., 1967, Growth and yield of well-stocked white spruce stands in Alaska, *U.S. Department of Agriculture Forest Service Research Paper PNW-53,* Portland, Oreg., 30p.

Franklin, J. F., and C. T. Dyrness, 1973, Natural vegetation of Oregon and Washington, *U.S. Department of Agriculture Forest Service General Technical Report PNW-8,* Portland, Oreg., 417p.

Fujimori, T., 1971, Primary production of a young *Tsuga heterophylla* stand and some speculations about biomass of forest communities on the Oregon coast, *U.S. Department of Agriculture Forest Service Research Paper PNW-123,* Portland, Oreg., 11p.

Henderson, J. A., R. L. Mauk, D. L. Anderson, R. Ketchie, P. Lawton, S. Simon, R. H. Sperger, R. W. Young, and A. Youngblood, 1976, *Preliminary Forest Habitat Types of Northwest Utah and Adjacent Idaho*, Department of Forestry and Outdoor Recreation, Utah State University Logan, 99p.

Hitchcock, C. L., and A. Cronquist, 1974, *Flora of the Pacific Northwest*, University of Washington Press, Seattle, 730p.

McArdle, R. E., W. H. Meyer, and D. Bruce, 1961, The yield of Douglas-fir in the Pacific Northwest, *U.S. Department of Agriculture Technical Bulletin 201*, U.S. Department of Agriculture, Washington, D.C. 74p.

Maclean, C. D., and C. L. Bolsinger, 1973, Estimating productivity on sites with a low stocking capacity, *U.S. Department of Agriculture Forest Service Research Paper PNW-152*, Portland, Oreg., 18p.

Meyer, W. H., 1961, Yield of even-aged stands of ponderosa pine, (revised) *U.S. Department of Agriculture Technical Bulletin 630*, U.S. Department of Agriculture, Washington, D.C., 59p.

Minor, C. O., 1964, Site index for young growth ponderosa pine in northern Arizona, *U.S. Department of Agriculture Forest Service Research Note RM-37*, Fort Collins, Colo., 8p.

Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby, 1977, Forest habitat types of Montana, *U.S. Department of Agriculture Forest Service General Technical Report INT-34*, Ogden, Utah, 174p.

Reed, K. L., and R. H. Waring, 1974, Coupling of environment to plant response: A simulation model of transpiration, *Ecology* **55**:62–72.

Van Cleve, K., and J. C. Zasada, 1976, Response of 70-year-old white spruce to thinning and fertilization in interior Alaska, *Can. J. For. Res.* **6**:145–152.

Viereck, L. A., 1973, Ecological effects of river flooding and forest fires on permafrost in the taiga of Alaska, in *Permafrost: The North American Contribution to the Second International Conference*, National Academy of Sciences, Washington, D.C., pp. 60–67.

Viereck, L. A., and E. L. Little, Jr., 1975, Atlas of United States trees, 2: Alaska trees and common shrubs, *U.S. Department of Agriculture Forest Service Miscellaneous Publication 1293*, U.S. Department of Agriculture Forest Service, Washington, D.C., 19 p., 105 maps.

Waring, R. H., 1969, Forest plants of the eastern Siskiyous: Their environmental and vegetational distribution, *Northwest Sci.* **43**:1–17.

Waring, R. H., and B. D. Cleary, 1967, Plant moisture stress: Evaluation by pressure bomb, *Science* **155**:1248–1254.

Waring, R. H., K. L. Reed, and W. H. Emmingham, 1972, An environmental grid for classifying coniferous forest ecosystems, in *Proceedings—Research on Coniferous Forest Ecosystems—A Symposium*, J. F. Franklin, L. J. Dempster, and R. H. Waring, eds., U.S. Department of Agriculture Forest Service, Portland, Oreg., pp. 79–91.

Waring, R. H., W. H. Emmingham, and S. W. Running, 1975, Environmental limits of an endemic spruce, *Picea breweriana, Can. J. Bot.* **53**:1599–1613.

Whittaker, R. H., 1961, Vegetation history of the Pacific coast states and the "central" significance of the Klamath region, *Madrono* **16**:5–23.

Wikstrom, J. H., and S. B. Hutchinson, 1971, Stratification of forest land for timber management planning on the western national forests, *U.S. Department of Agriculture Forest Service Research Paper INT-108,* Ogden, Utah, 38p.

Zasada, J. C., 1976, Alaska's interior forests, *J. For.* **74**:333–341.

Zobel, D. B., W. A. McKee, and G. M. Hawk, 1976, Relationships of environment to composition, structure and diversity of forest communities of the central western Cascades of Oregon, *Ecol. Monogr.* **46**:135–156.