

Chapter 17

Age-Dependent Changes in Environmental Influences on Tree Growth and Their Implications for Forest Responses to Climate Change

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Abstract Dendrochronology has long used tree-rings to better understand climate-tree-growth relationships within a site or across a region, with tree age often considered to contribute unwanted noise to the signal in question. Here I demonstrate that strong climate-tree-growth relationships exist across sites, on a global scale, and that these changes are correlated with variation in average net primary productivity. The age-specific tree-ring data analyses used here show that the sensitivity of tree growth to environmental variability changes predictably with tree age. Young trees were found to be particularly sensitive to each of the environmental factors investigated. These results are discussed in the context of climate change and established changes in tree morphology and physiological function with tree age or size. I argue that explicitly treating tree or forest age can yield tangible improvements in the projection of terrestrial carbon sink responses to climate change by increasing the accuracy with which forest to non-forest ecosystem boundaries can be projected.

1 Introduction

Understanding the processes that govern terrestrial ecosystem productivity is critical to predicting future concentrations of carbon dioxide in the atmosphere (Canadell et al. 2007). Forests make up a large portion of terrestrial productivity and their contribution to carbon stored in live trees, dead wood and soils keeps increasing long after the age in which maximum tree height is approached (Luyssaert et al. 2008). Since 1850, the total amount of carbon released by cutting and burning of

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forests is approximately one third of all carbon emissions (Houghton 1999). Indeed, many forests of the northern hemisphere are still recovering from this period of exploitative logging and land use practices, resulting in the northern hemisphere being identified as a major carbon sink over the past two decades (Keeling et al. 1996; Schimel et al. 2001; Nemani et al. 2003). Predictions by each of ten coupled carbon and climate change models suggest that northern forests will continue to be a sink (Friedlingstein et al. 2006; Qian et al. 2009). However, data from the most recent decade suggest that droughts, largely in the southern hemisphere, have reduced global net primary productivity (NPP) despite the continued sink in the northern hemisphere (Zhao and Running 2010).

There are three main processes that determine the portion of global NPP associated with forests: (1) tree mortality rates, (2) tree establishment/colonization rates, and (3) the growth rates of the trees present. These three processes rarely act independently because mortality rates of individual trees are strongly dependent on their radial growth rates (Kobe and Coates 1997; Wyckoff and Clark 2002) while the stand level balance between mortality and establishment greatly influences forest age/size distributions. Ultimately the interaction of these processes can affect the boundaries between forested and non-forested ecosystems. Substantial exceptions to the interdependence of these variables can occur when an exogenous factor such as climate change induces shifts in the likelihood or severity of disturbances or in the favorability of an environment for or against herbivores and plant pathogens to a degree that is not balanced by concomitant changes in tree growth, mortality and establishment rates.

One major challenge is to accurately model NPP responses to changes in climatic conditions for forests that differ in tree age/size distributions. Efforts are underway to accurately scale physiological or growth responses of forests from the tree or stand-level to landscapes (Bradford et al. 2008; Hudiberg et al. 2009; Duane et al. 2010). Low-frequency variation in tree growth or forest productivity is difficult to discern from most empirical data owing to the presence of large and often inaccessible carbon pools as well as the inter-annual variability in carbon fluxes of old forests. A review of forest inventory data suggests that the growth rates of extant forests have increased through the late twentieth century (Boisvenue and Running 2006). Likewise, other studies from tropical and temperate forests have shown increases in aboveground tree growth rates or total aboveground biomass production, although the amount varies by region and species and often parallels an increase in mortality rates (Caspersen et al. 2000; Laurance et al. 2004, 2009; Lewis et al. 2004; Phillips et al. 2008; Thomas et al. 2010). Some evidence suggests that the rate of change in radial growth in response to changing resources levels diminishes with tree age or size (Körner 2006; Voelker et al. 2006).

Another major challenge is to understand how boundaries of ecosystems will shift due to climate change and whether the persistence of forests along these boundaries is affected by tree age/size. Non-forested vegetated lands such as shrub, scrub, alpine, tundra or grassland contribute only about 75% of the terrestrial carbon uptake of forests growing under the same climatic conditions (Del Grosso et al. 2008). Consequently, any climate change-induced shifts in the area of forests versus

non-forest on the peripheries of these ecosystems will impact carbon uptake to at least this extent. Differences in tree age or size distributions can affect the three primary processes governing carbon storage in forests mentioned above, but are not explicitly represented in large scale models of forest extent or productivity. Moreover, the physiological mechanisms that determine growth and survival of tree seedlings are largely uncharacterized (Johnson et al. 2011). If tree age or size affects the ability of a tree to survive environmental stresses and thus for forests to sustain adequate regeneration and establishment, there exists some substantial risk that current vegetation models will be unable to project shifting boundaries between forested and non-forested regions. The thresholds determining a transition between these ecosystem types are particularly hard to predict because the amounts and distribution of forest versus non-forest vegetation can influence feedbacks on local water and nutrient availability and in some cases even impact regional weather conditions (Scheffer et al. 2005; Hirota et al. 2010). Therefore a determination of age-related responses in tree radial growth to relevant biophysical variables may shed light on the nature of threshold responses of ecosystem boundaries.

As forests age and increase in stature, they extend root systems deeper into the soil, attain sexual maturity and incur changes in the environmental conditions to which leaves and meristems are exposed. However, it is not well known whether these developmental patterns are accompanied by changes in the sensitivity of growth to biophysical drivers. A lack of insight on the physiological mechanisms determining forest growth and persistence severely restricts our ability to predict future terrestrial carbon uptake at landscape to global scales. Rather than undertake the daunting task of tracking each physiological mechanism over long periods in time, it may be possible to infer which processes are most affected by tree age or size by investigating the effect of different biophysical variables on tree growth at different ages. These broad scale patterns in growth can serve to guide further in-depth studies of tree size/age dependent physiological mechanisms. Towards this end, vast dendrochronological (tree-ring) datasets already exist. In this chapter I use a compilation of transformed tree-ring data to establish overall, age-averaged tree productivity responses to temperature, precipitation, relative humidity and an index of treeline proximity. I then quantify how tree age affects responses to these biophysical controls over productivity and discuss the implications of these results for forest responses to global climate change.

2 Methods

2.1 Tree-Ring Data

Data from 46 temperate and boreal tree species were obtained from the International Tree Ring Data Bank (ITRDB; <http://www.ncdc.noaa.gov/paleo/treering.html>). These species were largely selected on the basis of data availability from the ITRDB. Some species known to be very shade tolerant (i.e. *Tsuga* spp.) were not used

because variation in productivity from site to site was more likely to be confounded by the frequency of canopy disturbances. Within some species used here, data from certain sites were rejected because there were too few trees sampled or when data had obviously been artificially shortened (i.e. where each series began upon a decadal-year). Altogether the dataset used here includes measurements of more than ten million ring-widths from 60,457 ring-width series collected at 1,838 collection sites (Table 17.1).

Conventional dendrochronological methods use a sample population of predominately old trees where all ring-widths are aligned by calendar year after cross-dating verification. Each file from the ITRDB was inspected for data quality and then each ring-width series was manually re-aligned by cambial age at each site (as ring number from the pith) such that wood produced in the same developmental age could be compared within each species. This first step in data standardization is conceptually similar to the RCS (regional chronology standardization) method that has been used to infer other regional to hemisphere-scale climate investigations using tree-rings (Briffa et al. 1996; Esper et al. 2002; Cook et al. 2003). Because RCS-type methods are known to have end-fitting problems at the beginnings and ends of chronologies (Briffa 2011) the methods briefly described herein employ a series of standardizations aimed at eliminating the potential for this sort of bias within the raw ring-width data before they are combined into species-level growth curves plotted by cambial age (Fig. 17.1).

2.2 Standardization for Off-Center Tree Cores

Increment cores often do not reach the center of the tree due to imperfect increment borer alignment, heart-rot or eccentric cambial growth patterns. These unreported tree rings affect the perceived cambial age and if all cores are aligned by the earliest tree-ring reported, those with more “missing” rings near the pith would tend to underestimate tree growth. To minimize the potential for a systematic offset from older trees having more missing rings, it was assumed that the number of unreported rings and the resulting effect on productivity can be estimated from the number of rings reported. To determine an age to missing rings relationship, I visually inspected 2,606 increment cores from seven different principal investigators. Those increment cores outside of my own collections (about half) were from archived collections at the University of Arizona Tree-Ring Laboratory (TRL). Data from all TRL cores used here had been measured and the data reported in the ITRDB. TRL cores were collected from locations across the Western United States. The data used for the missing rings relationship were collected for the purposes of climatic reconstruction and were from the following species: *Juniperus occidentalis*, *Pinus flexilis*, *Pinus ponderosa*, *Pinus monophylla*, *Pseudotsuga menziesii* and *Quercus macrocarpa*. In most cases, my own work and the notes of others at the TRL indicated the cores were collected by more than one person, often two to four people at each site. Thereby the cores likely reflect the work of 15–20 or more collectors’ individual

Table 17.1 A list of the species used, specified by number of tree-ring series, number of sites sampled and the mean number of tree-rings reported across all ring-width series

Species	Tree-ring series	Sites	Tree-rings reported
<i>Abies alba</i>	1,266	52	127
<i>Abies lasiocarpa</i>	834	22	138
<i>Abies pindrow</i>	115	10	217
<i>Abies spectabilis</i>	600	23	236
<i>Austrocedrus chilensis</i>	759	32	257
<i>Cedrus excelsa</i>	235	7	376
<i>Cedrus libani</i>	459	16	203
<i>Fitzroya cupressoides</i>	344	10	733
<i>Juniperus occidentalis</i>	1,066	22	379
<i>Juniperus virginiana</i>	531	15	206
<i>Larix decidua</i>	349	14	282
<i>Larix lyallii</i>	306	6	273
<i>Larix sibirica</i>	1,358	48	247
<i>Larix gmelinii</i>	1,178	47	258
<i>Libocedrus bidwillii</i>	1,151	27	298
<i>Nothofagus pumilio</i>	1,077	38	188
<i>Nothofagus solanderi</i>	569	25	163
<i>Picea abies</i>	3,344	130	131
<i>Picea glauca</i>	4,267	112	180
<i>Picea mariana</i>	1,075	33	122
<i>Picea obovata</i>	725	28	181
<i>Picea rubens</i>	506	16	217
<i>Pinus albicaulis</i>	474	13	257
<i>Pinus aristata</i>	193	8	528
<i>Pinus cembra</i>	284	10	181
<i>Pinus contorta</i>	367	12	201
<i>Pinus echinata</i>	1,041	26	122
<i>Pinus edulis</i>	2,434	75	296
<i>Pinus flexilis</i>	1,162	24	319
<i>Pinus jeffreyi</i>	669	17	295
<i>Pinus longaeva</i>	767	15	647
<i>Pinus monophylla</i>	481	13	256
<i>Pinus nigra</i>	851	40	219
<i>Pinus palustris</i>	381	7	88
<i>Pinus ponderosa</i>	4,568	166	246
<i>Pinus resinosa</i>	678	22	215
<i>Pinus rigida</i>	210	3	97
<i>Pinus strobus</i>	610	19	164
<i>Pinus sylvestris</i>	8,459	190	159
<i>Pseudotsuga menziesii</i>	5,765	193	293
<i>Quercus alba</i>	2,574	65	188
<i>Quercus douglassii</i>	611	10	188
<i>Quercus macrocarpa</i>	1,033	38	124
<i>Quercus petraea</i>	240	11	135
<i>Quercus robur</i>	1,812	48	132
<i>Quercus</i> Spp. (European)	473	32	125
<i>Quercus stellata</i>	2,206	48	178

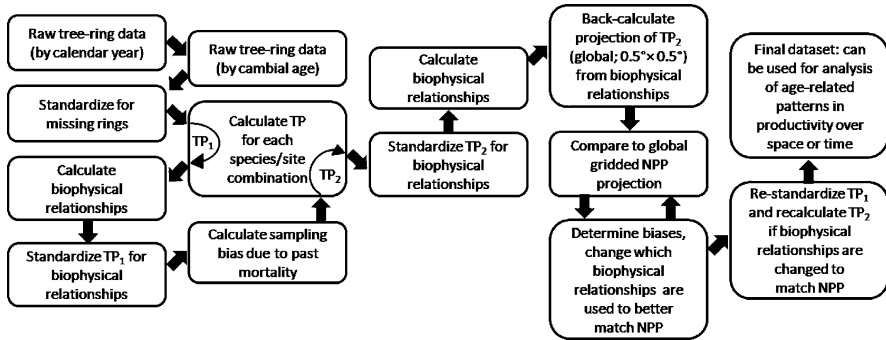


Fig. 17.1 Schematic flowchart showing the main steps used to produce a global tree-ring database that can be used to track tree productivity in space or time. TP is tree productivity; subscripts indicate iterations of tree productivity as affected by standardization scheme

habits. Because data in the ITRDB are also collected for dendroecological studies, included here were data that I and three assistants collected from *Pinus echinata*, *Quercus coccinea*, *Quercus macrocarpa* and *Quercus velutina*. These collections were made to determine stand establishment ages and compare tree growth rates during early development. Altogether these species and purposes for tree-ring collection should be reasonably representative of the larger ITRDB database.

The missing rings to pith were primarily estimated using the geometric calculation of Duncan (1989). In some cases where very few rings were missing or when growth ring arc height could not be accurately measured, the number of missing rings was visually estimated by comparing ring-width patterns and ray angles to “pith locator diagrams” (i.e. sets of concentric rings printed on clear plastic sheets). When available, notes on tree diameter measurements were also used in combination with core length and growth trends to help estimate the missing rings to pith.

From the age estimates for each tree-ring series the number of missing tree-rings to pith was estimated and combined with average ring-widths for each cambial age to calculate separate standardizations for each species (Fig. 17.2). This standardization was applied to each ring-width in the dataset and accounts for the smaller standardizations needed for species with cambial age patterns that varied little such as *Pinus longaeva* versus the larger standardizations needed for species with strong negative exponential patterns such as *Pinus ponderosa*.

2.3 Climate and Biophysical Standardizations

Each ring-width in the dataset was also standardized by productivity trends as predicted from three climate variables, and an index of treeline proximity. These standardizations used globally-gridded $0.5^\circ \times 0.5^\circ$ resolution monthly climate data for temperature, precipitation and vapor pressure from the IPCC data distribution center (<http://www.ipcc-data.org/>), which were originally made available through

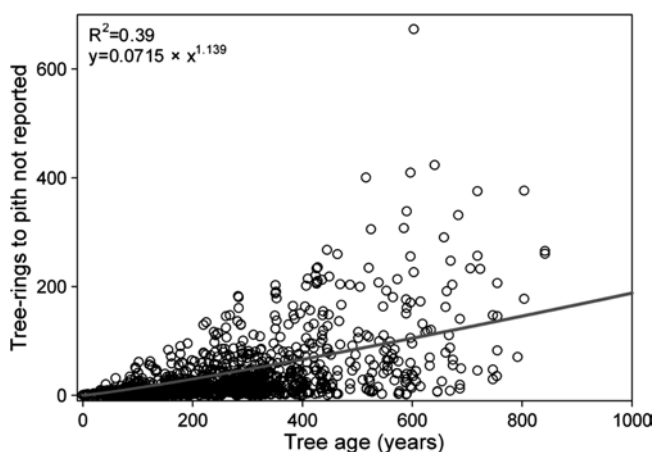


Fig. 17.2 The relationship of estimated number of tree-rings to pith not reported to tree age. Data are from 2,606 increment cores from nine species and numerous collectors (see Sect. 2 for details)

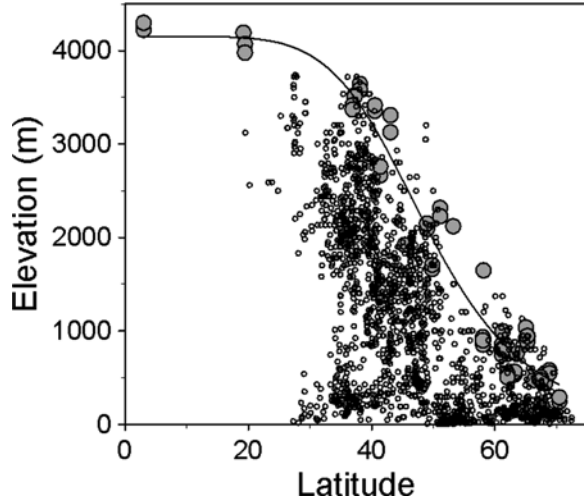
the Climate Research Unit at the University of East Anglia (<http://www.cru.uea.ac.uk/cru/>). Average growing season temperatures were calculated by weighting monthly mean temperatures with the growing degree days for the same month. Monthly relative humidity was calculated from the algorithm for saturated vapor pressure reported by Paw U and Gao (1988) that used ambient air and dew point temperatures. Monthly relative humidity values were weighted according to growing degree days for that month in each cell to calculate average growing season relative humidity. Mean annual precipitation was used to standardize tree-rings rather than growing season precipitation because of the ability of soil to store a certain amount of water that falls previous to the growing season.

The unique climate conditions at treeline can limit productivity not only through the effects on leaf-level physiology associated with the above climate variables, but also due to changes in plant form. A biophysical index of treeline proximity was calculated to help capture local elevation-related variation in site level productivity. Treeline position was estimated by using high resolution digital imagery and elevation models provided by Google earth software, version 4.2, Google Inc., Mountain View, CA. (Fig. 17.3). To these data was fit the following sigmoidal relationship:

$$\text{Treeline elevation} = \left(\text{LowTLE} \times \text{Latitude}^{-6.032} \right) / \left(\text{HighTLE}^{-6.032} + \text{Latitude}^{-6.032} \right),$$

where LowTLE is the low latitude treeline elevation (the best-fit relationship was 4,153 m), HighTLE is the high latitude treeline elevation (the best-fit relationship was 49 m), and -6.032 is a constant determining the shape of relationship (Fig. 17.3). To calculate treeline proximity the elevation at each tree-ring site was divided by predicted treeline elevation, and then the ratio was multiplied by 100 to yield a percentage.

Fig. 17.3 Position of global average treeline elevation in relation to latitude. The sigmoidal regression fit to the gray circles was significant ($R^2=0.95$, $P<0.0001$). Small open circles indicate the distribution tree-ring sampling locations



2.4 Standardization for Biases Due to Past Mortality and Tree-Ages Sampled

The extent to which ecological effects deriving from past stand dynamics or epigenetic differences may allow some slow-growing trees to disproportionately survive to very old ages was uncertain (*sensu* Black et al. 2008). This growth pattern could result in tree growth being overestimated for recent times if sites dominated by young trees were more likely to contain fast-growers that had undergone less selection against that growth strategy. To account for this potential bias in differential-survival, I quantified this pattern only after an initial round of climate and biophysical standardizations were completed. For each species with enough replication of tree-rings formed before 1850 (to avoid anthropogenic effects occurring later on) ring-width data were divided into 10 percentile bins according to relative age. Relative age was determined for each tree by dividing the maximum age of the species in the database by the age of the tree as indicated by the number of rings reported for a ring-width series. Each ring-width value for a progressively older relative age class was divided by the mean ring-width of the same cambial age from the youngest relative age class. For example, growth across the first 80 cambial ages were compared among 10 relative age classes for bur oaks (*Quercus macrocarpa*; max. age=315) while for bristlecone pines (*Pinus longaeva*; max. age=5,591) growth across the first 700 cambial ages were compared among 10 relative age classes. To plot the data as shown, the difference between one and the best-fit linear regression prediction of the Y-intercept for each species was used to reset data so that the slope of the line was the same but the Y-intercept was equal to one (Fig. 17.4). For clarity

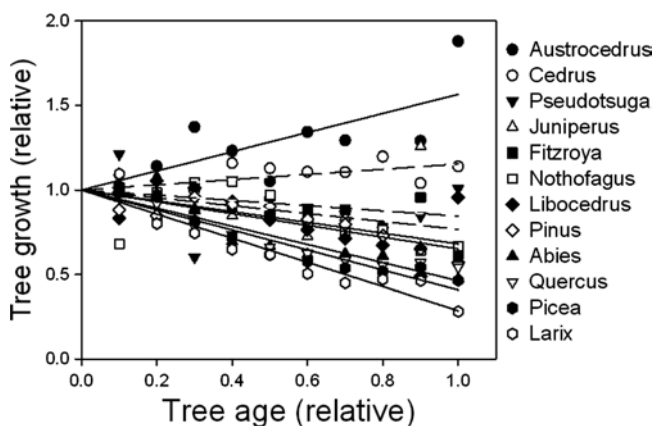


Fig. 17.4 Genera-level estimates for the effect of tree age on growth rates. Relative tree age was calculated from the maximum age in the database set equal to one. Relationships with solid lines were significant ($P < 0.05$). Although genera-level estimates are shown for clarity, species-level estimates were used to adjust for age biases within the database where enough data existed

only genera-level relationships were plotted. Therefore each species was standardized according to

$$Y = y \times (1 + G_{\max} \times A_r)$$

where Y is the post-standardization ring-width index value, y is the pre-standardization ring-width index value, G_{\max} is the predicted growth of a species sampled at its maximum age (i.e. relative age = 100%) and A_r is relative age. Some species (generally those with less than 500 ring-width series reported) were standardized with the genera-level relationships because this paucity of data did not allow for adequate replication across relative age classes.

2.5 Model Validation with NPP

Validation is needed to judge the effectiveness of a model. In this case tree productivity can be compared against biophysical variables which may differ in the amount of control they exert over tree productivity across the range of a biophysical variable. It is uncertain, however, whether co-variation of some biophysical variables may cause unwanted biases to be introduced to estimates of tree productivity. To validate a model of tree productivity that derives from empirical relationships between tree growth and biophysical data, a back-prediction of tree productivity across the globe was attempted using age-specific growth in combination with $0.5^\circ \times 0.5^\circ$ climate and elevation data. Gridded elevation data were obtained from the University Corporation for Atmospheric Research (<http://dss.ucar.edu/datasets/>).

By comparison to similarly gridded NPP data projections (Cramer et al. 1999) spatial patterns in differences can be assessed. These spatial patterns between projections can then help diagnose whether weighting certain biophysical variables or adding others can significantly improve the model so as to better match patterns in NPP. In this manner tree productivity modeling efforts can be validated with spatial data and changes made to reduce bias in the standardizations applied. This will improve the accuracy of future efforts at constructing tree productivity chronologies aimed at detecting whether differences in long-term trends exist within certain subsets of the data.

3 Results

When averaged across ages 1–300 years, tree productivity as affected by temperature, precipitation and treeline proximity all had predicted minimum values (i.e. where trees still grow) that were about 60% of maximum (Fig. 17.5). Minimum predicted tree productivity under low relative humidity conditions was approximately 80% of maximum indicating this variable was less important. Constraints on tree productivity at sites with low annual precipitation formed the steepest relationship shown for these biophysical variables indicating that productivity over this range is most sensitive. This sensitivity to precipitation may have been equaled by treeline proximity, had species-specific trends in tree height been used to more accurately estimate productivity.

To investigate age \times environment interactions, sigmoidal curves were fit to each of the 31 ages investigated within each of the four biophysical relationships. When plotted across tree ages, treeline and relative humidity described half as much of the variation for old trees as for young trees (Fig. 17.6). There were no distinct long-term trends in variability of productivity with age for temperature or precipitation. Besides variation within the relationships, age-related trends in the minimum values predicted for productivity for each biophysical variable should also be an indicator of the strength of age \times environment interactions. Indeed, as shown by the age-related trends in variation (Fig. 17.6), the minimum values for treeline and relative humidity showed a weakening of their effect on productivity throughout the ages investigated (Fig. 17.7). Temperature and precipitation also showed some weakening in their effect on minimum productivity with age, but this trend was associated with tree ages less than 50 years (Fig. 17.7).

The first round of spatial validation for tree productivity found the back-prediction from the average relationship to the four biophysical variables to show a coarse-scale agreement with NPP (Fig. 17.8a, b). As expected for this initial round of validation, in some regions tree productivity did not correlate well with NPP. Underestimates of NPP by tree productivity generally occurred where high elevations coincided with colder or drier regional climates (Fig. 17.8c). Overestimates of NPP tended to be greatest in regions where annual NPP is dominated by grass, shrub, savanna or woodland ecosystems (Fig. 17.8c).

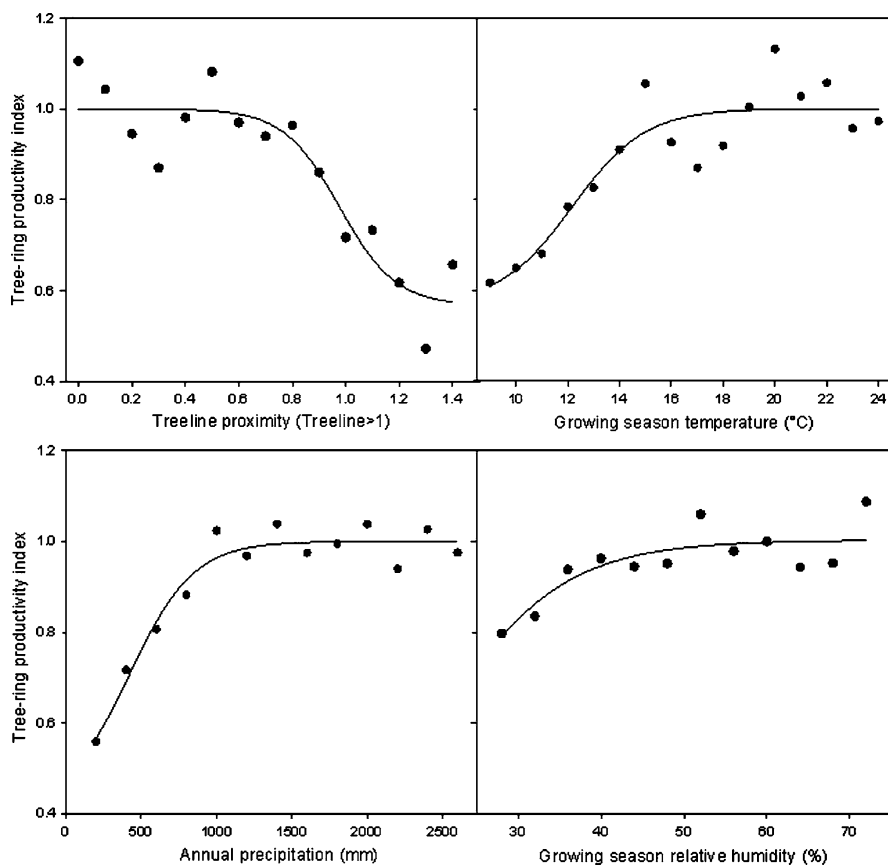


Fig. 17.5 Overall trends in tree productivity plotted against four biophysical variables. Data were binned at intervals of 0.1 for treeline proximity, 1°C for temperature, 200 mm for annual precipitation and 4% for relative humidity

4 Discussion

4.1 Age-Dependence of Tree Productivity to Biophysical Variables

Tree productivity is equivalent to changes in radial growth rate, and biomass increment scales, albeit roughly, with radial growth rate to the third power. Minimum levels of age-averaged tree productivity ranged from about 0.55–0.8 across the range of the biophysical variables investigated (Fig. 17.5). In terms of biomass increment these minimum values are equivalent to a range of 0.55^3 – 0.80^3 , or approximately 17–51% of the maximum biomass increment than at maximum tree productivity equal to one. Tree productivity was found to be strongly related to temperature,

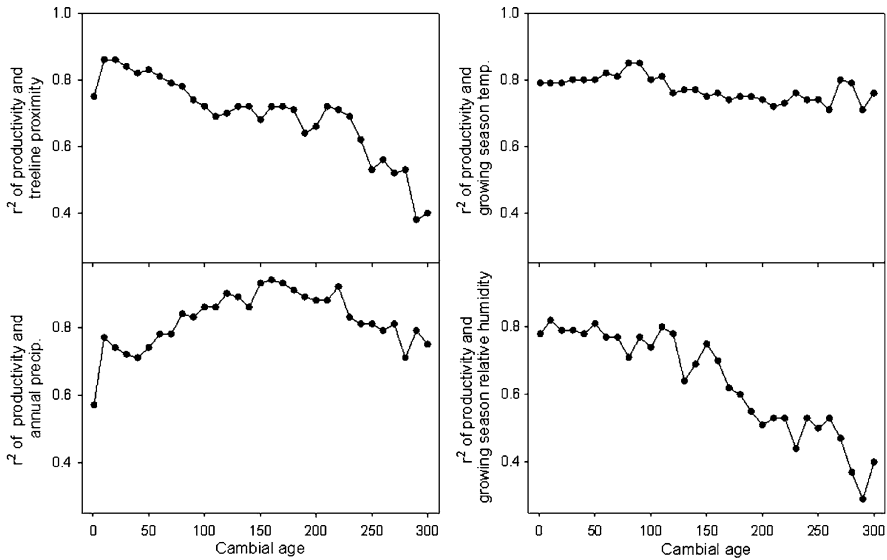


Fig. 17.6 Age-specific changes in the coefficient of determination (r^2) describing the relationship between tree productivity and four biophysical variables. Age specific regressions used to calculate r^2 values were of the same sigmoidal form as those shown in Fig. 17.5

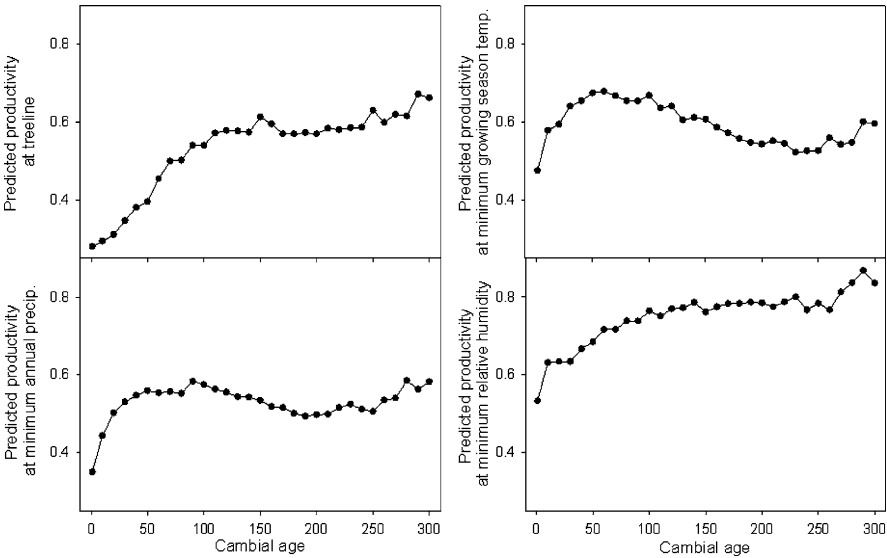


Fig. 17.7 Age-specific changes in the productivity predicted by regressions fit to minimum or maximum values for four biophysical variables. Minimum or maximum values are for the same bins specified in Fig. 17.5. Age specific regressions were of the same sigmoidal form as those shown in Fig. 17.5

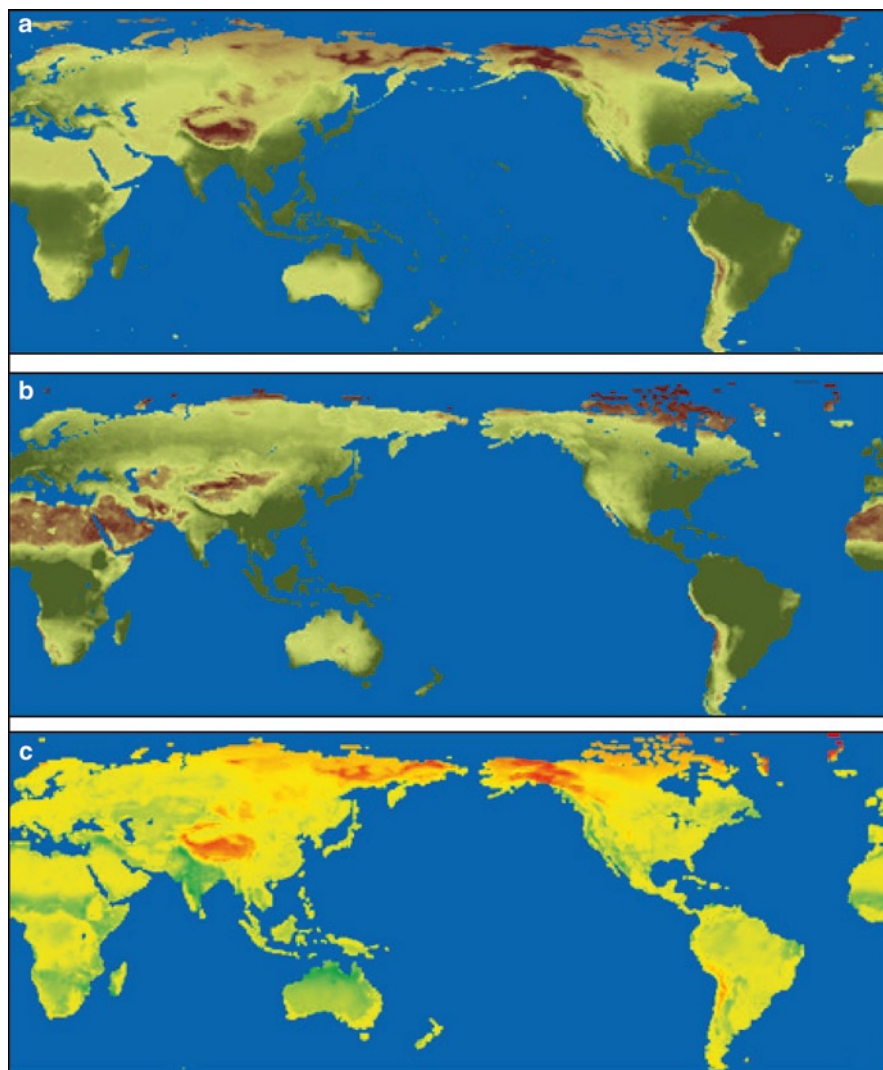


Fig. 17.8 Comparison of $0.5^\circ \times 0.5^\circ$ projections of (a) tree productivity, (b) model averaged annual net primary productivity and (c) the differences between the projections. For panels a and b, green indicates high productivity and brown indicates low productivity. Gridded NPP in panel b, ranging from 0 to $1,270 \text{ C m}^{-2}$, and are plotted after Cramer et al. (1999). For panel c green indicates where tree productivity overestimates modeled NPP and red indicates where tree productivity underestimates modeled NPP

precipitation, and treeline proximity while relative humidity had a smaller influence (Fig. 17.5). These age-averaged results are generally similar to the findings of other empirical studies of how temperature and precipitation influences vegetation productivity (Lieth 1972; Schuur 2003; Anderson et al. 2006).

For modeling efforts at landscape to global scales, the effects of tree age have often been assumed to average out. On the other hand, patterns in tree growth or vegetation productivity integrate many complex physiological processes that can be predicted to undergo directional changes as forests grow older and larger. As a general rule, the growth of older trees appears to be more buffered from large variations in climate. However the pattern of this age-dependence as well as the overall strength of the effect differed among biophysical variables (Fig. 17.7).

Accurately predicting the effects of climate change on terrestrial carbon storage will depend on an ability to accurately delimit forest cover and forest productivity at those sites. Compared to other carbon sinks within a tree the allocation of carbon to stem growth is generally a low priority (Oliver and Larson 1996). Hence, trees that chronically grow very slowly for their species and size are much more likely to succumb to competition, pests and diseases (Kobe and Coates 1997; Bigler et al. 2007; Wyckoff and Clark 2002; Voelker et al. 2008). As such, at some minimal level of forest productivity or average tree growth, the likelihood that a forest will persist at that site will be severely diminished. After a transition to non-forest, the re-colonization of that same site may require a more amenable climate for trees than the threshold value that caused the initial ecosystem transition. For example, if a mix of woodlands and forests persisted across a landscape where annual precipitation was 600 mm but was replaced by a grassland/savanna when decades of drought caused average precipitation to drop to 400 mm, the re-colonization of that site may require annual precipitation to significantly exceed the 600 mm that had previously sustained the forests and woodlands. This can occur because of a loss of seed sources, nurse trees or other safe sites for seedling/sapling establishment. Moreover, increased precipitation must persist above a certain threshold for a long enough period that the seedlings can establish as trees and bypass the early growth stages that could otherwise succumb to short-term droughts if their rooting depth and soil water supply are limited. Most models of tree/grass coexistence do not incorporate these tree age/size-related effects (Sankaran et al. 2004) and in most cases it could only be guessed at how long this establishment phase may take or the shape of the curve. It may be nearly impossible to measure the actual shape of this age/size-related hysteresis in sensitivity to climatic variables, but the age-dependent patterns described here should provide a reasonable first-order approximation.

4.2 *The Influence of Precipitation*

Tree productivity was estimated at sites with annual precipitation that ranged from 200 to 2,600 mm. This range covers the vast majority of forests across the globe. Like tree productivity (Fig. 17.5) NPP saturates above 1,600 mm annual precipitation (Schuur 2003). On the few rare sites where precipitation exceeds 4,000 mm/year NPP is somewhat reduced (Schuur 2003; Del Grosso et al. 2008), likely because the forests are radiation limited. There are also regions that receive less than 100 mm annual precipitation in which both hardwood or conifer trees can grow, albeit very

slowly and only as scattered trees (Abdoun et al. 2005; Andersen and Krzywinski 2007). These species are likely relicts of a formerly wetter climate in Northern Africa whose widely scattered trees are sensitive to anthropogenic uses and presumably to continuing aridity. For both of these species the adults persist while seedlings of *Cupressus* are very rare and regeneration of *Acacia* is largely from re-sprouting rather than seed origin (Abdoun et al. 2005; Andersen and Krzywinski 2007).

At larger scales of inference, precipitation is undoubtedly one of the strongest determinants of the rates of successional development, or the amount of forest cover, vegetated cover, leaf area and NPP (Lieth 1972; Gholz 1982; Churkina et al. 1999; Schuur 2003; Sankaran et al. 2005; Scheffer et al. 2005; Anderson-Teixeira et al. 2008). As expected, tree productivity follows a broadly similar pattern (Fig. 17.5). However, these variables are not entirely similar in their sensitivity to precipitation. Average NPP decreases dramatically between 1,500 and 2,000 mm of annual precipitation (Lieth 1972; Schuur 2003) whereas the upper bounds for woody cover decrease sharply at about 650 mm (Sankaran et al. 2005) and vegetation cover is reduced near a threshold of 350 mm annual precipitation (Scheffer et al. 2005). In comparison, maximum tree productivity occurs midway between these thresholds, with an inflection point at approximately 1,000 mm annual precipitation.

For most growing conditions the greatest change affecting the water status of a tree as it grows larger is the development of a more extensive root system that can provide access to water in deep soil layers when upper soil layers are dry (Fritts 1976; Kozłowski and Pallardy 1997; Canadell et al. 1996; Cairns et al. 1997). However the occurrence of branch dieback and mortality after regional droughts has been found to be greater in older and/or taller trees (Voelker et al. 2008; Zhang et al. 2009). Perhaps it is this contrast in sensitivity to drought of younger versus older trees that has prevented any systematic effort to determine a global average age-dependence of responses to climate variables including precipitation. For the data summarized here, trees older than 50 years accrued biomass four times more rapidly than the youngest trees at the minimum annual precipitation sampled, 200 mm (Fig. 17.7). This radical change in sensitivity to precipitation is best explained by changes in maximum rooting depth that would be expected to occur during the first few decades of development for most tree species.

Although a critical rooting depth to access deep soil water is likely reached in the first few decades of a tree's life, some trees may increase in height for another 100 years or more. Associated with increasing tree size are greater tensions on the xylem stream which may require a tradeoff between xylem efficiency and safety (Ryan et al. 2006; Domec et al. 2008) as well as changes in leaf morphology and stomatal functioning (Koch et al. 2004; Woodruff et al. 2009, 2010; McDowell et al. 2011; Woodruff and Meinzer 2011). All else equal this height-related change in tree function would impinge on the water status of leaves on the uppermost branches, potentially making the growth of a 200-year-old tree more sensitive to drought stress than a shorter 80-year-old tree. To help compensate for the greater hydrostatic tensions at height, large old trees can alter their wood properties, sapwood area and crown morphology. These processes can benefit the tree by providing a greater whole

crown light use-efficiency via the production of epicormic sprouts (Ishii 2011) or promoting increased water storage that can buffer extremes in evaporative demand (Phillips et al. 2003; Domec et al. 2005; Meinzer et al. 2006). The greater reliance on stored water suggests that the oldest trees may need to more conservatively regulate water status as the asymptotic height is approached for that species and site. Taken together, the difference in timing and relative importance of these influences may explain the complex shape of the response to minimum rainfall (Fig. 17.7).

4.3 The Influence of Relative Humidity

Greater vapor pressure deficits can directly cause reductions in stomatal conductance (Leuning 1995). At the global scale of this investigation, stomatal sensitivity of the species investigated should be reasonably coupled to local vapor pressure deficit regimes that are in turn largely influenced by growing season temperatures. Indeed, stomatal sensitivity to vapor pressure deficit scales with average canopy conductance for a species (Oren et al. 1999). However, low canopy conductance can occur in cold, low productivity regions or in hot and arid low productivity regions. Because the temperature dependence of tree growth was already of interest, I investigated the sensitivity of tree productivity to relative humidity to better isolate the effects of atmospheric drought from low temperatures on canopy conductance and thus productivity. A recent study showed that branches excised from increasing tree heights and thus uncoupled with *in situ* xylem tensions still had maximum stomatal conductance values which occurred at greater vapor pressure deficits (Woodruff et al. 2010). This response of stomatal sensitivity is apparently a response to those branches being formed at different osmotic pressures necessary to balance the increasing xylem tensions at greater tree heights. Hence, *in situ* responses of stomatal conductance are expected to be similar among tree heights and ages while age-related decreases in sensitivity to both precipitation and relative humidity (Figs. 17.6 and 17.7) are likely a function of changes to whole plant water status as affected by age-related changes in rooting depth. At sites where trees grew at the minimum average growing season relative humidity, older trees were characterized by biomass increments that were about threefold greater than the youngest trees. The change in relative humidity response was greatest for young trees, less than 50 years old, which corresponds better to expected differences in rooting depth rather than a limitation imposed by tree height which would continue to increase for many decades after this age.

Relative humidity also plays a large part in determining the rates of evapotranspiration and site water balance. Because low summer relative humidity values can occur even in regions with high annual precipitation, variation in relative humidity connotes a likelihood of drought stress that would not be represented by precipitation alone. Ideally, the precipitation and relative humidity variables would be combined with other meteorological data for each site to produce a water balance function, but these calculations and analyses are still underway.

4.4 *The Influence of Treeline Proximity*

The influence of treeline proximity was investigated because gridded meteorological data do not capture local orographic effects on meteorological variables. Treeline elevation changes on average with latitude (Fig. 17.3) yet is not absolute in a given locality considering the itinerant nature of regional climates at decadal to millennial timescales. Another source of variation in treeline elevation is that at mid-latitude treelines can be substantially lower on average when the mountain range has a maritime climate in comparison to the higher treeline position of drier continental slopes. Despite these considerations, the equation given here for average treeline position agrees well with the upper boundary elevations for tree-ring collection sites (Fig. 17.3).

Reductions in growth with elevation and the related treeline phenomena are often correlated with an array of meteorological, soil and site factors that are known to be temperature dependent (Körner 1998; Sveinbjörnsson and Hofgaard 2002; Holtmeier and Broll 2005; Malanson et al. 2007; Anderson-Teixeira et al. 2008). Some research suggests that variation in photosynthetic assimilation is not important because low temperatures, especially soil temperatures, provide a direct and primary limitation on growth metabolism (Körner and Hoch 2006; Hoch and Körner 2009). However other work suggests that differences in resource availability that affect photosynthetic carbon capture cannot be discounted and that there is likely a gradient between limitation of growth by carbon demand and limitation of growth by carbon supply (Bansal and Germino 2008; Susiloto et al. 2010; Sveinbjörnsson et al. 2010). Moreover, carbon gain of seedlings at some treelines can depend critically on cloudy, high humidity conditions (Johnson and Smith 2008), an aspect of local climate that is poorly understood at present.

Dwarf tree forms or twisted Krummholz forests, are a common sight at many treelines, yet rarely have radial growth rates of trees been accurately determined as they vary across elevation gradients or proximity to treeline. Regional studies of radial growth rates have been undertaken by two research groups, and in each case they established a non-linear effect of altitude (Paulsen et al. 2000; Coomes and Allen 2007). These studies are in agreement with the more general curve provided here for treeline proximity (Fig. 17.5). The age-dependence of growth is stronger at treeline than for any other biophysical variable investigated (Fig. 17.7). Near tree-line, the biomass increment of old trees should be approximately 12-fold greater than that of young trees. This suggests that growth is so slow for young trees at treeline that even infrequent disturbances, drought or herbivory have a good chance to kill most trees before they ever reach an effective reproductive size.

As discussed for precipitation, the conditions that limit growth at treeline likely require an extended period of more favorable conditions for substantial treeline expansion to occur. The mechanisms behind this age-dependence are not clear. Observational data have shown the timing of cambial activity can be initiated much later for old- growth versus young montane forests, suggesting age/size-related interactions with temperature thresholds may be important for predicting forest growth responses (Rossi et al. 2008a, b). It also seems likely that the trees themselves

ameliorate the microsite conditions that may have previously limited the growth of more exposed trees (i.e. shifts in snowpack depth, air temperature, windspeed or the trapping of plant litter and sediments that can provide water and nutrients). Finally, age-related changes in growth form may play a role as there is some evidence from high-latitude treelines that upright growth forms tend to produce greater tree growth (Devi et al. 2008).

4.5 *The Influence of Temperature*

Growing season temperatures had a strong, non-linear effect on tree productivity when averaged across all ages (Fig. 17.5). Similar to the gross primary productivity and mean annual temperature data summarized by Lieth (1972) I found that a sigmoidal function had the best fit to tree productivity. This contrasts with other extensive studies of gross primary production rates that show a linear trend with winter minimum temperatures (Gholz 1982) and no saturation at high growing season temperatures (Anderson et al. 2006). The data compiled by Anderson et al. (2006) were all from relatively moist sites which contrasts with the tree-ring database employed here where data from most sites with higher temperatures were from semi-arid regions. The theory provided by Anderson et al. (2006) suggests biomass accumulation should increase linearly with temperature owing to the temperature response of Rubisco carboxylation. However, for plants growing within any particular environment, net photosynthesis declines above a certain threshold temperature. This occurs at approximately 24°C for most C3 species (Long et al. 2006). Therefore some reduction in photosynthesis and growth would be expected for high temperatures alone. In comparison to relative humidity or treeline proximity, the age-dependence of growth responses to temperature were more complex (Figs. 17.6 and 17.7). As observed for the response to precipitation, the minimum predicted growth at low temperatures increased across ages 1–50 (Fig. 17.7), but this response declines again thereafter. It is unclear whether this trend has a biological or ecological basis. However, one could speculate that this complex shape could result from younger trees growing in an open stand (at boreal or sub-alpine sites) being able to trap more heat near the ground level in spring which would locally thaw the soil while the shade of canopy closure could result in an insulating blanket of snow persisting longer into the spring and causing the soil to stay frozen for a longer period.

Leaf temperatures would also be expected to change with tree age or size as leaves are exposed to changes in irradiance, wind speeds, boundary layer conditions and xylem tensions. Evidence of leaf temperatures across a wide latitudinal range suggest that trees modify their form and hydraulic characteristics to promote optimal photosynthesis near leaf temperatures of 21.4°C (Helliker and Richter 2008). Further investigations are needed to determine whether similar morphological changes occur in trees as they age to help keep a consistent leaf temperature as this effect could help explain the complex shape of age-dependence of the growth response to temperature (Fig. 17.7).

4.6 Potential Biases of Tree Productivity Estimates

Estimates of tree productivity do not account for changes in the number of trees per unit area, which can affect NPP independent of leaf area index. For example, as forests transition to savannas and then grasslands the grass component can sustain equivalent leaf area, but NPP is generally lower even if the ecosystem change is due to fire and/or grazing and the climate is very similar (Del Grosso et al. 2008). Therefore the threshold precipitation value causing a rapid decline in NPP (Schuur 2003; Del Grosso et al. 2008) is greater than the threshold causing a similar decline in vegetated cover. The steep decline in tree productivity (Fig. 17.5) occurs between that for the vegetated cover by grasslands and the global average NPP including all vegetation types. This indicates that the decline in NPP is influenced by disturbance (fire, grazing or anthropogenic) that reduces tree frequency before tree growth is affected. Because of this offset, tree productivity would be expected to overestimate NPP for disturbance-dependent ecosystems.

Part of the age-dependence of growth on the four biophysical variables documented here could occur if young trees at low productivity sites consistently allocated a greater fraction of growth belowground compared to older trees (Fig. 17.7). However, this situation seems unlikely because a large datasets on biomass components suggest the ratio of above to belowground allocation is more or less independent of tree size (Enquist and Niklas 2002).

4.7 Comparison of Spatial Patterns of Tree Productivity and NPP

Spatial patterns of tree productivity and NPP show substantial agreement (Fig. 17.8a, b). Regional differences did occur (Fig. 17.8c), but the importance of these differences needs to be assessed with respect to the goals of this research. Rather than being a direct diagnostic of shortcomings of tree productivity estimates, the projected deviations from the NPP projection should be thought of as a guide to potential biases. In this way it can be determined whether using biophysical variables to standardize tree-ring data can back-predict realistic spatial results and thus validate the opposite approach for calculating unbiased estimates of tree productivity back in time.

Tree productivity projections across deserts, tundra and wet tropical forests are bound to be less accurate because no tree-ring data are available for these regions. Nonetheless, it is instructive to compare productivity and NPP projections across all terrestrial ecosystems. Overall, the methods employed here may need little further improvement where differences arise due to differences in disturbance regimes that affect the vegetation types and reduce NPP below what would be expected for the potential vegetation type at the site. These differences (Fig. 17.8c, see green-colored regions) are most evident in portions of sub-Saharan Africa, India and Australia. These regions correspond strongly to savanna or grassland ecosystems

(see Del Grosso et al. 2008) where frequent fires and/or grazing reduce NPP from the potential maximum expected for those climatic conditions. For these types of overestimates of NPP no further changes should be required for the purposes of this model.

The largest underestimates of NPP (Fig. 17.8c, see red-colored regions) strongly correspond to ecosystems classified as tundra by Del Grosso et al. (2008). These tend to occur in relatively higher elevations at cooler northerly latitudes or, for example, in high elevation regions that are relatively dry and cold such as the Tibetan Plateau (Fig. 17.8c). The underestimate of NPP for these regions likely results from low precipitation values (<400 mm/year) predicting extremely low tree productivity (Fig. 17.5) even though evapotranspiration and resulting drought stress may rarely limit the vegetation in these cold regions. These differences can likely be corrected to better match NPP by employing a water balance function that uses annual evapotranspiration and precipitation estimates. The rate of reductions in tree productivity due to low temperatures and treeline proximity might also be attenuated by correcting for the number of hours of sunlight received at each site. Finally, the structure of the model right now employs a mean response to the four biophysical variables. Further tree productivity projections should attempt to optimize performance by employing decisions as to which factor is most limiting at each site. For example, treeline proximity was included to differentiate local to regional effects of elevation that might not be captured by temperature alone but this effect may not need to be incorporated at high latitudes where sites are already clearly limited by growing season temperature irrespective of elevation. The incorporation of decision algorithms that differentiate between temperature and precipitation limitations should also implicitly determine forest/grassland transitions while transitions to treeline proximity from another variable should implicitly determine forest/tundra boundaries. By incorporating age-specific responses of tree productivity and comparing current versus predicted future climate projections, the locations and direction of change in NPP as affected by tree age might be coarsely estimated for the first time.

5 Conclusion

The database described here is an improvement over previous empirical modeling because it permits the establishment of global trends in the age dependence of tree growth responses to biophysical variables. These data are important for justifying the need for further characterization of changes to physiological function with tree age to help incorporate mechanisms into predictions of forest cover and rates of future terrestrial carbon sequestration.

The findings presented here argue that the growth of older forests may be more resilient to climate change effects, making old-growth forests all the more valuable considering that they can increase their carbon storage for centuries after peak production is reached (Luyssaert et al. 2008). Although older forests may be initially

buffered from the effects of smaller changes in mean temperature and precipitation, the data here cannot speak to whether they are indeed more buffered from an increased incidence of extreme events such as severe droughts. Moreover, it may prove that the ever more dynamic and unpredictable disturbance regimes and cycles of pest and pathogen abundance may have stronger effects on NPP than the direct effects on tree function from shifts in average climate.

Old growth forests receive much attention, but the data here suggest that the growth and establishment of younger trees are more sensitive to shifts in climate. Because establishment can take a number of years, or even decades for slow-growing trees, an increase in the frequency of severe drought events without a change in the mean levels of precipitation could also cause major changes to the populations of sensitive tree species. Consequently, if a changing climate causes species migrations and shifts in ecosystem boundaries, the early growth stages should be thought to represent the greatest potential for bottlenecks in the persistence of forests or colonization by new forests. In turn, these changes can have far-reaching effects on the location of ecosystem boundaries and the resulting differences in carbon storage and other services they provide.

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