INHIBITION OF CONIFERS GROWING UNDER A DECIDUOUS CANOPY: DEGREES, SEASONALITY AND CAUSES OF SUPPRESSION

by

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ABSTRACT

The physiological response of conifers to a deciduous overstory is unstudied in the cool temperate zone despite the widespread occurrence of the association. The object of this study is therefore to determine the degree that understory conifers are inhibited by a deciduous overstory, and to identify the factors responsible. Thus, three conifer species (*Juniperus scopulorum, Pseudotsuga menziesii, Abies lasiocarpa*) growing with and without a deciduous *Populus* canopy were contrasted in regards to environment, seasonal performance, and physiological response to environmental factors.

Understory conifer stands were darker, and especially so when the overstory had leaves. Understory environments of *P. menziesii* and *A. lasiocarpa* were cooler and had lower vapor pressure deficits than open sites, but were similar in relative humidity and soil water. In contrast, understory sites of *J. scopulorum* had similar temperature, vapor pressure deficit, and soil water.

Relative to conifers in the open, photosynthesis of understory conifers was reduced by roughly the same amount (~10%), regardless of photosynthetic rate. While at intermittent times photosynthesis was reduced by much greater amounts, the expected increase of summertime suppression (>10%) was not seen. Understory conifer suppression was not linked to any seasonally limited resource, such as light, water, or nutrients. The slight suppression over the year was due to an unidentified factor, perhaps the lower temperature of the understory environment (-2C), or seemingly unlikely, an allelopathic effect from *Populus.* In instantaneous measures, photosynthesis was better correlated with day of year and RH than light, VPD, or temperature. The correlated phenomena relate to season and precipitation rather than canopy condition under study.

Slight photosynthetic inhibition of understory conifers is supported by similar observations of suppression in the diameter growth and one-year's twig growth.

INTRODUCTION

Successional displacement of a deciduous overstory by coniferous trees is observed in many forests across the cool temperate zone including those in New England (Henry and Swan 1974), the Rocky Mountains (Mueggler 1985), Alaska (Helm and Collins 1997), Scandinavia (Bradshaw and Lindbladh 2004), Siberia (Schulze et al. 2005), and eastern Asia (Chen et al. 2003). Although this widespread occurrence has been recognized, there appears to be few empirical studies that examine the physiology of conifers in competition with a deciduous overstory (cf. Burkle and Logan 2003, Cornett et al. 1998, and Shainsky and Radosevich 1992). Empirical measures of conifers' tolerance and physiological responses to suppressing conditions could create opportunities to better manage timber practices (Cornett et al. 1998), restoration (Karel et al. 2001, Parker 1997, Young et al. 2005) and to predict vegetation responses to global climate change (Bachelet et al. 2000, Sykes and Prentice 1996).

To expand knowledge regarding conifer tolerance to the seasonally variable environmental conditions under a deciduous overstory, four hypotheses were tested by comparing performances of conifers with and without a deciduous overstory:
1) Understory conifers have fewer resources available across seasons e.g. light, water, than conifers growing in the open. 2) While the existence of conifers in the understory demonstrates degrees of shade tolerance, conifer growth remains suppressed.
3) Conifer inhibition in the understory is greatest in the summer and less in the spring and autumn when the overstory is leafless. 4) Suppression of understory conifers is primarily correlated with the lack of light.

Conifer tolerance to conditions of low resource availability is necessary if conifers are to either 1) overtop and replace the deciduous overstory or 2) persist in the understory and become dominant only after the deciduous overstory senesces (Picket et al. 1987). Therefore, the objectives of this study are to demonstrate conifer tolerance in four ways: 1) To show understory conifers have fewer resources than unshaded conifers. 2) To contrast annual net productivity between deciduous shaded and unshaded conifers. 3) To contrast the seasonality of conifer performance in deciduous shaded and unshaded environments. 4) To identify controlling factors by correlating presumptive environmental factors to physiological responses of shaded and unshaded conifers.

To identify controlling factors, instantaneous photosynthetic and respiration rates of conifers were correlated to photosynthetic active radiation (PAR), temperature, relative humidity, vapor pressure deficit (VPD), and soil moisture. While other physiological factors such as chlorophyll content (Leverenz 1987), photosynthetic potential of leaf cohorts (Fuchs et al. 1977), and environmental factors such as mychorrizhae (Nara and Hogetsu 2004), and soil nutrients (Leuschner and Rode 1999) are important to understanding conifer's tolerance to low resource availability, logistical constraints concentrated the study on effects of water, light, and atmospheric conditions.

These hypotheses were tested in three systems to support generalizations about conifers growing under deciduous trees throughout the cool temperate zone: 1) junipers (*Juniperus scopulorum*) growing under riparian cottonwoods (*Populus accuminata*) versus in the open, 2) lower montane Douglas-firs (*Pseudotsuga menziesii*) growing

under aspens (*Populus tremuloides*) versus in the open, and 3) upper montane subalpine firs (*Abies lasiocarpa*) growing under aspens versus in the open.

Annual and seasonal conifer performance were compared with Generalized Additive Mixed Models (GAMM) that modeled trees in open and closed stands for each species and correlated their physiological response to presumptive environmental factors. Model coefficients were contrasted to determine how season, time of day, resource use, and resource quality differentially influenced conifer production in open and closed stands.

METHODS

Species Studied

In the northern Rocky Mountains post disturbance succession often progresses from deciduous *Populus* to a dominant coniferous overstory. Post primary disturbance in the riparian zone sometimes begins with cottonwoods (Boggs and Weaver 1994), which can transition to juniper. Post secondary disturbance in the montane sometimes begins with aspen and leads to Douglas-fir (Mueggler 1985). In the subalpine, the sere sometimes starts with aspen and transitions to subalpine fir (Mueggler 1985).

Early Seral Species

Lanceleaf cottonwood is a common riparian species across the West (Sargent 1965). Its wind-blown seeds establish in a short window after floods on freshly deposited surfaces, which must remain moist to support germination and establishment (Wilson 1970, Boggs and Weaver 1994). Post-establishment, river deposition gradually deposits organic matter and mineral soil, which contributes to the allogenic transition to the next seral stage (Boggs and Weaver 1994). Cottonwoods typically span the riparian zone laterally, but their distribution tapers temporally as succession, geomorphologic and hydrologic processes gradually displace cottonwood stands (Amlin and Rood 2003). Cottonwoods can be replaced by species such as *Pascopyrum smithii* (Boggs 1984), *Fraxinus pennsylvanica* (Wilson 1970), or *Juniperus scopulorum*.

In the Rocky Mountains, aspen occupies montane environments, where it can be either an early seral or late successional species (Mueggler 1985). It is one of the most

widespread species in North America, and grows in both low and high elevation sites, dry, moist, nutrient poor or rich soils (Mueggler 1985). Coniferous species tend to invade aspen communities and in time can replace aspen according to site conditions and disturbance levels (Mueggler 1985). Coniferous invaders include: lodgepole pine (*Pinus contorta),* Englemann spruce (*Picea engelmannii*), Colorado spruce (*Picea pungens*), ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*) and subalpine fir (*Abies lasiocarpa*) (Mueggler 1985). The existence of uneven aged, late successional aspen stands, especially in the Central and Southern Rocky Mountains (Mueggler 1985), is evidence that aspen can also replace itself.

Late Seral Species

Rocky mountain juniper is a widespread species that grows in arid grasslands/steppe communities and on drier riparian sites (Sargent 1965). Birds and rodents disperse its fleshy berries (Chambers et al. 1999). Once established, it associates with species ranging from *Pinus monophylla* to *Artemesia* in the Great Basin, savanna grasslands of *Bouteloua* and *Stipa* in the plains (Daubenmire 1943). Juniper species have expanded over most of their range in the twentieth century (Miller and Rose 1995). It has been suggested that expansion results from fire suppression and/or increased grazing, because grazing reduces grass competition with out damaging the unpalatable juniper. (Miller and Rose 1995, Owens 1996).

Douglas-fir can be either an early or late successional species that grows in moister, cooler, montane zones (Daubenmire 1943). It has a wide range across the western US. Douglas-fir is considered somewhat drought and shade tolerant (Hofman

1920). Douglas-fir seeds are dispersed by wind (Lanner and Vander Wall 1980), birds and rodents (Hofman 1920). Older stands have diverse understories ranging from herbaceous to shrubby communities (Daubenmire 1943).

Late successional subalpine fir grows throughout the Rocky Mountains between the Douglas-fir zone to timberline (Daubenmire 1943). Subalpine fir needles are cold tolerant at least in part due to a tight needle arrangement that accumulates heat (Smith and Carter 1988). Subalpine fir's winged seeds are wind dispersed (Lanner and Vander Wall 1980). Subalpine fir can establish in the shade and invade *Populus, Pseudotsuga menziesii,* and *Pinus contorta* stands. It can codominate with *Picea engelmannii,* and has understories that vary from shrubby *Vaccinium scoparium* to herbaceous *Arnica cordifolia* and *Carex geyerii* communities (Daubenmire 1943).

Site Descriptions

Performance of juniper under cottonwood, Douglas-fir under aspen and subalpine fir under aspen were studied on three separate sites. Adjacent to all study sites, various conifer-deciduous successional stages were observed; including deciduous trees overtopped by conifers and senesced deciduous trees with a dominant conifer overstory. Hence, it is speculated that in all study sites, the coniferous understory will become the dominant overstory.

Junipers growing underneath fully established cottonwoods were studied on private land 15 miles east of Livingston, Montana in the riparian zone along the Yellowstone River (Table 1). The stands are little managed and receive only light cattle grazing. High densities of whitetail deer and annual flooding may contribute to the

maintenance of a relatively uniform *Bromus inermis* understory. Junipers were monitored in three subsites: Group 1 was the furthest from the river, had the highest organic material in the soil, and its junipers were ~30 years old. Group 2 was more open with junipers ~50 years old. In Group 3, cottonwoods and junipers appeared stressed by drought inducing sandy soils. The average juniper age was ~24 years old. All stands were on older river deposits and were high above the river. During analysis, these groups were analyzed separately, and then combined as one group. The Livingston area is noted for having an average wind speed of 13 miles per hour, with gusts often over 40 miles per hour (Weather Underground 2009).

Douglas-fir growing under aspen was studied on private land in the rain shadow of the Bridger Mountains in Bridger Canyon, 15 miles northeast of Bozeman, MT (Table 1). The slightly south-facing site is mesic and until the past decade, had an ephemeral spring. The soils have high organic matter in the A horizons. It is unknown when the aspens established at the site. Douglas-fir outside the aspen stand were thinned in the 1980's.

Subalpine fir growing underneath aspen were studied on slightly north facing private land 7 miles north of the Douglas-fir site on the east side of the Bridger Range in Bridger Canyon. The time of aspen establishment is unknown. Both the open and closed sites are mesic, well drained and have deep O-horizons in the soil. The aspen stand sits in a slight depression. The subalpine fir site was thinned in the 1980's, but the aspens were undisturbed.

Trees were selected in adjacent open and closed sites. The unequal sample size amongst conifer species stems from the lack of availability of tree pairs and a lack of access in the winter.

Table 1. Environmental conditions and descriptions of the juniper, Douglas-fir and subalpine fir sites (wunderground.com).

	Juniper	Douglas-fir	Subalpine fir
Lat/long	45.723375/-110.447788	45.790446/-110.887241	45.84515/-110.870934
Elevation (m)	1380	1700	1800
Precipitation (cm)	41	88	88
Snowfall (cm)	165	566	566
Jan min/max (˚C)	-8/2	-14/0	-14/0
July min/max (˚C)	10/28	4/24	4/24
Overstory	Cottonwood	Aspen	Aspen
Understory Closed	*Bromus inermis* *Iris missouriensis* *Solidago canadensis*	*Amelanchier alnifolia* *Calamagrostis rubescens*	*Calamagrostis rubescens* *Maiinthemum stellatum* *Poa pratensis*
Understory Open	same as closed stand	*Amelanchier alnifolia* *Arctostaphylos uva-ursi* *Mahonia repens*	*Aquilegia coerulea* *Poa pratensis*
Mean conifer age	36	22	41
# of sample pairs	9	6	3
# of sample dates	19	15	15

Environmental Measurements

Environmental conditions under juniper, Douglas-fir and subalpine fir were measured from mid-March to early-November 2008 simultaneously with measures of instantaneous net photosynthesis and dark respiration. Measurements were not taken in winter before mid-March or after mid-November as sub-freezing temperatures caused instrument battery power to be irregular, which in turn caused calibration errors to exceed measured values. Thus, the data were suspect and not used.

The environments of conifers growing under deciduous trees were contrasted with the environments of trees growing in the open to compare overstory influence on

available resources, especially light, temperature, atmospheric water and groundwater. Temperature, light, and relative humidity were measured with a LCA-2 infrared gas analyzer (Analytical Development Co., Hoddeson, England).

Water status in open and closed stand water status was measured in two ways. First, Bouyocous gypsum blocks were buried at 10 cm, 25 cm, and 75 cm at one site in each open and closed stand. Blocks were placed vertically against the sides of the pit. The blocks were installed shortly after snowmelt in late April and measurements commenced after a fortnight to give block water content time to equilibrate with soil water (Aho and Weaver 2008). The open and closed juniper stands had three replicated block sets for the three sub groups, while Douglas-fir and subalpine fir stands had one set each in the open and closed stands. Gypsum blocks were read when gas exchange measurements were made fortnightly. Meter readings were converted to water potential values (Aho and Weaver 2008).

Second, in late-August, predawn water-stress measurements were taken on twigs from north and south aspects of each tree using a Scholander (1965) pressure chamber following the instructions of Ritchie and Hinkley (1975). On measurement dates temperatures exceeded 35°C and were amongst the hottest days of the year. Water stress of trees in open and closed stands were compared using a t-test.

Conifer Production

Conifer production in open and closed environments was contrasted by three methods. First, diameter growth over the trees' lifetime was calculated from measures of diameter and annual rings. Second, in order to compare integrated growth across a single

season, dry biomass was measured on one year's growth of a twig adjacent to each twig examined for instantaneous physiological performance. Third, instantaneous gas exchange was measured at 16-19 dates throughout the 2008 growing season.

Average Diameter and Growth

Diameter growth of each conifer was calculated from tree age and diameter. All conifers were aged by counting annual rings in cores. Diameters and cores were taken at the tree's base to obtain an accurate age. Linear regressions with a zero intercept term were fit between the natural log scale of tree diameter and age. Regressions between open and closed stands were compared using a t-test.

Twig Biomass

Dry biomass, and therefore growth, of a twig during 2008 was measured by harvesting and weighing a twig adjacent to the 'instantaneous twig.' The 'annual growth' twig was selected on the same branch as the 'instantaneous' twig to approximate the same environmental conditions. Biomass was not measured on juniper due to the impossibility of assessing annual growth of its twigs.

Physiological and Environmental Measurements

Instantaneous carbon dioxide exchange and associated environmental conditions were measured with a LCA-2 infrared gas analyzer in the open system mode (Analytical Development Co., Hoddeson, England). Measurements were separately made at the stand level and at the leaf level. Ambient CO_2, temperature, relative humidity and photosynthetically active radiation (PAR) were measured roughly 1-2 meters away from

each tree on the north side to be used as a general measure of stand conditions. The location of stand level measurements was such that the tree did not shade it.

The same environmental conditions were measured at four positions on each tree, i.e. two leaves on the north aspect, and two on the south aspect to assess variation in microclimate within a tree. Throughout this paper, the "leaf" is defined as a roughly 4 cm long twig with needles attached. Differential CO_2 exchange, relative humidity and PAR were then measured on each leaf. The same leaves were used in every measurement throughout the study to reduce variance and more accurately track variation in photosynthesis. All leaves were roughly 1.5 meters off the ground, and were in the lower third of the bole in most trees. However, in the shortest trees, measured leaves were in the middle half of the tree. Any new growth on the subject leaf was clipped to keep leaf surface area constant. Photosynthesis and respiration rates of leaves adjacent to the monitored leaves were compared to rates of monitored leaves to assure that there was no effect from clipping or repeated measurements on the same leaves.

Net Photosynthesis

Net photosynthesis measurements were made in the morning (~9-11 am) and afternoon (~2-4 pm) to represent hydrated and midday slump conditions (Hodges 1967). Sunny days were chosen to standardize light conditions. Measurements were taken fortnightly beginning in mid-March and ending early in November.

Respiration

Dark respiration was measured on the same leaves as for photosynthesis, but at midday between the morning and afternoon photosynthetic measurements i.e. between

12-2pm. Prior to measurement, each leaf was sealed in a lightproof black cloth bag for 30-60 minutes to eliminate photosynthesis. A large lightproof black cloth was then placed over the gas analyzer, the sealed leaf, and the technician. The bag was then removed and the leaf cuvette was clamped on the leaf. CO_2 exchange, temperature and relative humidity were simultaneously measured on each leaf in the dark. The respiration rates calculated in gross photosynthesis may be high relative to morning photosynthesis and low relative to the afternoon photosynthesis, as noon temperatures are between morning and afternoon temperatures (Ryan 1994).

Leaf Surface Area

Leaf surface area was used as a basis to express photosynthesis and respiration rates. Surface area of the sample leaves was measured with a LI-3000 leaf area meter (Li-Cor Inc. Lincoln, Nebraska). The instrument measures leaf area as a function of light interception. Each leaf sample was measured ten times and the readings were averaged. The area values recorded are two-dimensional projections of leaf surface area and underestimate conifer needle surface area. To compensate for three-dimensional surfaces, juniper projected leaf area values were multiplied by 3.2 (Cregg 1992), Douglas-fir surface areas were multiplied by 2.0, and subalpine fir surface areas were multiplied by 2.5 (Smith et al. 1991).

Photosynthesis and Respiration Calculations

Specific measurement procedures and calculations used are outlined in the LCA-2 users manual (ADC 1985), and Long and Hallgren (1987). Flow rate, CO_2 exchange, transpiration and stomatal conductance were calculated from ADC (1985) and Long and

Hallgren (1987). Vapor pressure deficit was calculated from the Arden Buck equation (1981).

The flow rate calculations were corrected as those presented in the manuals were designed for standard pressure and standard volume of air. Rates were calibrated at sea level and were therefore separately recalculated for each site to compensate for thinner air at higher altitudes.

Transpiration measures were also corrected. These changes seem relatively minor but are essential to accurately reflect the environment's influence on gas exchange. The formula for transpiration in Long and Hallgren (1987) is:

$$E = (f/s) * (\chi_o-\chi_e)/(1-\chi_o) \qquad (1.1)$$

where E = transpiration rate (mol $H_2O/m^2/s$)
f = mole flow of air (mol/s)
s = leaf surface area (m^2)
χ_o = mole fraction of water vapor at chamber outlet (mol/mol)
χ_e = mole fraction of water vapor at chamber inlet (mol/mol)
P = measured atmospheric pressure (Pa)
P_o = standard pressure as a function of elevation (Pa)

The ADC Manual (1985) suggests calculating transpiration by:

$$E = (f/s) * (\chi_o/P-\chi_o) \qquad (1.2)$$

Equation 1.1 and 1.2 were combined to take into account elevation's influence on pressure and therefore flow of air, and difference in water vapor between chamber inlet and outlet

$$E = (f/s) * (\chi_o-\chi_e)/((P/P_o)-\chi_o) \qquad (1.3)$$

Data Analysis

Open and Closed Stand Comparison with T-tests

A t-test was used to directly compare the differences in photosynthesis, respiration and presumptive environmental factors of trees in open and closed stands for each species. T-tests were performed on each season, and the entire year for all three species.

Longitudinal Analysis

All data were analyzed using the statistical program R (R Development Core Team 2007). The figures were produced using xyplot (lattice package; Sarkar 2007) or the base package. Photosynthesis and respiration rates were analyzed with gamm (mgcv package; Wood 2004), which uses lme (nlme package; Pinheiro et al. 2008).

Photosynthesis, respiration, and transpiration rates were all longitudinal in nature because they involved repeated measurement of the same leaf over time. Longitudinal data analysis was therefore needed to cope with the resulting correlation between repeated measurements (Diggle et al.1995). Longitudinal analysis accurately distinguishes variation in the response variable over time for an individual versus the variation across the cohort (Diggle et al. 1995). Thus, leaves were assumed independent, but repeated measurements over time on that individual leaf were correlated (Diggle et al. 1995, Singer and Willet 2003).

The general model for longitudinal data is:

$$Y_{ij}=\beta_o+\beta_c x_{i1}+\beta_L(x_{ij}-x_{i1})+\epsilon_{ij} \qquad (1.4)$$

where Y_{ij} =response for observation j and subject i
β_o = model intercept
β = model explanatory variable, either cross-sectional or longitudinal
x_{i1} = cross-sectional effect
x_{ij}-x_{i1} = longitudinal effect
ϵ_{ij} = zero mean random variation variable (Diggle et al. 1995).

Generalized Additive Mixed Models

Generalized Additive Mixed Models (GAMM) (Lin and Zhang 1999) fit within the longitudinal framework and were used to model the data. GAMM's combine Generalized Additive Models (GAM's) (Hastie and Tibshirani 1990) with mixed-effects models (Pinheiro and Bates 2000).

GAM's are penalized versions of Generalized Linear Models (GLM's) combined with an additive structure. GAMM's are similar to Generalized Linear Mixed Model (GLMM's), but use additive nonparametric functions to model covariates. These nonparametric smoothers assist in data interpretation and estimate dependence of the response on the predictors (Hastie and Tibshirani 1990). Within the GAMM, GAM's provide the general model shape and the smoothed responses to the covariates. GAMM's cope with correlation between individuals through mixed-effects parameters and are therefore well suited for hierarchical data (Lin and Zhang 1999). The mixed model manages variability between individuals and their hierarchy.

In concert, GAM's and mixed-effects models provide a more powerful platform than GAM's or mixed models alone. A general description of GAMM components follows. However, for technical details on longitudinal analysis refer to Diggle et al. (1995) or Singer and Willet (2003). For GAMM's and smoothers, refer to Wood (2004, 2006) and Lin and Zhang (1999).

Generalized Additive Models

GAM's use two individual algorithms to maximize model fit. The first algorithm establishes a smooth relationship between variables on the data with a spline. Evenly spaced points (knots) are placed throughout the data and then unique polynomials are fit between knots. Each polynomial is then flexed like a thin strip of wood until the ends of each polynomial within knots smoothly meets the adjacent polynomial. The spline is smoothed within sections then between sections so that it is continuous both visually and in the first and second derivatives. Thin plate regression splines were used for this model (Wood 2003). These splines optimize weights between data and the smooth function without the use of knots (Wood 2003).

The second algorithm maximizes model fit through penalized likelihood maximums to reduce overfitting or 'wiggliness' (Wood 2006). These smoothers summarize the response as a function of the explanatory variables. Penalized fits are multiplied by a smoothing parameter as a compromise between overpenalizing and poor fit.

An additive mixed model has a general form

$$Y_i=X_i\beta+f_1(x_{1i}) +f_2(x_{2i},x_{3i})+\ldots+Z_ib+\epsilon_i$$

where Yi = univariate response
β = fixed parameter vector
X_i = row of fixed effects model matrix
f_j = smooths of the covariates x_k
Zi = row of random effects matrix
$b\sim N(0,\psi_\theta)$ is a vector of random effects coefficients, with parameter θ
$\epsilon\sim N(0,\Lambda)$ is the residual error vector
Λ = covariance matrix (Wood 2006).

Mixed-Effects Models

Variability is expected between individuals in a sample population. Fixed effects models attribute individual effects to each individual instead of the population. Fixed effects models are too flexible and confound the general response with individual response, and therefore create pseudoreplication across samples (Bolker et al. 2009), and artificially increase the degrees of freedom. Inference can only be expanded to include individuals outside of the sample population if individual variability is insignificant. Dependence is induced if individual response is ignored. To deal with the potential for confounding individual response and dependence, a random effects parameter was added.

Parameters that affect individuals from the experimental unit are 'random effects,' and therefore only affect the variance of the response. Parameters that affect the entire population are 'fixed effect,' and are of primary interest, as these affect the mean of the response. The combination of fixed and random effects form mixed-effects models (Pinheiro and Bates 2000).

Mixed effects models are used to find the relationships between the response and explanatory variables that are grouped by a classification factor (Pinheiro and Bates 2000). Mixed-effects models handle longitudinal data, repeated measurements, multilevel data, and block designs (Singer and Willet 2003).

Variance and Normality

Data heteroskedacity was reduced in models with varPower (nlme package; Pinheiro and Bates 2000), which weighted values to a proportional normality. As a simple example, a value near the mean would be given a weight of one, and a value two

standard deviations away would be given a weight of 0.25. The reduction of heteroskedacity makes r^2 unreliable and so r^2 was only used in preliminary models.

GAMM's require the data to be normally distributed. Some data points exceeded the mean by orders of magnitude. Each erratic point was investigated individually and then discarded as all erratic points were determined to be instrument error through contamination of the air stream by the technician.

GAMM Smoothing

GAMM's use Bayesian approaches to smoothing. By minimizing penalized least squares covariate smooths and bases are chosen for the models. Smooths give models more flexibility and therefore more wiggliness than is often appropriate. A prior, i.e. a penalty of the degrees of freedom, is added to cope with the over-flexibility of the model and leads to one that is simpler and less wiggly. Penalties come from the integrated square of the model's second derivative. Each smooth has an unpenalized fixed effect, and a penalized random effect. These are absorbed into the model as $X_i\beta$ and Z_ib respectively. Random effects are assumed by the prior to be Gaussian for the wiggliness measure, while fixed effects are non-Gaussian. The random and fixed effects are then reparameterized with eigen-decomposition. The reparameterization provides a Gaussian smooth with a mean of zero to each coefficient in the model (Wood 2006).

Gamma values were increased in overfit models to 1.4, which increases the weight of the effective degrees of freedom (Kim and Gu 2004). Gamma values increase the penalty of overfitting, which ultimately decreases wiggliness, and therefore overfitting, at the cost of a slight decrease in r^2 values. While increasing the gamma

values reduces overfitting, some caution should still be used in interpretation of the final GAMM curves due to the high number of degrees of freedom used in the models relative the number of degrees of freedom available.

GAMM Selection

Each covariate was modeled independently to see if there was a response and if the data were represented across a gradient. Model covariates were then backwards selected based on four criteria: 1) Residuals had to be normally distributed and homoscedastic. 2) GAM's of covariates modeled independently of other covariates could not be overly wiggly, have overly large confidence intervals, or have insignificant influence on the response. 3) P-values had to be significant at alpha=0.05 for both GAM and mixed model components. 4) AIC had to be near the lowest level.

Optimal GAMM's were chosen by first maximizing r^2 values of fixed covariates with p-values<0.05. P-values on the cusp on 0.05 were thrown out as p-values are not considered overly robust in GAMM (Wood 2006). Random effect parameters were then optimized based on p-values (Pinheiro and Bates 2000). Fixed effect GAMs and random effects were then optimized in concert for an optimal GAMM using AIC.

Table 2. All models were tested for each response, species, and subset. Note that in the full models, open and closed stand data were pooled. The full-oc also models pool open and closed stands, but a 'splitter' is used that partitions each covariate by open and closed stand.

Response	Species	Subset	Number of trees	Number of leaf samples	Number of observations	Estimated df used in model
Net Photosynthesis	Juniper	Open stands	9	36	1119	21
		Closed stands	9	36	1211	17
		Full	18	72	2402	30
		Full-OC	18	72	2402	38
	Douglas-fir	Open stands	6	24	655	12
		Closed stands	6	24	649	15
		Full	12	48	1304	23
		Full-OC	12	48	1304	9
	Subalpine fir	Open stands	3	12	314	10
		Closed stands	3	12	305	10
		Full	6	24	619	4
		Full-OC	6	24	619	21
	All Species	Open stands	18	72	2178	32
		Closed stands	18	72	2181	21
		Full	36	144	4359	30
		Full-OC	36	144	4359	27
Respiration	Juniper	Open stands	9	36	364	9
		Closed stands	9	36	399	7
		Full	18	72	763	9
		Full-OC	18	72	763	18
	Douglas-fir	Open stands	6	24	267	12
		Closed stands	6	24	276	15
		Full	12	48	543	23
		Full-OC	12	48	543	9
	Subalpine fir	Open stands	3	12	111	10
		Closed stands	3	12	128	10
		Full	6	24	239	4
		Full-OC	6	24	N/A	N/A
	All Species	Open stands	18	72	742	5
		Closed stands	18	72	803	5
		Full	36	144	1545	11
		Full-OC	36	144	1545	15

Table 3. Description of model covariates

Covariate	Description	Retained in at least one model
Date	Day of the year	Yes
Time	Time of day	Yes
Stand PAR	PAR measured 1m north of tree	No
Stand Temperature	Temperature measured 1m north of tree	Yes
Stand RH	Relative humidity measured 1m north of tree	Yes
Stand VPD	Calculated vapor pressure deficit 1m north of tree	Yes
Stand CO_2	Ambient CO_2 levels 1m north of tree	Yes
PAR	Photosynthetically active radiation external to leaf chamber	Yes
Temperature	Temperature in leaf chamber	Yes
RH	Relative humidity in leaf chamber	Yes
VPD	Calculated vapor pressure deficit in leaf chamber	Yes
Transpiration	Calculated transpiration rate	Yes
Stomata	Calculated stomatal aperture	No
OC	Open or closed stand; only used in full models	Yes
NS	Leaf with north or south aspect	Yes
Canopy shade	Categorical leaf out period	No
Daylight	Number of hours of daylight calculated from date	No
Soil Moisture 75cm	Soil moisture measured at 75 cm	No
Soil Moisture 25cm	Soil moisture measured at 25 cm	No
Soil Moisture 10cm	Soil moisture measured at 10 cm	No

GAMM and Graph Interpretation

GAMM smoothed model response curves approximate the process. Values are not absolute, and instead show relative response to a parameter, or assist in explaining variance. Some parameters have small responses, yet are included in the model due to their additive interaction with other parameters. Smoothed responses are assumed more influential to the response than linear responses. This belabors the fact that responses of individual covariates should be considered general, and not absolute due to the large number of degrees of freedom relative to the number available. However, the general final predicted model is considered valid.

Linear responses are common to many environmental factors. Smoothed responses are most common for date and time. For clarity, x-axis labels were omitted,

and placed inside plots. Solid black lines are the mean smoothed response, and dotted lines are confidence intervals. Ticks above the x-axis label of covariate graphs are "rugs," and indicate one or more measurements at that location. The model covariate graphs are in order from smoothed parameters in the top left. Leaf covariates appear before stand covariates. All models are normally distributed and are the optimum models for each category. Normality graphs and model iterations leading up to optimal models are not included.

GAMM Comparison

Optimal models were validated against the raw data to assess goodness of fit of the models. Parametric and nonparametric responses of covariates were compared within a species, and between species to assess importance of an environmental variables' influence to the physiological response.

Date was not significant in all models. The predicted values from each GAMM were then fitted with a GAM over Date. This allowed direct comparison of photosynthesis and respiration over the year. Refitting predicted values underestimates photosynthesis and respiration by double-smoothing the response. However, the differences appear negligible, so the model has less overfitting and more is precise for model comparisons.

Integrals

Integrals of photosynthesis over time were approximated for each GAM by Riemmann sums and the trapezoidal rule. Integral and standard error approximations were made with predict.gam (mgcv package; Wood 2004) with 10,000 intervals. Gross

photosynthesis was calculated from these integrals. Although respiration was not taken at the exact same time as net photosynthesis, the difference in time between measurements was typically less than two hours. Therefore, measured respiration should be accurately reflected in the calculated gross photosynthesis.

Net photosynthesis, gross photosynthesis, and dark respiration were compared for each species and the combination of species. T-tests were used on the integrals to compare open and closed stands, seasonality, and net photosynthesis versus respiration. Integrals for each season were converted to a percent of total, and then compared between open and closed stands using a proportion test.

RESULTS

Environments of Trees in Open versus Closed Stands

Several environmental factors were hypothesized to differentiate performance of trees growing in adjacent sites in the open and under a deciduous canopy. The comparison of environments between open and closed stands demonstrates overstory influence on abiotic factors, including light, water, temperature and relative humidity. Environmental measurements were made at both the stand level, i.e. between trees, and at the leaf level, i.e. in the gas-exchange chamber.

Light

Light is required for photosynthesis, and is usually considered a major determinant of photosynthetic rate (Kozlowski et al. 1991). While there was some variability in PAR in open stands, average annual PAR at the leaf level was ~40 μmol/m²/s in juniper stands, and ~50 μmol/m²/s in Douglas-fir and subalpine fir stands. PAR was less in closed stands of all three species and decreased from ~30 μmol/m²/s before deciduous leaf-out and decreased to ~15 μmol/m²/s after the deciduous trees leaf-out (Tables 4, 5). When the deciduous trees lost their leaves, PAR increased in shaded Douglas-fir stands to 25 μmol/m²/s, while in shaded juniper and subalpine fir, PAR did not increase from summer PAR levels (Table 5, figure 1). PAR of trees in closed stand was always lower than trees in open stands due to persistent leaves, stems, and branches. Northern aspects of subject trees had lower PAR than southern aspects in the spring and autumn, but the difference decreased in summer (Figure 3). Light available at the stand

level correlated poorly with light available at the leaf level in closed stands or on the north aspects of trees in open stands (Figures 3, 4). Sunflecks contribute much to the light variability in closed stands, and contribute to the differences between stand and leaf light levels.

Temperature

Temperature influences enzyme activity of both photosynthesis and respiration (Ryan 1994, Tanja et al. 2003). Noon respiration is high as compared to morning respiration, and respiration is low as compared to afternoon respiration, due to the low and high temperature under which photosynthesis was measured respectively. The overall temperature trend was parabolic over the year, with a peak in late August (Figure 1). There was little temperature variation between open and closed stands of juniper, Douglas-fir or subalpine fir (Figure 1). Stand and leaf temperatures are almost identical (Figure 5). There was little variation between north and south aspects of individual trees in either open or closed stands (Figure 3). While there was no difference between average temperatures in open juniper stands and those under cottonwoods (Tables 4-7, figure 1), environments of conifers under the aspen understory were two degrees cooler than in open stands.

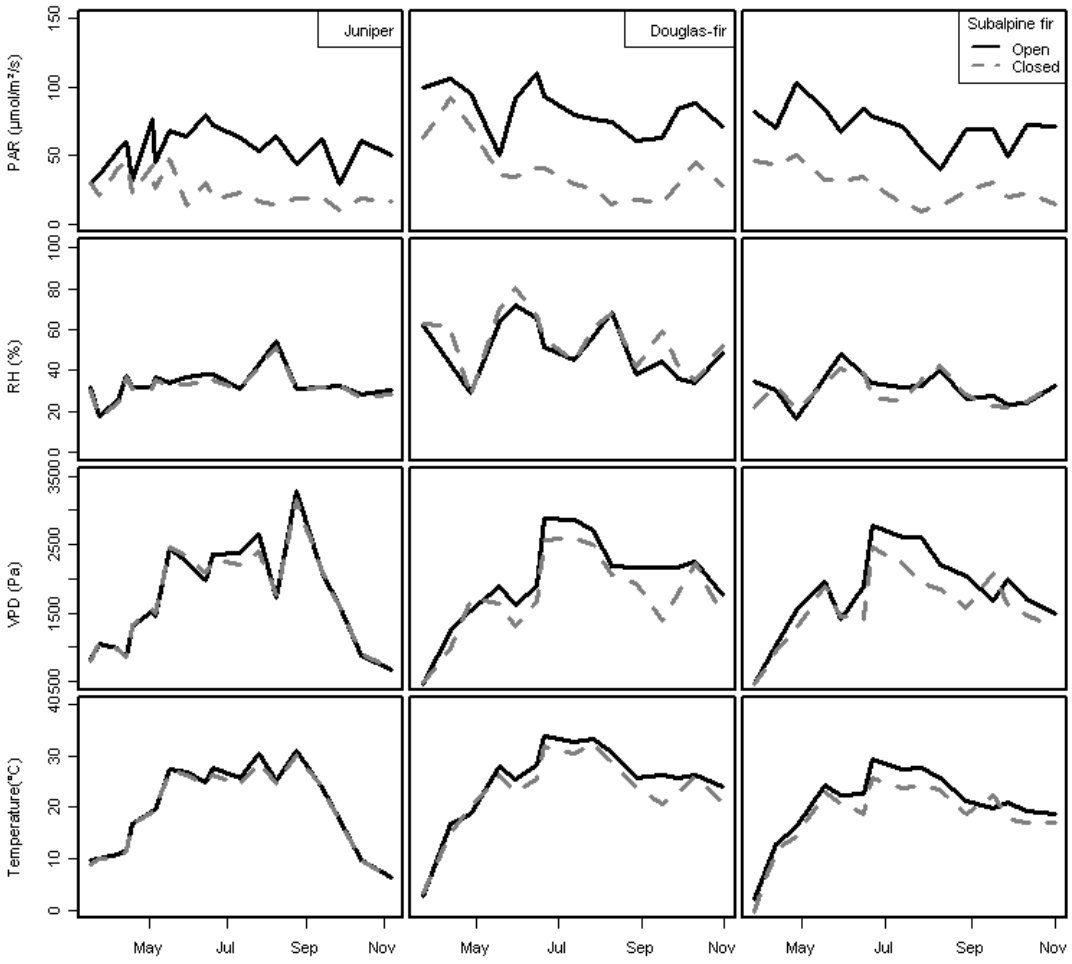

Figure 1. Comparisons of leaf photosynthetically active radiation, relative humidity, vapor pressure deficit, and temperature of open and closed stands of three species during 2008.

Table 4. Comparison of stand environments between open and closed stands of three conifers. Means and standard errors are calculated across seasons and between seasons.

	Juniper				Douglas-fir				Subalpine fir			
	Closed	*se*	*Open*	*se*	*Closed*	*se*	*Open*	*se*	*Closed*	*se*	*Open*	*se*
PAR spring (mol/m^2/s)	35	1.5	55	2	45	2.9	76	4.1	58	3.6	87	5.1
PAR summer (mol/m^2/s)	25	1.4	70	2.3	28	1.7	80	2.8	20	2.2	78	4.1
PAR autumn (mol/m^2/s)	16	1.7	55	3.4	34	3.6	76	4.9	11	2.3	71	6.5
PAR annual (mol/m^2/s)	28	0.9	62	1.4	34	1.4	78	2.1	30	1.8	80	2.9
Temperature spring (˚C)	17.5	0.2	17.5	0.2	16.2	0.4	16.7	0.4	16	0.6	17.2	0.6
Temperature summer (˚C)	25.3	0.2	25.7	0.2	23.6	0.2	25.8	0.2	23.2	0.3	25.5	0.3
Temperature autumn (˚C)	8.1	0.2	8.4	0.2	21.4	0.3	26.2	0.2	17.3	0.1	19.9	0.3
Temperature annual (˚C)	20.1	0.2	20.3	0.2	21.2	0.2	22.8	0.2	20.2	0.3	22.3	0.3
RH spring (%)	22	0.4	22	0.3	27	0.7	26	0.5	27	0.7	27	0.8
RH summer (%)	28	0.4	28	0.4	23	0.4	24	0.4	24	0.8	25	0.7
RH autumn (%)	20	0.5	24	0.6	17	0.4	17	0.4	18	0.9	18	0.7
RH annual (%)	25	0.2	25	0.2	23	0.3	24	0.3	24	0.5	24	0.5
VPD spring (Pa)	1663	27.3	1664	28.6	1495	40.3	1536	37.8	1429	48	1546	50.4
VPD summer (Pa)	2492	33.3	2550	34	2322	30.4	2616	32.7	2287	54.4	2635	61.1
VPD autumn (Pa)	883	14.6	862	15.6	2183	45.7	2295	31.2	1651	24.4	1946	47.2
VPD annual (Pa)	1967	23.5	1991	24.5	2064	24.7	2262	26.6	1941	38.2	2226	44.2
Soil water 75 cm spring (Pa)	0	0	0	0	0	0	0	0	0	0	0	0
Soil water 75 cm summer (Pa)	-3.0E5	4.2E4	-2.0E5	2.2E4	-2.0E6	2.0E5	-3.0E6	2.0E5	0	0	0	0
Soil water 75 cm autumn (Pa)	-9.0E6	6.0E5	-1.0E6	1.0E5	-2.0E6	6.9E4	-1.8E4	1.8E4	0	0	-1026	46
Soil water 75 cm annual (Pa)	-1.0E6	9.9E4	-2.6E5	2.2E4	-2.0E6	1.0E5	-2.0E6	1.0E5	0	0	0	0
Soil water 25 cm spring (Pa)	0	0	0	0	0	0	0	0	0	0	0	0
Soil water 25 cm summer (Pa)	-5.1E5	5.0E4	-6.5E5	4.0E4	-3.0E6	2.0E5	-4.0E6	2.0E5	0	0	-4.0E6	3.0E5
Soil water 25 cm autumn (Pa)	-1.5E4	505	-1.0E4	116	-3.0E6	2.0E6	-1.5E4	1.1E4	-3009	557	-3785	466
Soil water 25 cm annual (Pa)	-2.4E5	2.4E4	-3.1E5	2.0E4	-2.0E6	1.0E5	-2.0E6	1.0E5	-159	429	-2.0E6	2.0E5
Soil water 10 cm spring (Pa)	0	0	0	0	0	0	0	0	0	0	0	0
Soil water 10 cm summer (Pa)	-6.8E5	6.2E4	-6.9E5	4.2E4	-5.0E6	3.0E5	-3.6E5	2.6E4	-1.2E4	3481	-3.0E6	2.0E5
Soil water 10 cm autumn (Pa)	-3.5E4	1950	1.5E4	445	-2.0E6	1.0E5	-7461	148	-7.7E4	8523	-4.9E5	5.6E4
Soil water 10 cm annual (Pa)	-3.3E5	3.1E4	-3.3E5	2.1E4	-3.0E6	2.0E5	-2.0E5	1.6E4	-1.8E4	2615	-2.0E6	1.0E5
Precipitation spring (cm)	0.18	0.05	0.18	0.05	0.07	0.02	0.07	0.02	0.07	0.02	0.07	0.02
Precipitation summer (cm)	0.06	0.01	0.06	0.01	0.12	0.03	0.12	0.03	0.12	0.03	0.12	0.03
Precipitation autumn (cm)	0.08	0.04	0.08	0.04	0.04	0.03	0.04	0.03	0.04	0.03	0.04	0.03
Precipitation annual (cm)	0.11	0.18	0.11	0.18	0.13	0.03	0.13	0.03	0.13	0.03	0.13	0.03

Table 5. Comparison of leaf environments between open and closed stands of three conifers. Means and standard errors are calculated across seasons and between seasons.

	Juniper				Douglas-fir				Subalpine fir			
	Closed	*se*	*Open*	*se*	*Closed*	*se*	*Open*	*se*	*Closed*	*se*	*Open*	*se*
PAR spring (mol/m^2/s)	23	1.3	35	1.6	39	2.7	61	3.6	27	3.1	53	5
PAR summer (mol/m^2/s)	13	0.9	41	1.9	18	1.3	54	2.7	14	1.8	42	3.4
PAR autumn (mol/m^2/s)	11	1.6	37	3.7	24	3.1	54	5.7	12	2.7	48	7
PAR annual (mol/m^2/s)	17	1.7	38	1.2	25	1.2	56	2	18	1.4	46	2.6
Temperature spring (˚C)	17.6	0.2	17.7	0.2	16.8	0.5	16.5	0.4	16.5	0.6	17.9	0.6
Temperature summer (˚C)	25.7	0.2	26.3	0.2	23.9	0.2	26.7	0.2	22.5	0.2	25.1	0.3
Temperature autumn (˚C)	8.3	0.2	8.7	0.2	21.6	0.3	22.6	0.1	17.3	0.1	19.1	0.2
Temperature annual (˚C)	20.3	0.2	20.7	0.2	21.5	0.2	23.2	0.2	19.9	0.3	22.2	0.3
RH spring (%)	28	0.3	28	0.3	34	0.8	32	0.7	30	0.9	33	1.1
RH summer (%)	35	0.4	35	0.4	32	0.4	29	0.4	29	0.8	31	0.8
RH autumn (%)	28	0.6	29	0.6	25	0.6	23	0.5	27	0.8	27	0.7
RH annual (%)	31	0.2	32	0.3	31	0.3	29	0.3	29	0.5	31	0.6
VPD spring (Pa)	1564	26	1564	27	1400	36	1384	33	1398	45	1482	51
VPD summer (Pa)	2305	31	2354	32	2098	27	2549	34	2014	42	2319	52
VPD autumn (Pa)	815	16	818	15	2010	49	2127	30	1448	20	1640	32
VPD annual (Pa)	1830	22	1852	23	1884	22	2156	27	1749	30	1982	38
Stomatal aperture spring (m)	1.1E-6	1.7E-7	1.0E-6	1.6E-7	2.7E-6	5.3E-7	3.0E-6	8.2E-7	1.6E-6	6.1E-7	2.8E-6	5.5E-7
Stomatal aperture summer (m)	1.2E-6	1.2E-7	9.8E-7	9.0E-8	1.3E-6	1.4E-7	1.2E-6	1.5E-7	7.3E-7	1.6E-7	1.1E-6	1.6E-7
Stomatal aperture autumn (m)	9.7E-7	7.7E-8	1.2E-6	8.6E-8	7.7E-7	8.0E-8	6.5E-7	5.9E-8	8.3E-7	8.2E-8	1.0E-6	6.0E-8
Stomatal aperture annual (m)	1.0E-6	7.8E-8	1.1E-6	8.1E-8	1.6E-6	1.7E-7	1.6E-6	2.5E-7	9.8E-7	2.0E-7	1.6E-6	1.8E-7

Water

Soil water scarcity causes a decrease in instantaneous net photosynthetic rate from a corresponding reduction in stomatal aperture, and therefore CO_2 absorption (Farquhar and Sharkey 1982). Due to water's relevance in controlling photosynthesis, soil moisture, atmospheric water, and tree water status were measured. Water in the riparian zone of the Yellowstone River and Bridger Canyon comes from rain, snowmelt, and possibly via subsurface flow (Figures 1, 4). Most rain fell in April-June in the juniper site and April-May in the Douglas-fir and subalpine fir sites (Figure 6). In both sites, erratic afternoon

summer thunderstorms yielded on average 0.1-0.5 cm and up to 2.25 cm in a single storm in Bridger Canyon (Figure 6).

Soil water measurements show that water was available most of the year for all three species (Figure 7). In open stands, there was no time when soil moisture was less than –5 MPa in at least one soil layer. In closed stands, only Douglas-fir had a period in which water stress in all three layers was less than –5 MPa. Both Douglas-fir open and closed stands were drier than those of the juniper and subalpine fir. Soil moisture blocks were replicated for each stand and not individual trees, so while generalizations at the stand level can be made, they cannot be correlated with instantaneous measures of photosynthesis and respiration.

While soil water affects water uptake, atmospheric water affects loss. At all three sites, average annual relative humidity was around 30% (Tables 4, 6, figure 1). While open and closed juniper stands experienced similar VPD ($p>0.05$), VPD was greater in open stands than closed stands of both Douglas-fir and subalpine fir ($p<0.05$) (Tables 4-7, figure 1). There was no significant difference of relative humidity between aspects of individual trees, or in stand versus leaf level relative humidity (Figures 1, 8).

Tree water status integrates the influence of soil and atmospheric water. The cottonwood overstory had little effect on water potential of the juniper understory (-8 MPa) as compared to open stands (-10 MPa) ($p>0.05$). Water stress was high in both Douglas-fir closed stands (-17 MPa) and open stands (-17 MPa) ($p>0.05$). Subalpine fir closed stands had much less water stress (-9 MPa), than open stands (-17 MPa) ($p<0.05$).

Production of Trees in Open and Closed Stands

Production in open and closed stands was compared to quantify any suppression caused by the deciduous overstory. Performance was measured in the long term by conifer diameter growth, in the current year by twig biomass increase, and instantaneously by net photosynthesis and respiration rates.

Diameter growth was used to compare performance over the tree's lifespan between open and closed stands. Average diameter growth indicates that all three species are slightly suppressed in the closed stands ($p<0.05$, all r^2 of linear regressions>0.95), with Douglas-fir being the most suppressed (Figure 11).

Twig biomass production was used to compare current 2008 production in open and closed stands. Differences in current year twig biomass between open and closed stands of Douglas-fir and subalpine fir were insignificant (pvalue>0.05) (Figure 12). Juniper was not measured, as annual twig growth was indistinguishable between years.

Instantaneous net photosynthesis and respiration rates of trees in open and closed stands were compared using t-tests for each season. In all three species, net photosynthesis was significantly less in the closed canopy stands during the summer and the year as whole (Table 8). Net photosynthesis was not significantly reduced in the leafless spring and autumn for juniper and Douglas-fir (Table 8). In contrast, photosynthesis of subalpine fir was significantly less in trees of closed stands in the autumn than trees of open stands (Figure 7). Respiration in juniper and Douglas-fir tree did not differ between open and closed stands (Table 8). Respiration of subalpine fir was lower under an aspen canopy in the spring, but not in summer or autumn (Figure 7).

Table 8. P-values of tests between net photosynthesis and respiration trees of open and closed stands for three seasons and three species. P-values significant at the 0.05 level are **bolded**.

Response	Species	Season	Closed Stand Reduction	P-value	Df
Net Photosynthesis	Juniper	Spring	No	0.26	729
		Summer	Yes	**3.8E-6**	1112
		Autumn	No	0.23	275
		Annual	Yes	**6.9E-5**	2375
	Douglas-fir	Spring	No	0.35	379
		Summer	Yes	**2.9E-1**	612
		Autumn	No	0.95	175
		Annual	Yes	**3.0E-1**	1214
	Subalpine fir	Spring	No	0.27	178
		Summer	Yes	**4.6E-6**	312
		Autumn	Yes	**0.004**	75
		Annual	Yes	**1.7E-5**	533
Respiration	Juniper	Spring	No	0.42	249
		Summer	No	0.53	525
		Autumn	No	0.22	139
		Annual	No	0.73	1124
	Douglas-fir	Spring	No	0.47	172
		Summer	Yes	**0.03**	358
		Autumn	No	0.57	75
		Annual	No	0.05	604
	Subalpine fir	Spring	Yes	**0.02**	90
		Summer	No	0.65	155
		Autumn	No	0.06	32
		Annual	No	0.48	316

Net photosynthesis varies with season and canopy. Seasonal net photosynthesis trends are parallel in trees of open and closed stands (Figure 10). Total net photosynthesis and integrated growth of conifers growing under a deciduous canopy show slight suppression (Figure 7, 8). Mean annual photosynthesis of closed stands of juniper and Douglas-fir are 80% as compared to open stands (Figure 13). Subalpine fir closed stands

have around 65% mean annual photosynthesis as open stands (Figure 13). Differences of net photosynthesis between trees of open and closed stands are greatest during the summer (Figure 7), when deciduous trees apparently reduce resource availability of understory conifers. Most of the photosynthetic differences between open and closed stands stem from the spring peak and the autumn peak. There is only slight suppression of photosynthesis for the remainder of the year.

Respiration varies with season and canopy. Seasonal trends in respiration are similar to photosynthetic trends, but oscillate less (Figure 10). Respiration rates of junipers in closed juniper are 77% of junipers in open stands. In Douglas-fir and subalpine fir, the rates of trees in closed stands are 87% and 70% of trees in open stand rates respectively (Figure 10).

Determinants of Production

To determine the effect of presumptive environmental factors, photosynthetic response was correlated with environmental variables separately measured at both the stand and leaf levels (light, relative humidity, VPD, temperature) and correlated factors (aspect, open/closed, time of day, date). GAMMs compare within season performance and resource availability between trees of open and closed stands of all three species. For each of three species there is a 1) a closed stand model 2) an open stand model 3) a pooled model that tests open and closed tree differences 4) pooled model that test differences in environmental differences between open and closed stands.

Seasonal Differences in Tree Models between Open and Closed Stands

Integrated net photosynthesis, gross photosynthesis, and dark respiration of trees in open stands are greater than trees in closed stands for all species ($p<0.05$) (Table 9, figures 13-15). In the spring, when the overstory is leafless, there is no significant difference in net photosynthesis between trees of open and closed stands for all species ($p>0.05$) (Figure 13). There are small and marginally significant differences between trees in open and closed stands in the summer when the deciduous canopy had leaves (juniper, $p=0.06$, Douglas-fir and subalpine fir, $p=0.04$). In the autumn, after deciduous leaves had dropped, photosynthesis and respiration were lower in closed juniper stands than in open stands ($p<0.05$), but differences were insignificant between trees of open and closed stands of Douglas-fir and subalpine fir ($p>0.05$). Spring and autumn photosynthesis did not differ between trees of open and closed stands for all three species ($p>0.05$). Integrated annual net photosynthesis of trees in open stands are statistically larger than trees of closed stands for all three species ($p<0.05$), despite the small seasonal differences of integrated net photosynthesis.

Dark respiration values of trees in open stands are greater over than the year than trees in closed stands of juniper and subalpine fir ($p<0.05$). Respiration of Douglas-fir closed and open stands are not different for any season across the year ($p>0.05$) (Table 9, figure 14). In the spring and autumn, respiration rates of trees in open stands of juniper and subalpine fir are greater than trees of closed stands ($p<0.05$). However, summer rates of trees in open stands are slightly higher than trees in closed stands ($p<0.05$)

All gross photosynthetic rates of trees in open stands are greater than trees in closed stands for all species ($p<0.05$) (Table 9, figure 15). In the spring, subalpine fir gross photosynthesis rates are greater in trees of open stands than of closed stands ($p<0.05$), while juniper and Douglas-fir were smaller ($p>0.05$). In the summer, all gross photosynthesis rates of trees in open stands, across species are statistically greater than trees in closed stands ($p<0.05$). In parallel with spring observations, autumn photosynthesis in subalpine fir was not different ($p>0.05$), but photosynthesis of trees in open stands were greater than trees in closed stands of Douglas-fir and juniper ($p<0.05$). Significant differences in gross photosynthesis between trees in open and closed stands disappear when comparing the spring and autumn leafless shoulder seasons for any species ($p>0.05$).

Net photosynthesis, gross photosynthesis, respiration rates (Table 9, figures 13-15), and growth (Figures 11, 12) of trees in open stands are slightly higher than trees in closed stands. These differences are small and while significant at the 5% level, are rarely significant at the 1% level.

The relative rates of net photosynthesis, gross photosynthesis and respiration for each season was calculated as a percentage of the year and compared between trees of open and closed stands, e.g. the integral of spring photosynthesis in closed juniper stands was divided by total annual integral of photosynthesis of closed stands, and then compared to the same ratio of juniper open stands. Relative rates show no significant differences in tree production between open and closed stands of absolute response values for each season ($p>0.05$) (Table 10, figures 16-18). The only exception is that

proportionately, juniper and Douglas-fir open stands have greater gross respiration values in the autumn than closed stands ($p<0.05$).

Photosynthetic Response of Trees in Open and Closed Stands to Environmental Factors

Models correlating the performance of each species with presumptive factors identify environmental factors that influence photosynthesis. Open and closed models allow direct comparison between tree performance of open and closed stands. Full models and full-oc models provide an alternative method for comparing differences between tree performance in open and closed stands. Full models pool data from both open and closed stands and use an open/closed covariate to determine whether there is a difference between stands. Similarly, full-oc models pool data from open and closed stands, but specify differences between stands for each factor. Simply put, full models indicate in a binary manner if there is a difference between open and closed stands. Full-oc models quantify the influence of each factor to photosynthesis in open and closed stands.

Table 9. Cross season p-values of photosynthesis (Ps), respiration (resp) and gross photosynthesis (gross) closed (C) to open (O) stands of three species. The comparison is based on the ratio of physiological response of trees in closed to open stands integrated across seasons. Significant p-values are **bolded**. Shoulder refers to the deciduous leafless spring and autumn.

Measure	Comparison	Juniper	Douglas-fir	Subalpine fir	All Species
Ps	Spring O v C	0.17	0.56	0.08	0.16
Ps	Summer O v C	0.06	0.06	**0.04**	**0.04**
Ps	Autumn O v C	**0.01**	0.60	0.13	0.10
Ps	Shoulder O v C	0.12	0.56	0.09	0.12
Ps	Full year O v C	**0.04**	0.05	**0.03**	**0.03**
Ps	Shoulder v Summer C	**0.04**	**0.04**	0.13	**0.04**
Ps	Shoulder v Summer O	**0.03**	**0.03**	**0.08**	**0.03**
Resp	Spring O v C	0.22	0.15	0.06	0.11
Resp	Summer O v C	**0.03**	0.13	**0.04**	**0.05**
Resp	Autumn O v C	0.12	0.16	0.33	0.12
Resp	Full year O v C	**0.03**	0.07	**0.03**	**0.003**
Resp	Shoulder O v C	0.23	0.15	0.09	0.12
Resp	Shoulder v Summer C	**4.5E-5**	**0.03**	**0.02**	**0.04**
Resp	Shoulder v Summer O	**0.04**	**0.03**	0.21	**0.04**
Gross	Spring O v C	0.09	0.17	**0.04**	0.09
Gross	Summer O v C	**0.02**	0.05	**0.03**	**0.03**
Gross	Autumn O v C	**0.04**	**0.01**	0.12	0.05
Gross	Full year O v C	**0.02**	**0.04**	**0.02**	**0.03**
Gross	Shoulder O v C	0.07	0.15	0.05	0.07
Gross	Shoulder v Summer C	0.17	0.13	0.34	0.17
Gross	Shoulder v Summer O	0.13	0.12	0.28	0.15

Photosynthetic models fit the data well (Figures 19-22), and this is confirmed by the similarity of trends across seasons between models and raw data (Figure 23, 24). Open and closed stand photosynthetic values are parallel across seasons in all species, but net photosynthesis is slightly less in closed stands ($p<0.05$) (Table 8, figures 25-28).

That PAR had extremely low slopes and sporadic appearance in models discounts it as a controlling factor. PAR was positively, but weakly correlated with photosynthesis in most Douglas-fir models, all species open models, and all species full models (Table

11, figures 31, 33, 35, 36, 42, 43, 44). PAR never influences photosynthesis in closed models.

Temperature may be responsible for the weak hyperbolic rise and fall in photosynthesis from spring to fall. Temperature appears in all but in closed models and juniper models (Table 11, figures 33, 35-44). Temperature positively correlates with photosynthesis in the models (Figures 29-44).

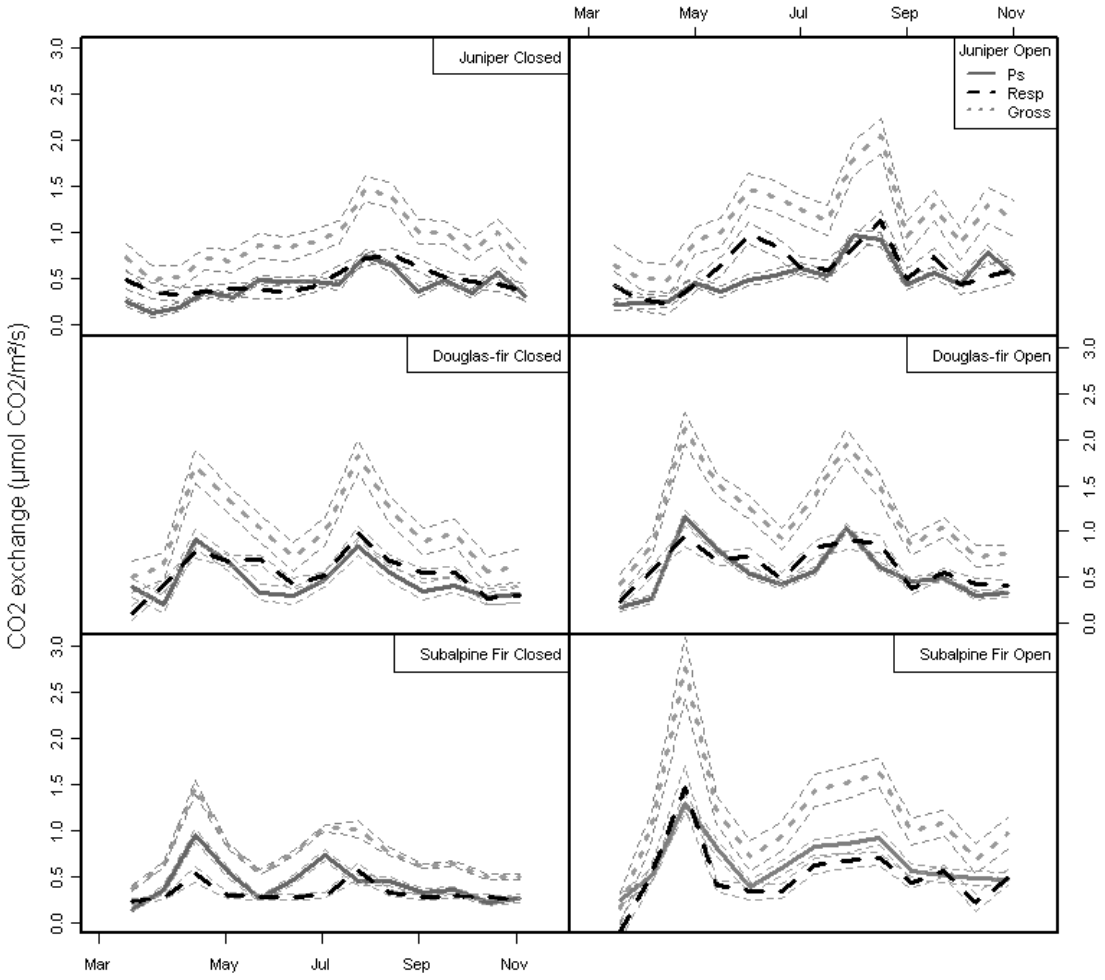

Figure 24. Modeled annual gross photosynthesis, net photosynthesis, and respiration for trees growing in open and closed stands of juniper, Douglas-fir, and subalpine fir. Because respiration reduces gross photosynthesis to net photosynthesis, gross photosynthesis was calculated as the sum of net photosynthesis and respiration.

Table 11. Generalized mixed model slopes of all factors in determining net photosynthesis. Shading indicates relationship: clear indicates no overall trend, light gray indicates photosynthesis increases when the factor increases. Dark gray boxes indicate photosynthesis decreases when the covariate decreases. A "smooth" means the response was not linear. Bold text indicates slopes with slopes >0.01. The term OC is only in full models. Boxes around terms in full-oc indicate the factor had different effects between open and closed stands. Refer to table 3 for explanations of model covariates.

	Model	Intercept	*Date*	*PAR*	*S. RH*	*RH*	*S. VPD*	*VPD*	*Trans*	*Time*	*Temp*	*OC*	*NS*	*S.CO2*
Closed	Juniper	0.784	smooth		smooth	**-0.01**								
	Douglas-fir	-0.030	smooth		**0.01**			1E-4		smooth				
	Subalpine fir	0.386	smooth		**0.01**									
	All species	0.399	0.0003		smooth	smooth	smooth			**-0.49**	**0.01**			
Open	Juniper	0.514	smooth		smooth	smooth				smooth				
	Douglas-fir	0.032	smooth	1E-4	smooth						**0.017**			
	Subalpine fir	0.950	smooth		**0.02**	-0.01					**-0.02**		**-0.05**	
	All species	-0.080	0.0009	7E-4	smooth	smooth	smooth	-3E-4	-0.008	**-0.64**	-0.076			
Full	Juniper	0.367	smooth	9E-4	smooth	smooth				smooth		**0.11**		smooth
	Douglas-fir	-0.012	smooth	9E-4	smooth			smooth			**0.02**			
	Subalpine fir	0.450			**0.01**					**-1.20**	**0.02**			
	All species	1.892	smooth	7E-4	0.01	smooth	-0.001	-4E-4		**-0.58**	smooth	**0.08**		
Full-OC	Juniper	0.462	smooth		smooth	smooth				smooth				
	Douglas-fir	-0.195	0.0008	9E-4	0.002						smooth			
	Subalpine fir	0.470	smooth		**0.01**					**-0.99**	**0.01**			
	All species	1.437	0.0005	5E-4	**0.01**	smooth	-4E-4	-2E-4		**-0.57**	**0.06**			

Water influenced the response in all the models as shown in three ways (Table 10, Figures 29-44). 1) Relative humidity is highly correlated to the net photosynthesis peaks superimposed on the parabolic trend. These peaks also correlate with availability of surface water, i.e. with spring snowmelt in Douglas-fir and subalpine fir, and with August rain showers in all sites (Figure 8). 2) Stand relative humidity appears positively correlated with photosynthesis in all models. An erroneous leaf relative humidity effect is ignored as an artifact of modeling and not as a genuine response for two reasons. Firstly, leaf relative humidity negatively correlates with photosynthesis in models (Table 11,

figures 29-32, 38, 41-44). Secondly, when modeled independently of other factors, or when plotted against raw data, leaf relative humidity also positively correlates with photosynthesis. 3) VPD at both the stand and leaf level are negatively correlated with photosynthesis in full all species models i.e. as VPD rises, photosynthesis decreases (Table 11, figures 34, 35, 41-44). Within species, VPD only appeared in Douglas-fir closed and full models.

The effect of the pseudo-factor season on photosynthesis was not significantly different between trees in open and closed stands. Net photosynthesis is parallel, but slightly less in closed stands than in open stands across all seasons. Trees in closed stands did not photosynthesize less in the shaded summer than in the unshaded spring and autumn shoulder seasons. Instead, net photosynthesis follows a low hyperbolic curve that rises in spring and decreases in autumn (Figures 29-44). Peaks in June and August punctuate the hyperbolic curve in Douglas-fir and subalpine fir. Juniper lacks the June peak; instead, the photosynthetic rate rises gently toward an August peak before dropping off in the autumn.

Advancing time of day consistently reduced photosynthesis in juniper models (Figures 29-32), but had only sporadic effects in other models (Figures 34, 39, 40, 43). Photosynthesis generally decreased over the course of the day.

Influence of ambient CO_2 (Figure 31) transpiration (Figure 42), and leaf aspect (Figure 38) were too irregular to generalize. However, their inclusion sometimes increased model performance.

Respiration Response of Trees in Open and Closed Stands to Environmental Factors

Date and water were the best predictors of respiration. Dark respiration responses across seasons and environments are similar to trends of net photosynthesis (Figure 24), but with smaller oscillations. As in net photosynthesis models, the respiration models fit the data well (Figure 45-48).

Respiration in trees of open and closed stands are parallel across seasons in all species (Figures 24, 49, 50-53). Seasonal respiration follows a parabolic trend with two errant peaks in June and August in Douglas-fir and subalpine fir (Figures 24, 49). Juniper photosynthesis shows a mild peak in August, but as in net photosynthesis, does not show an early season peak.

Atmospheric water conditions were an important predictor in all respiration models as shown in two ways (Table 12, figures 50-68). 1) Stand relative humidity was the most commonly used water covariate, and its effect was found in all but subalpine fir closed, and juniper full models. Leaf relative humidity was less common, and as in net photosynthesis was shown to erroneously decrease when the response increased (Figures 60, 61, 67, 68). The decreasing response of relative humidity was not seen when modeled independently of other covariates, or observed as raw data. Therefore, the unusual response was ignored as an artifact of the models. 2) Respiration decreased when VPD increased but was used only intermittently in the models (Figures 64-68). It appeared in all pooled models at the leaf or stand level.

Date was an important predictor in over half of the models (Figures 24,49,50-53), in contrast to all net photosynthesis models. There did not appear to be any seasonal difference between respiration of trees in open and closed stands.

Table 12. Generalized additive model slopes of all factors in determining respiration. Shading indicates relationship: clear indicates no overall trend, light gray indicates photosynthesis increases when the factor increases. Dark gray boxes indicate photosynthesis decreases when the covariate decreases. A "smooth" means the response was not linear. Bold text indicates slopes with slopes >0.01. OC is only in full models. Boxes around terms in full-oc indicate the use of the oc splitter. Refer to table 3 for explanations of model covariates.

	Model	*Intercept*	*Date*	*S. RH*	*RH*	*S.VPD*	*VPD*	*Time*	*S. Temp*	*Temp*	*NS*
Closed	Juniper	0.748	**smooth**								
	Douglas-fir	0.112	**smooth**	**0.05**							
	Subalpine fir	1.083	**-1.28**								
	All species	-0.342		0.007			-4E-4		**0.04**		**0.11**
Open	Juniper	0.065	**smooth**	**smooth**							
	Douglas-fir	-0.682		**0.01**					**0.04**		
	Subalpine fir	-1.050	0.002	**0.02**						**0.03**	
	All species	-0.481		0.009		-3E-4			**0.06**		**0.12**
Full	Juniper	1.042	**smooth**					**-0.938**			
	Douglas-fir	-0.336		**0.02**	-0.009					**0.03**	
	Subalpine fir	1.048		0.008			1E-4	**-1.284**			
	All species	-0.266	**smooth**	**0.01**	-0.007	-3E-4			**0.06**		
Full-OC	Juniper	0.535	**smooth**	**smooth**						**smooth**	
	Douglas-fir	0.400	**smooth**	**0.02**	**-0.02**						
	Subalpine fir	NA									
	All species	-0.008	**smooth**	**smooth**	-0.007	-2E-4			**0.06**		

Time of day, temperature and aspect were occasionally used as predictors of respiration, but other presumptive factors were not. Time of day was not an important covariate, as respiration was only measured in a two-hour time window, and therefore variation in time was insufficient to detect a response. Temperature (Figures 57, 59, 60,

63 65-68) and aspect (Figures 65,66) were used intermittently in the models with no recognizable pattern. No other covariates were used to model respiration.

DISCUSSION

The objectives of this study were 1) to contrast the differences between conifer environments and unshaded of shaded environments) to contrast annual performance of shaded and unshaded conifers 3) to contrast seasonality of conifer performance in deciduous shaded and unshaded environments 4) to contrast physiological responses of shaded and unshaded conifers to presumptive environmental factors.

Differences in Environmental Factors between Trees in Open versus Closed Stands

Net photosynthesis is expected to be determined by light, which affects instantaneous rate (Chazdon and Pearcy 1991), temperature, which controls enzyme activity and thus photosynthesis's seasonal course (Neilson et al. 1972), and soil and atmospheric water, which influence the instantaneous photosynthetic rate via stomatal aperture (Farquhar and Sharkey 1982). Since environmental conditions influence photosynthesis, PAR, temperature, vapor pressure deficit, relative humidity, and soil water were monitored over the year. Understory conifers were found to have less light in all three species as hypothesized (Table 4). However, neither soil water nor any other presumptive factor measured was significantly less available in the understories of deciduous trees. PAR contrasted the environments of open and closed stands more than any other measured environmental variable (Table 4). The onset of *Populus* leaves caused ~50% PAR reduction in available light from spring PAR levels (Figure 1). In Douglas-fir and subalpine fir understories, both temperature and vapor pressure deficit decreased in the coniferous understory after deciduous leaf-out due to the interception of

solar radiation by leaves (Figure 1). In contrast, junipers in open and closed stands experienced similar temperatures and vapor pressure deficits. The similarity was probably due to the mixing of the air from wind. Relative humidity and soil water showed similar patterns in the environments of shaded and unshaded sites for juniper, Douglas-fir and subalpine fir (Figures 1, 7).

Annual Production of Trees in Open versus Closed Stands

Annual production of conifers growing with and without a deciduous overstory was compared via 1) diameter growth, 2) twig production, and 3) net photosynthesis. Taken together, the results show slight suppression of conifers growing under a closed canopy (Figure 11) and support the hypothesis that trees under a deciduous canopy are slightly suppressed.

First, tree growth, as indexed by diameter and age, shows long-term performance of the whole tree (Douglas 1919). Diameter growth of trees in closed stands was slightly less than trees in open stands.

Second, twig production, was used to index one year's growth. Twig biomass did not differ significantly between trees in open and closed stands of Douglas-fir or subalpine fir (Figure 12). Juniper twig production could not be measured. While actual photosynthetic gain is underestimated by twig biomass because the photosynthates are distributed throughout the tree, the proportion of photosynthates retained in the twig is likely equal between trees in open and closed stands. However, twig biomass is most likely influenced by physical position and allometry due to the relationship of the twig as a support structure for leaves (Westoby and Wright 2003).

Third, T-tests and integrals under GAMM production curves contrast differences between the instantaneous measurements of photosynthesis and respiration for a year. T-tests showed that trees in open stands had greater annual production than trees in closed stands for all three species ($p<0.05$) (Tables 7, 9, figures 13-15). The same result was found when rates were summed across the year by integrating under GAMM production curves. Relative to photosynthesis of trees in open stands, photosynthesis in closed stands over the year was less in juniper (80%), Douglas-fir (85%), and subalpine fir (65%) (Figure 13). Average suppression was around 10% on most measurement dates. The low production of subalpine fir might be explained by the fact that measurements were made on the leaves in the lower canopy, and could have inherently lower photosynthetic rates (Westoby and Wright 2003). Suppression could arise from an unmeasured factor that was competed for, or alleochemics from *Populus*, which seems unlikely, but would provide an explanation.

Influence of Deciduous Leafy and Leafless Seasons on Conifer Performance

Photosynthesis of understory conifers was hypothesized to be most inhibited in the summer when the deciduous overstory was leafy, due to either reduction in light or root competition associated with an active deciduous overstory. This hypothesis was tested by comparing photosynthesis of understory conifers against the photosynthesis of a control, i.e. conifers growing in the open. It was expected that photosynthesis of understory conifers would be more reduced in the summer than in the spring or fall.

The hypothesis is rejected (Tables 8, 10, Figures 16-18) on three counts. First, T-tests of photosynthesis by season between open and closed stands support the hypothesis that there is less summer net photosynthesis, gross photosynthesis, and respiration in trees in closed than open stands. However, net photosynthesis, gross photosynthesis and respiration of trees in open stands are not proportionately greater than trees in closed stands. There does not appear to be any seasonal suppression, rather trees in closed stands consistently photosynthesize and respire at rates about 80% that of trees in open stands throughout the year. Trees in both open and closed stands had springtime values of net photosynthesis, gross photosynthesis, and respiration around 40% that of the total annual values. Summer net photosynthesis, gross photosynthesis and respiration values of trees in both open and closed stands made up 50% of the annual measured values, and autumn values made up around 10% of the year (Figures 16-18). If there was seasonal suppression from the deciduous overstory, photosynthetic and respiration rates of trees in open stands would be proportionately greater than trees in closed stands during the summer.

Second, the hypothesis was retested with the integrals of GAMM by season. These integrals were used to compare production by season. This integration showed less photosynthesis in the autumn and fall than in the summer for understory conifers as compared to conifers growing in the open. However, as a percent of total annual photosynthesis, there was no difference between seasons. Suppression of understory conifers was constant of the course of the year, not more in the summer as hypothesized.

Third, models reject the shade season binary covariate used in the GAMM's that identifies summer versus the spring-autumn shoulder season, which suggests there is nothing categorically unique about the shaded season. There was no photosynthetic decrease in understory conifers that coincided with a reduction of a seasonally limited resource during the shaded summer (Table 8, figures 1, 24). Net photosynthesis did not correlate well with either PAR nor soil water. Year-round resource availability within the understory at lower levels is a more likely driver of lower photosynthetic rates (Day and Monk 1977, Xu and Baldocchi 2003), not the deciduous leaf-out (Burkle and Logan 2003).

Response to Presumptive Environmental Factors

The responses of net photosynthesis and respiration to environmental variables can be used to understand the differences in performance of trees in open and closed stands by values derived from integrals of time and photosynthesis measures (Figures 16-18). Thus, models were used to evaluate both the importance of individual presumptive factors for each species, e.g. light, temperature and water, and the importance of time e.g. time of day and season.

Environmental factors were of primary interest, but did not explain all model variability. The inclusion of date into all models suggests that something other than a measured environmental factor triggered phenological response. Triggers and limiting factors are confounded and require additional experimental work for elucidation (Billings 1952) and will not be further addressed here.

Response of Photosynthesis to Light

While lack of light for understory conifers in summer was hypothesized to inhibit net photosynthesis, data show that PAR availability had little effect on net photosynthesis. The null hypothesis is supported by three observations.

First, while PAR availability greatly decreased in the leaf-out period in closed stands (Figure 1), there was no photosynthetic rate decrease of understory conifers during the leafless periods not matched in open stands. Light did not appear in any closed model, and only appeared in open models with extremely low slopes (Table 11, figures 33, 36, 39, 43, 44).

Second, while north aspects of open trees have light levels only one-third the south aspect (Tables 4, 5), there was no difference in photosynthetic rate between aspects. Thus, the data suggest that juniper, Douglas-fir, and subalpine fir are shade tolerant and photosynthesis was not limited by light, as shade tolerant species have lower light saturated photosynthetic rates than shade intolerant species (Bassow and Bazzaz 1997). While unshaded spring-autumn shoulder seasons may be significant to photosynthesis in evergreen species, evergreens may not be acclimatized to the extra light, and are unable to use more than in the shaded period (Landhausser 1997). Any reduction in photosynthesis may be compensated by a reduction in photorespiration (Marek et al. 2002). Thereby, more photosynthates would be available to the tree for other uses.

Third, shade conifers did not respond like shade adapted understory plants, as there was no response to sunflecks (Figures 31, 33, 35, 36, 42, 43, 44)(Chazdon and

Pearcy 1991). Shade-tolerant species reach light-saturation between 5-10% full sunlight (Loach 1967, Kaufman 1982), and do not respond to additional light (Landhausser 1997).

If deciduously shaded conifers are not inhibited by shading, shade may provide an advantage for young conifers, as shaded conifers may be able to persist in the understory through indirect facilitation (Pages et al. 1995, Levine 1999). Herbaceous forbs compete with emergent tree seedlings for water and nutrients (Pages et al. 1995). Simultaneously, overstories reduce light available for seedlings and herbaceous forbs, which decreases the herbaceous species competitive ability for water and nutrients and favors shade tolerant emergent seedlings (Cornett et al. 1998, Pages et al. 1995). If the reduction of forb competitive effects through shading exceeds the effect of light lost through shading on tree seedling, then the reduction in forb competition for water or nutrients indirectly facilitates understory trees (Levine 1999).

Response of Photosynthesis and Respiration to Temperature

Increasing temperature is known to increase physiological processes within the tolerable range (Larcher 1969, Ryan 1994, Tanja et al. 2003). Photosynthesis and respiration were influenced by temperature at three levels: across seasons, across canopy coverage, and within stands. First, seasonal change in temperature is likely responsible for the parabolic rise and fall of respiration over the year (Neilson et al. 1972). Warm temperature initiates photosynthesis and transpiration in the spring in cold climates when soil temperatures rise above freezing (Jarvis and Linder 2000, Tanja et al. 2003), but inhibits photosynthesis at low temperatures through restriction of enzyme activity and stomatal opening as water cannot be transpired (Neilson et al. 1972, Öquist 1983). If

water is available, higher temperature will support higher photosynthesis via greater energy exchange and increased enzyme activity (Larcher 1969).

Second, open stands of Douglas-fir and subalpine fir consistently had two-degree higher temperatures than closed stands. Higher temperatures could have contributed to the slightly higher photosynthetic rates of trees in open stands (Larcher 1969). While, leafless aspen overstories provide decrease temperature even in shoulder seasons, the greatest cooling occurred in the shady summer (Figure 1). The reduction of photosynthesis in junipers in closed stands cannot be attributed to temperature because understory temperatures are not lower. The lack of temperature differences between open and closed stands of juniper may stem from wind mixing the air temperature.

Third, within-stand temperature variability was low in north and south aspects of trees in open and closed stands (Figure 3). Neither photosynthesis nor respiration responded to temperature variation from sunflecks in closed stands (Figures 31, 33, 35, 36, 42, 43, 44).

Response of Photosynthesis and Respiration to Water

Atmospheric water, tree water status and soil moisture were measured due to their expected influence on stomatal aperture and therefore CO_2 exchange (Turner et al. 1985). Despite soil waters' absence in the models, its importance is certain (Turner et al. 1985, Schulze 1986). Stand relative humidity was the presumptive factor most influential to photosynthesis and respiration in models (Tables 4, 6).

Three observations show water's influence on photosynthesis: 1) The large peaks punctuating the gently hyperbolic photosynthesis curve correspond to, and are likely due

to wet periods i.e. snowmelt in June in Douglas-fir and subalpine fir sites and afternoon thunderstorms in August in all three sites (Figures 6, 24). Early season photosynthesis is typically higher than late season photosynthesis due largely to water availability (Johnson and Smith 2007). 2) Stand relative humidity influenced photosynthesis in all models. Photosynthesis greatly increased when relative humidity increased (Figures 29-44). Relative humidity may influence stomatal aperture or be a simple correlative to soil water. 3) Photosynthesis decreased when VPD increased, likely for the same reasons as relative humidity (Figures 34, 35, 41-44). Inclusion of both VPD and relative humidity in the models suggests that relative humidity may be a surrogate for some unidentified factor, such as soil water (Oren et al.1998), as VPD is generally considered more relevant to photosynthesis because it influences the rate that water is drawn through the tree (Schulze et al. 1977b, Turner et al. 1985).

Water stress measurements, soil moisture blocks, and the time covariate in the models help quantify availability of soil water and the tree's interplay with atmospheric water. The water stress measurements show that water is not limiting for trees in either open or closed juniper stands or closed subalpine fir stands. However, water is limiting in open and closed Douglas-fir stands and open subalpine fir stands (Figure 7).

Soil water was excluded from the models due to a lack of replication in time and space. Soil moisture blocks show rapid draw of soil water at 10 cm and a subsequent recharge from precipitation in all three species in stands of open and closed trees (Figure 7). Precipitation is deposited in stands equally, but in closed stands, there could be greater competition from the deciduous overstory. Soil water at 25 cm and 75 cm takes longer for

the plants to exhaust, but also takes longer to recharge (Figure 7). While there may be more soil water initially available in *Populus* stands due to habitat preference (Horton et al. 2001) or snow retention in the spring (LaMalfa and Ryle 2008), the relatively high competition for water may decrease inherent water availability in closed stands. This may give trees not in competition for water an advantage (Bréda et al. 1994).

Photosynthesis is reduced during the day when the deciduous overstory and both the herbaceous and coniferous understories compete for soil water (Horton et al. 2001, Leffler et al. 2002). Photosynthesis was higher in the morning than the afternoon in open and closed juniper stands and Douglas-fir closed stands (Table 12). Douglas-fir showed a typical midday slump attributed to a drop in water potential (Hodges 1967), but juniper's response decreased steadily throughout the day in closed stands but not open stands. This suggests that junipers might be somewhat inhibited by water competition (Beadle et al. 1985). Factors that change over time of day in open but not closed stands indicate importance of an unmeasured factor that is competed for. The changes in temperature, relative humidity, and light throughout the day did contribute to the decline of photosynthesis in the afternoon.

Tolerance

Examination of conifer performance under deciduous canopies shows that there is high tolerance to the low resource availability, which is required by late successional conifers in order to replace early seral deciduous trees. Slow growing late successional trees dominate their environmental types unless disturbance excludes them (Bazzaz 1979). After disturbance, seral species occupy the site in the period between disturbance

and late successional dominance. Early seral species growth until viable seed is available must be rapid to provide escape through space via dispersal or through time via a seedbank (Bazzaz 1979). But that rapid growth is coupled with an inability to occupy the site in the long-term, e.g. inability to compete for water or nutrients, invest in alleleo-chemics, resist invasion, disease or to establish in their own shade or litter (Parrish and Bazzaz 1982). The inability of early seral species to occupy space for a long period of time provides opportunities for invasion by the slow growing, tolerant conifers.

That juniper, Douglas-fir and subalpine fir grow under *Populus* demonstrates tolerance. That they are only slightly inhibited by the *Populus* canopy demonstrates that they are quite tolerant of low resource availability. The low resource availability may have been due to interference (temperature and light), and competition (water and unstudied nutrients). Slight inhibition of conifer performance was shown in two ways. Firstly, diameter growth, net photosynthesis, and gross photosynthesis rates were slightly lower in understory conifers than in unshaded conifers. Secondly, conifers growing under the *Populus* canopy were not released when the overstory became noncompetitive i.e. during the spring and autumn leafless seasons. That photosynthetic values were parallel and proportionately the same across seasons for trees in open and closed stands of all three species (Figure 24), implies that resources significant to conifer growth were not absent in closed stands, but available in slightly lesser quantities.

In the absence of disturbance, conifer persistence in the understory could lead to their eventual dominance in the overstory as *Populus* senesces, if it is either overtopped, or fails to reproduce (Connell and Slatyer 1977). The change in dominant overstory will

occur either passively, if *Populus* senesces in the absence competition from the understory, or actively, if understory conifers overtop *Populus* and compete for light, water or nutrients (Picket et al. 1987).

Applications

Successful management of vegetation comes from the manipulation of vegetation using natural dynamics (Luken 1990). Failure to observe natural dynamics within a system can thwart the success of a land-manager (Luken 1990). Empirical measurements of physiological responses to different environmental conditions contribute to the understanding of succession and vegetation dynamics (Bazzaz 1979), which influence mixed forest management, restoration (Karel et al. 2001, Parker 1997, Young et al. 2005) and modeling vegetation response to environmental change (Bachelet et al. 2000, Sykes and Prentice 1996). The implications of the study are that managers of mixed evergreen-deciduous forests must either promote early seral species or take a laissez-faire approach, as suppression of conifers in these systems appears to be slight. Further, in the context of restoration and modeling climate change, this study shows how conifers can persist in the long-term under a deciduous canopy. While deciduous trees are desirable as they might trap sediment, water, or nutrients (Leucher and Rode 1999), restoration plantings may include conifers for the long-term maintenance of the site if the deciduous trees are short-lived. The results of this study have broad geographic and seral relevance, as deciduous to coniferous succession is observed across the cool temperate zone (Henry and Swan 1974, Mueggler 1985, Helm and Collins 1997, Bradshaw and Lindbladh 2004, Schulze et al. 2005, and Chen et al. 2003).

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APPENDICES

APPENDIX A:

TABLES

Table 6. P-values from t-tests of environmental variables between open and closed stands of three species. Highlighted boxes are values significant at $p<0.05$.

	Juniper	Douglas-fir	Subalpine fir
PAR spring	2.2E-15	5.6E-11	4.3E-6
PAR summer	2.2E-16	2.2E-16	2.2E-16
PAR autumn	2.2E-16	3.4E-11	2.6E-13
PAR annual	2.2E-16	2.2E-16	2.2E-16
RH spring	0.76	0.41	0.96
RH summer	0.99	0.18	0.58
RH autumn	2.7E-16	0.24	0.74
RH annual	0.29	0.49	0.56
VPD spring	0.97	0.46	0.09
VPD summer	0.22	6.7E-11	2.5E-5
VPD autumn	0.32	0.04	2.0E-7
VPD annual	0.47	5.5E-8	1.2E-6
Temperature spring	0.99	0.48	0.15
Temperature summer	0.14	2.2E-16	5.5E-7
Temperature autumn	0.25	1.5E-4	5.5E-13
Temperature annual	0.43	2.0E-8	6.5E-7
Soil water 75 cm spring	1	1	1
Soil water 75 cm summer	0.02	0.20	1.3E-3
Soil water 75 cm autumn	2.2E-16	2.2E-16	2.2E-16
Soil water 75 cm annual	2.2E-16	0.50	0.48
Soil water 25 cm spring	1	1	1
Soil water 25 cm summer	0.02	0.001	2.2E-16
Soil water 25 cm autumn	2.2E-16	2.2E-16	0.29
Soil water 25 cm annual	0.03	0.37	2.2E-16
Soil water 10 cm spring	1	1	1
Soil water 10 cm summer	0.95	2.2E-16	2.2E-16
Soil water 10 cm autumn	2.2E-16	2.2E-16	2.9E-10
Soil water 10 cm annual	0.97	2.2E-16	2.2E-16
Df spring	1193	504	241
Df summer	1114	921	414
Df autumn	293	259	89
Df annual	2606	1690	750

Table 7. P-values from t-tests of environmental variables between leaves of open and closed stands of three species. Highlighted boxes are values significant at $p<0.05$.

	Juniper	Douglas-fir	Subalpine fir
PAR spring	1.5E-8	3.5E-16	6.0E-6
PAR summer	2.2E-16	2.2E-16	2.2E-12
PAR autumn	9.9E-10	6.9E-6	6.0E-6
PAR annual	2.2E-16	2.2E-16	2.2E-16
RH spring	0.17	0.18	0.04
RH summer	0.13	2.2E-4	0.05
RH autumn	0.11	0.04	0.80
RH annual	0.02	8.7E-5	0.008
VPD spring	0.99	0.75	0.20
VPD summer	0.27	2.2E-16	5.7E-6
VPD autumn	0.86	0.04	1.3E-6
VPD annual	0.47	1.5E-14	1.5E-6
Temperature spring	0.64	0.66	0.10
Temperature summer	0.03	2.2E-16	1.4E-11
Temperature autumn	0.15	1.4E-3	5.1E-12
Temperature annual	0.17	9.5E-5	9.3E-9
Stomatal aperture spring	0.81	0.80	0.11
Stomatal aperture summer	0.25	0.58	0.08
Stomatal aperture autumn	0.04	0.20	0.09
Stomatal aperture annual	0.50	0.95	0.02
Df spring	1337	513	225
Df summer	1248	818	411
Df autumn	278	222	91
Df annual	2869	1559	733

Table 10. P-values of photosynthesis (Ps), respiration (Resp) and gross photosynthesis (Gross) for integral ratios of the whole season between open and closed stands for three species. Significant pvalues are in **bold**.

Measure	Comparison	Juniper	Douglas-fir	Subalpine fir	All Species
Ps	Spring Ratio O v C	0.65	0.12	0.56	0.38
Ps	Summer Ratio O v C	1	0.39	0.97	0.91
Ps	Fall Ratio O v C	0.34	0.97	0.4	0.52
Ps	Shoulder Ratio O v C	1	0.13	0.95	0.85
Resp	Spring Ratio O v C	0.09	0.88	0.69	0.82
Resp	Summer Ration O v C	0.42	0.56	0.99	1
Resp	Fall Ratio O v C	0.93	0.25	0.57	0.15
Resp	Shoulder Ratio O v C	0.21	0.45	0.97	0.73
Gross	Spring Ratio O v C	0.08	0.47	1	0.35
Gross	Summer Ration O v C	0.57	0.86	1	0.91
Gross	Fall Ratio O v C	**0.004**	**2.2E-16**	1	0.06
Gross	Shoulder Ratio O v C	0.39	0.77	1	1

APPENDIX B:

FIGURES

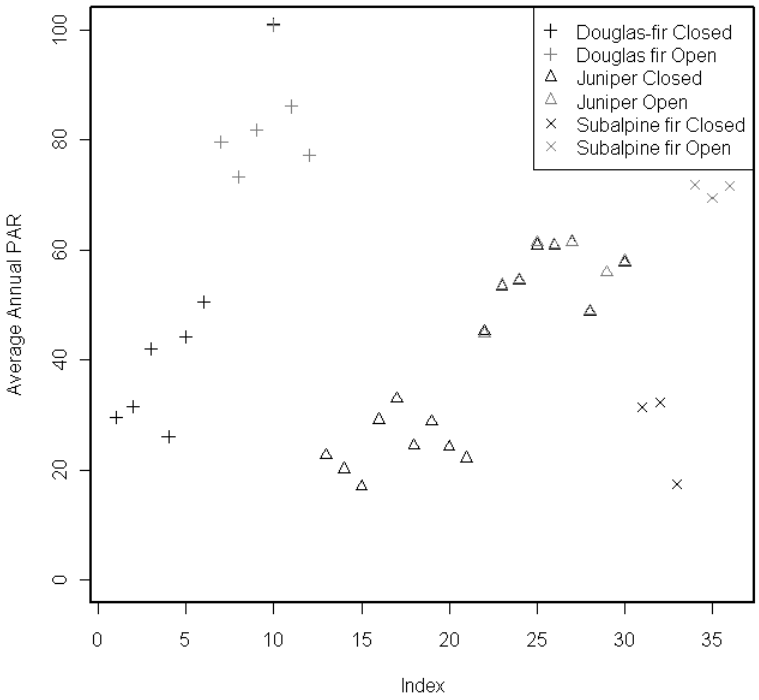

Figure 2. Average annual PAR of open and closed stands of three species.

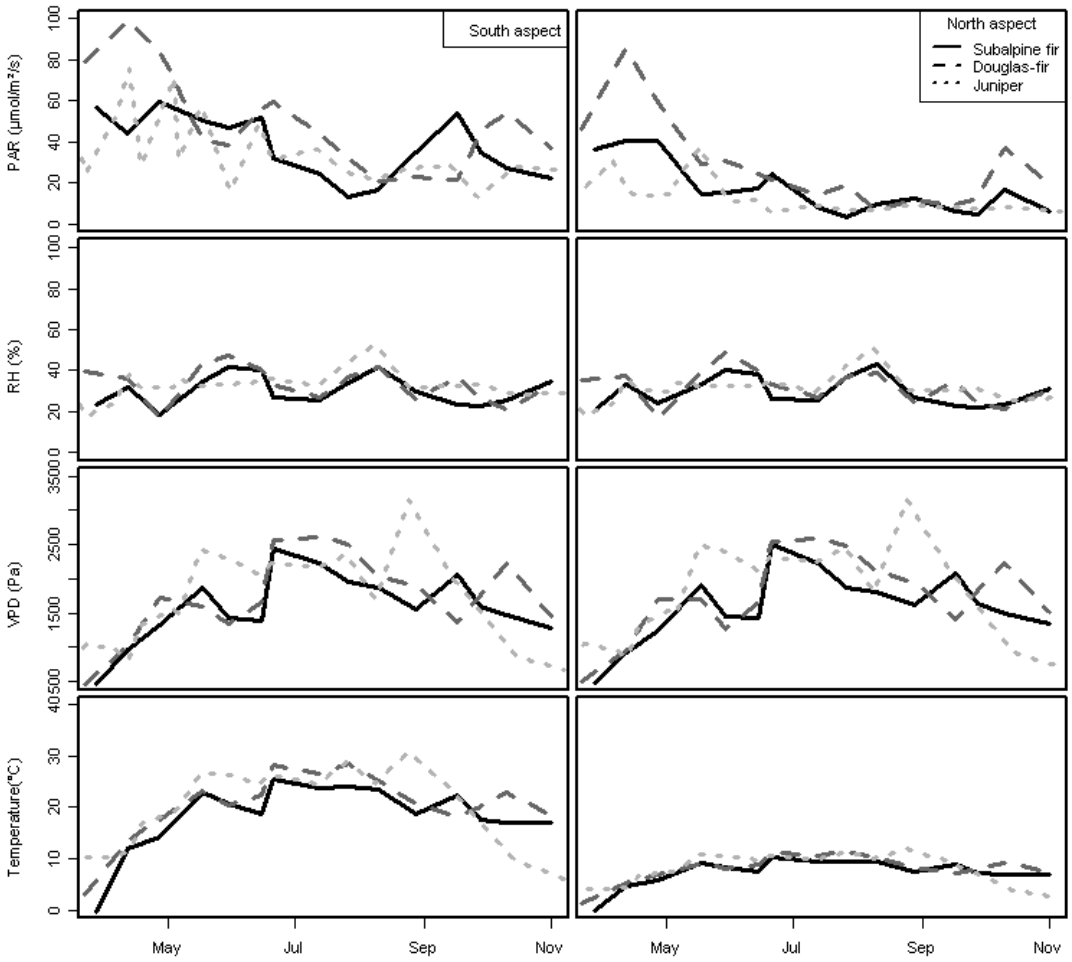

Figure 3. Mean PAR, RH, VPD, and temperature on north and south aspects in closed stands of three species over the year.

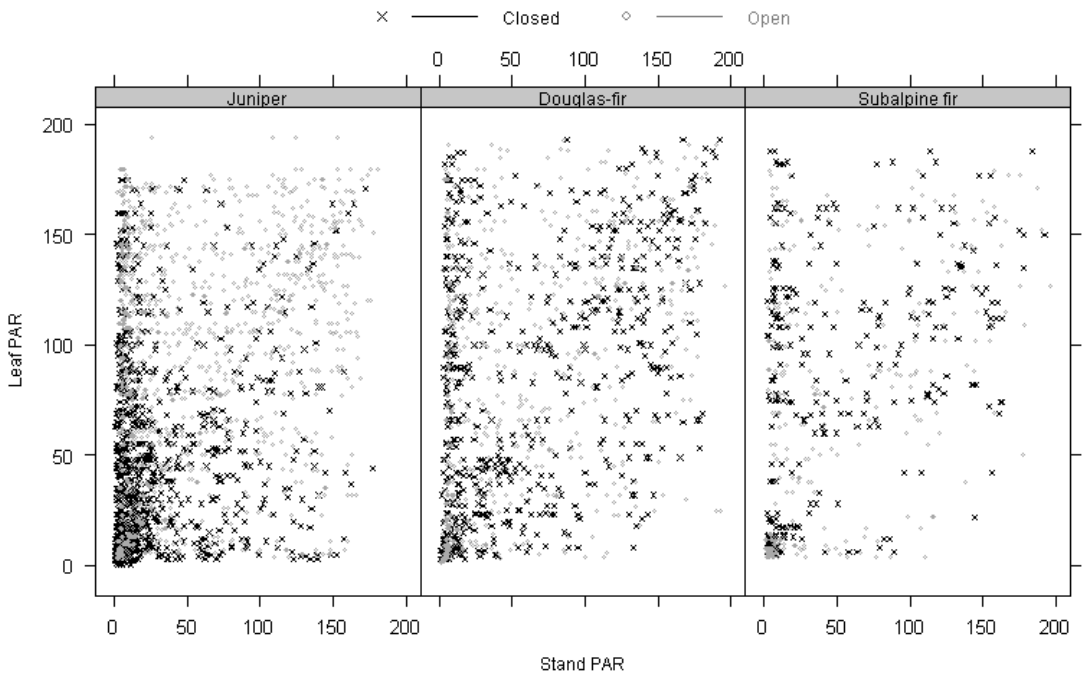

Figure 4. Stand and leaf PAR for three species.

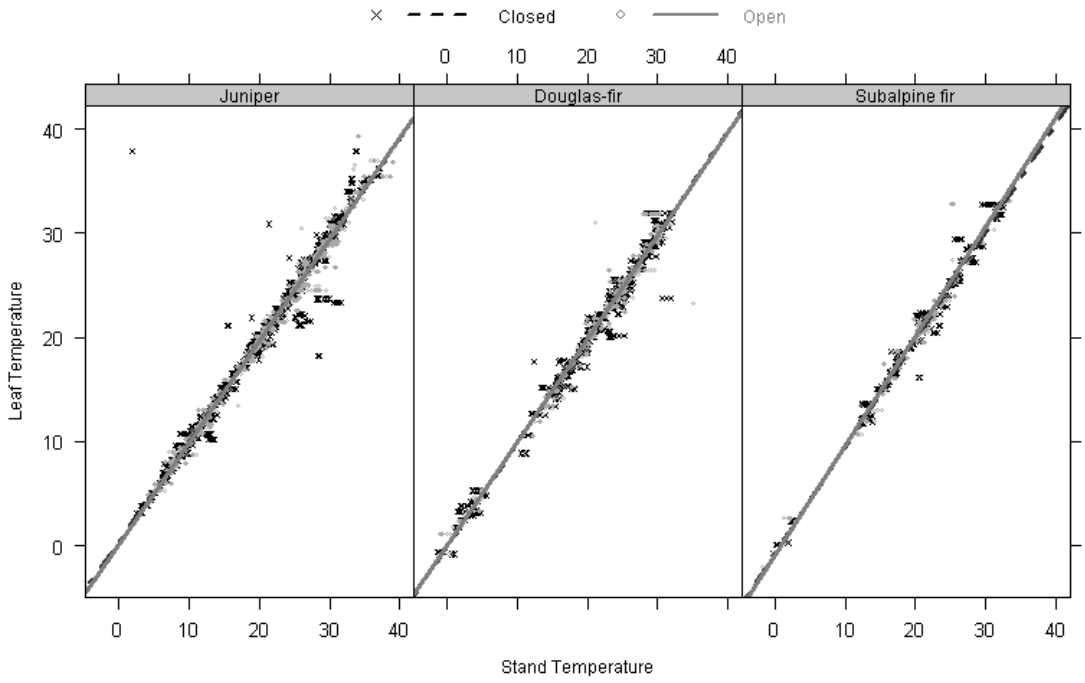

Figure 5. Stand and leaf temperatures for three species.

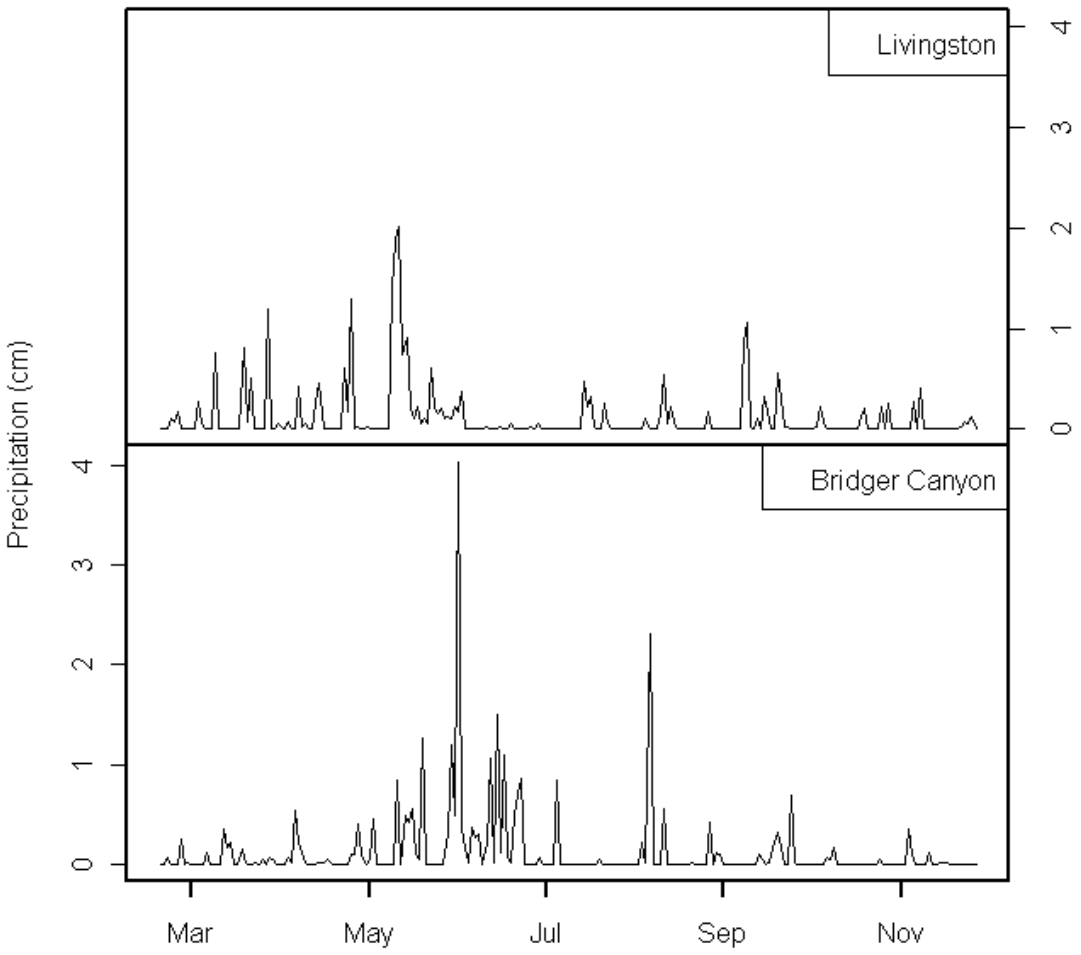

Figure 6. Annual precipitation in Livingston and Bridger Canyon

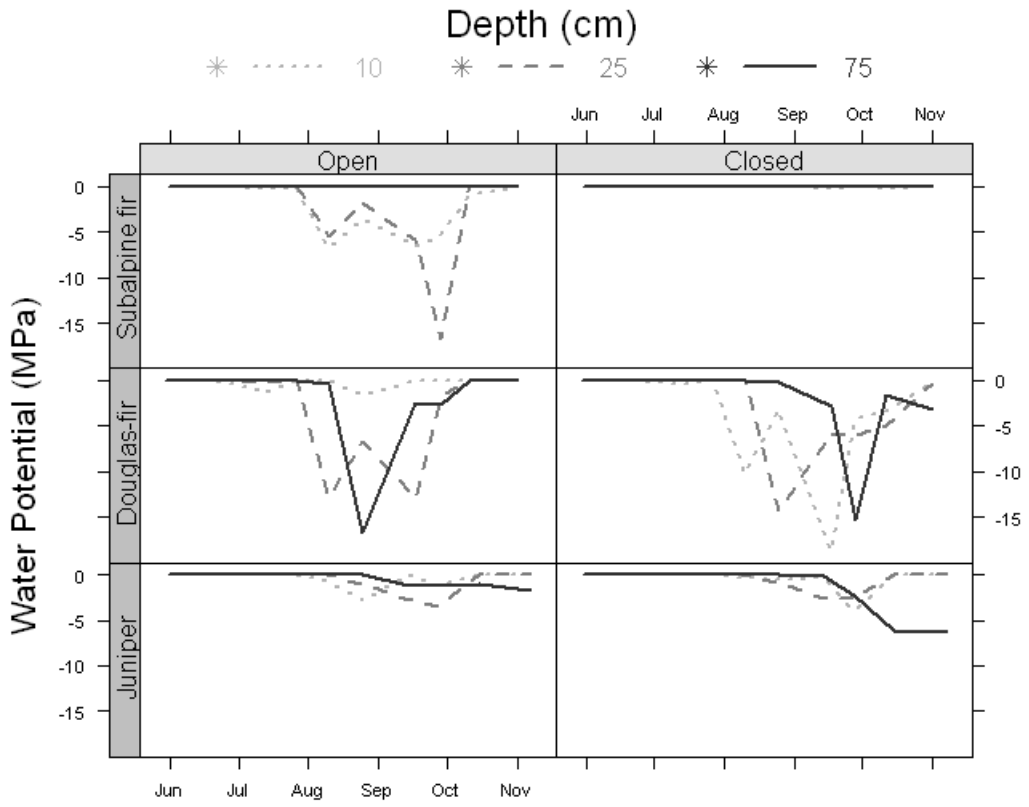

Figure 7. Soil water potential at 10, 25, and 75 cm for three species in open and closed stands.

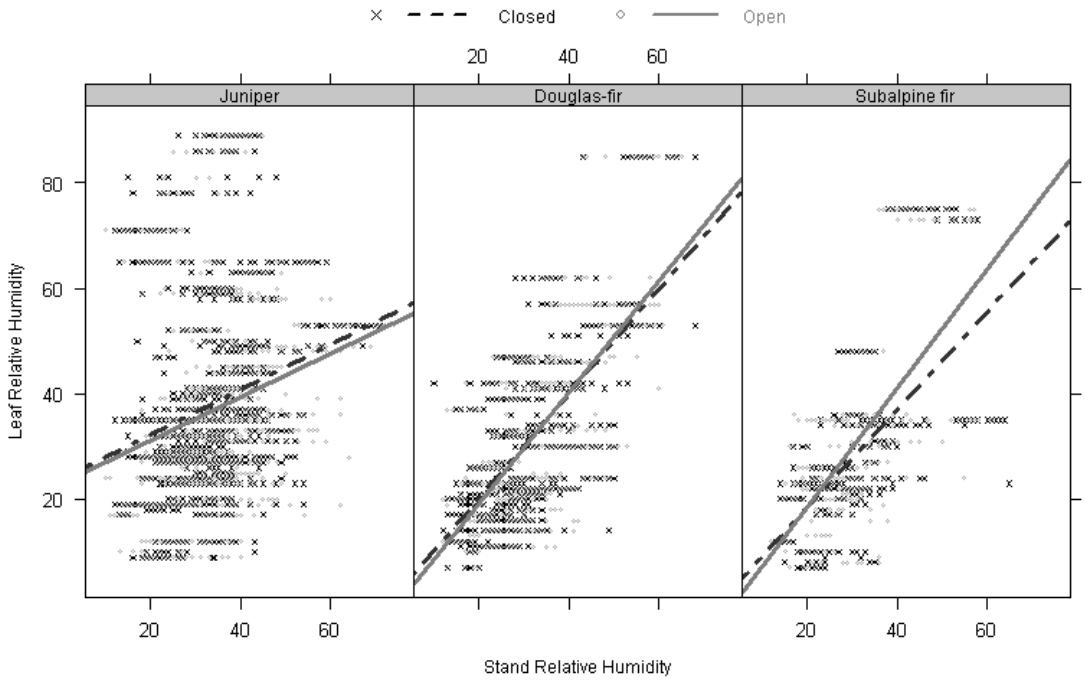

Figure 8. Stand and leaf RH for three species.

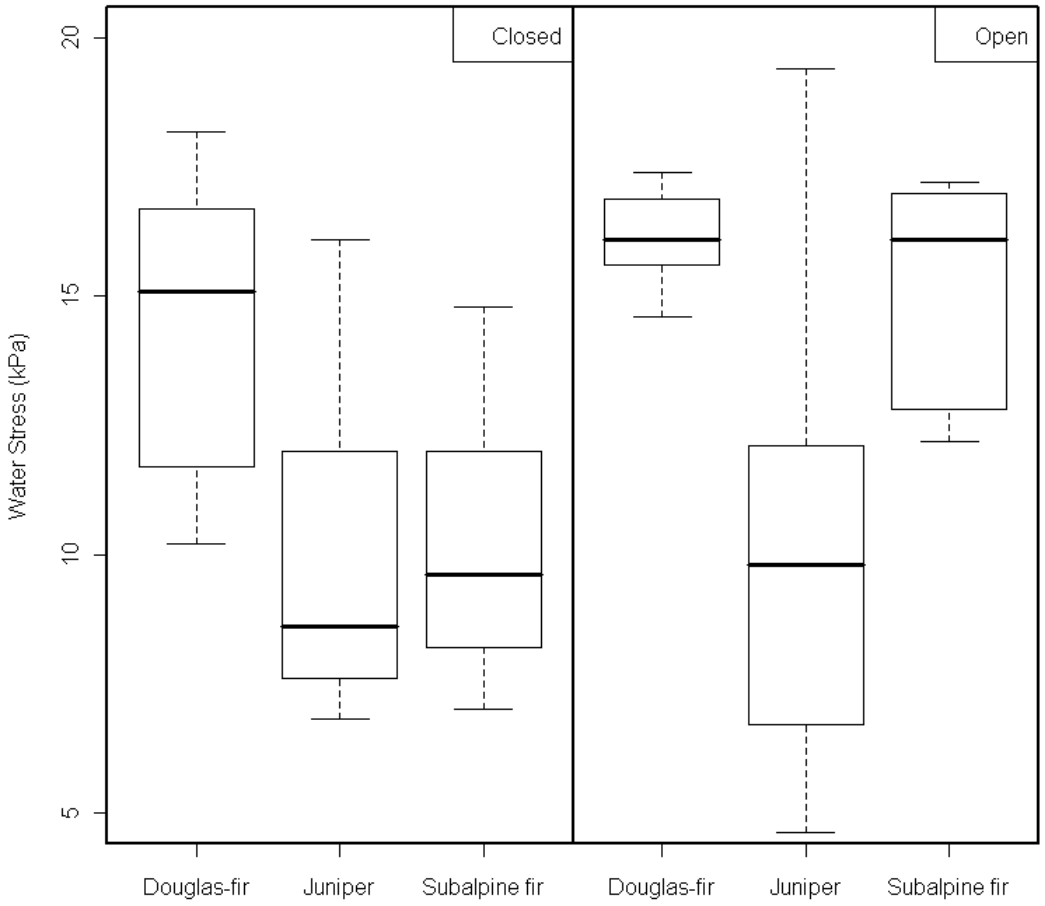

Figure 9. August predawn water potential of three species in open and closed stands.

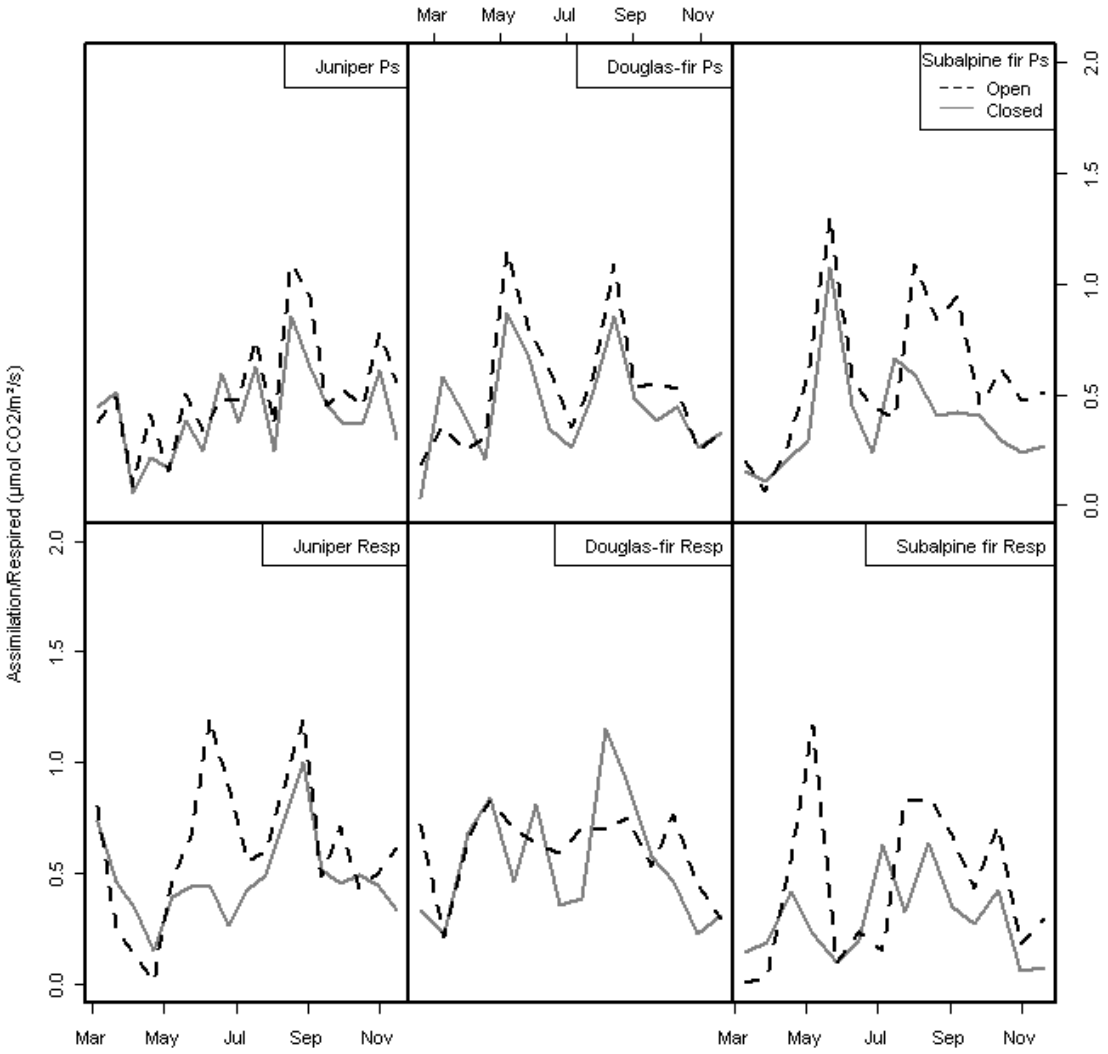

Figure 10. Mean net photosynthesis and dark respiration of open and closed stands of three species.

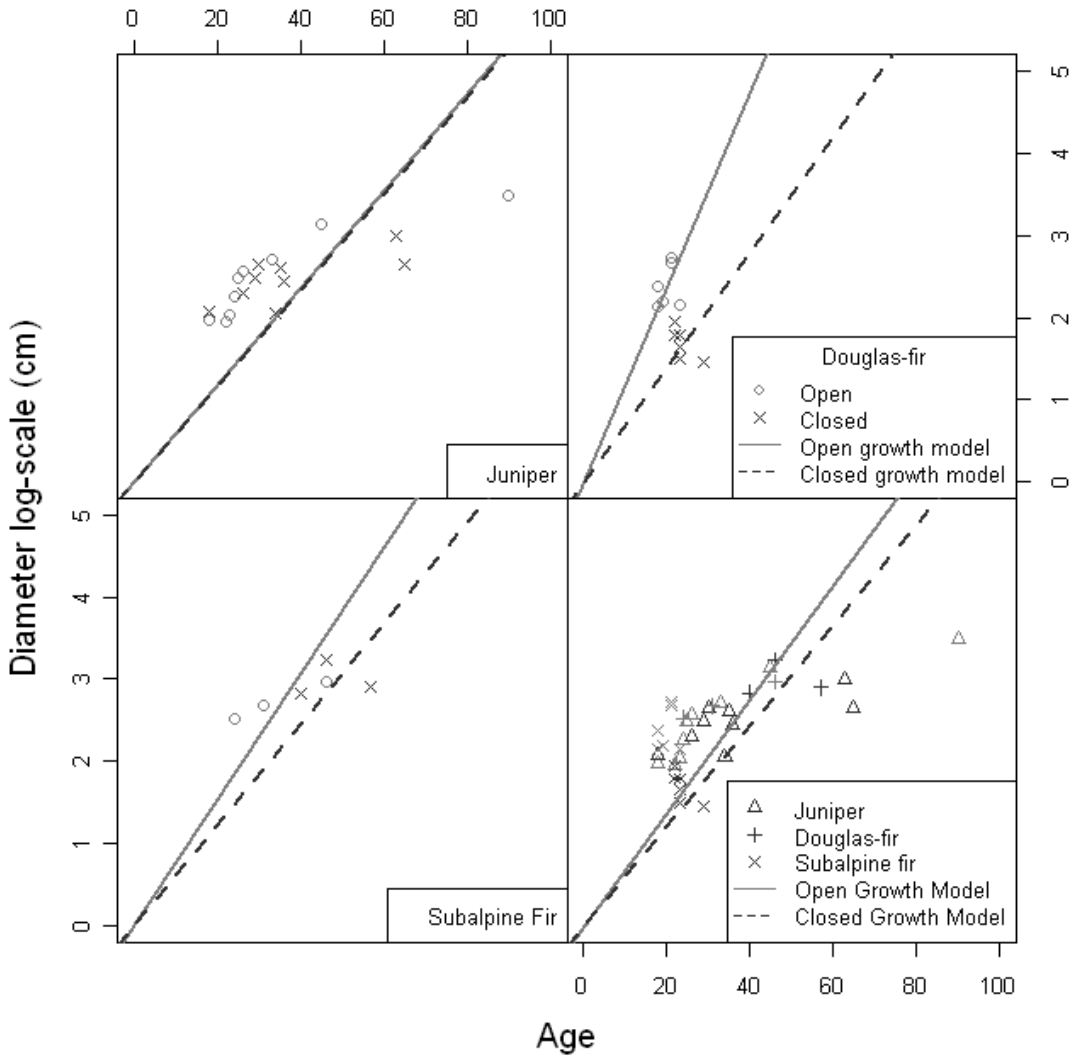

Figure 11. Age and log of diameter for juniper, Douglas-fir, subalpine fir, and all species for open and closed stands.

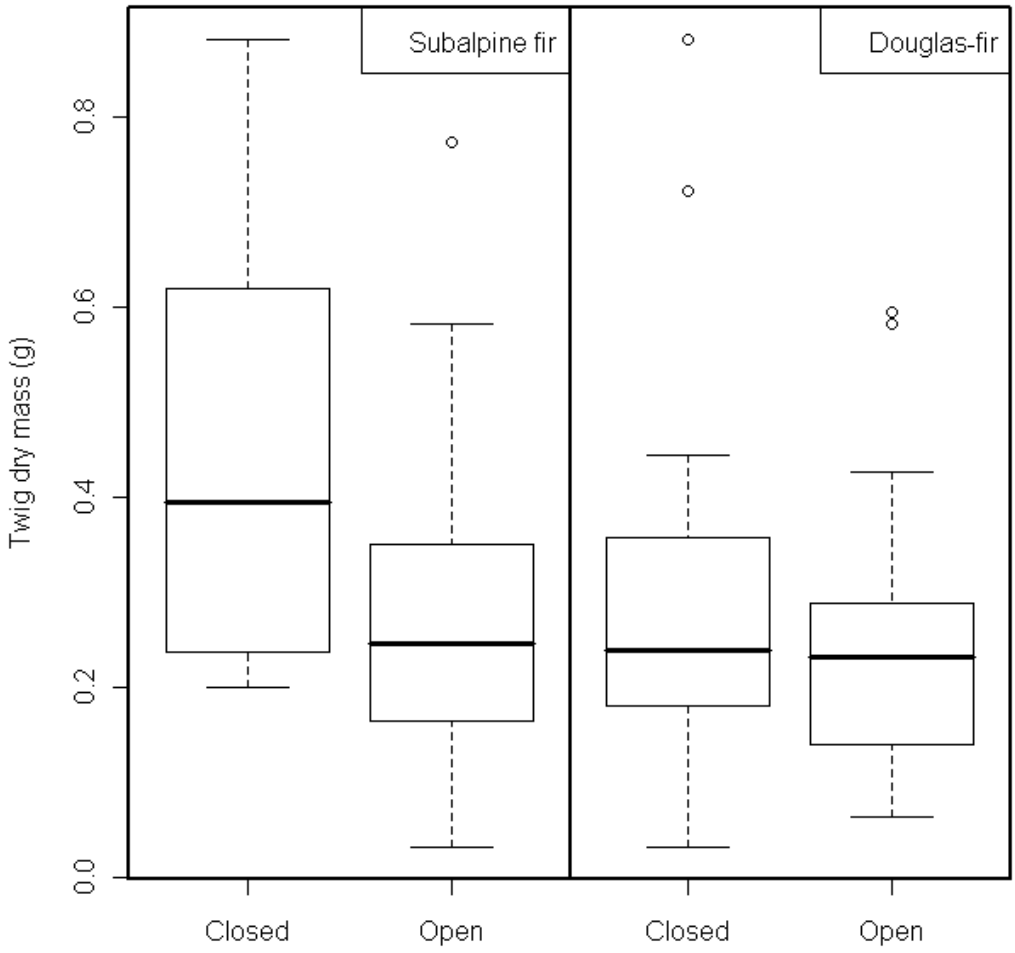

Figure 12. Twig dry biomass of open and closed stands of two species.

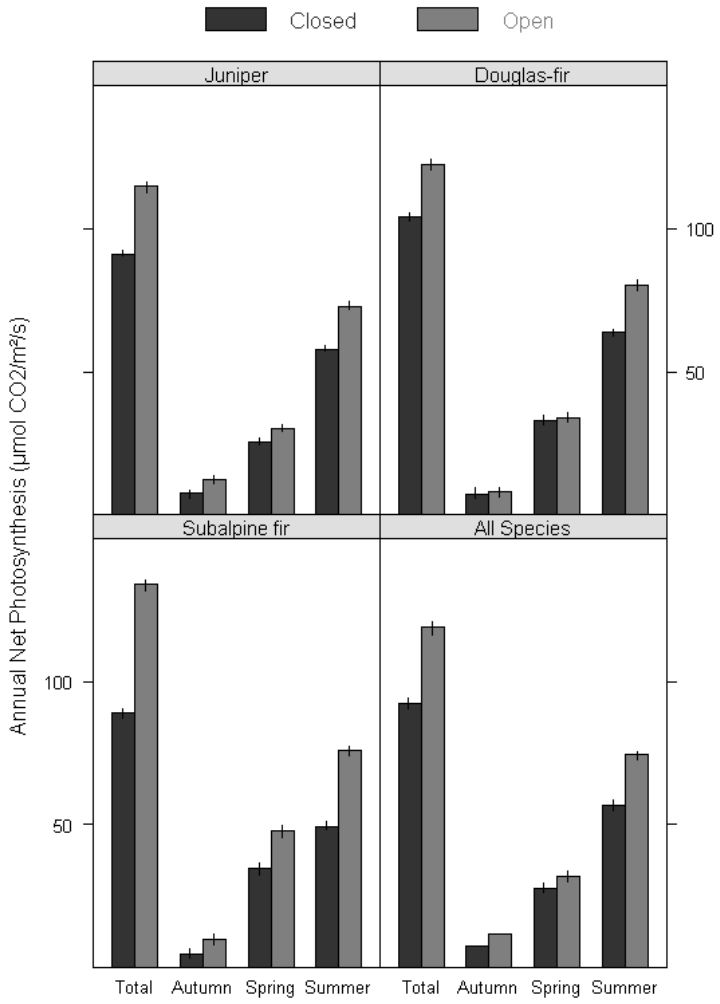

Figure 13. Annual net photosynthesis across seasons of three species and all three species pooled.

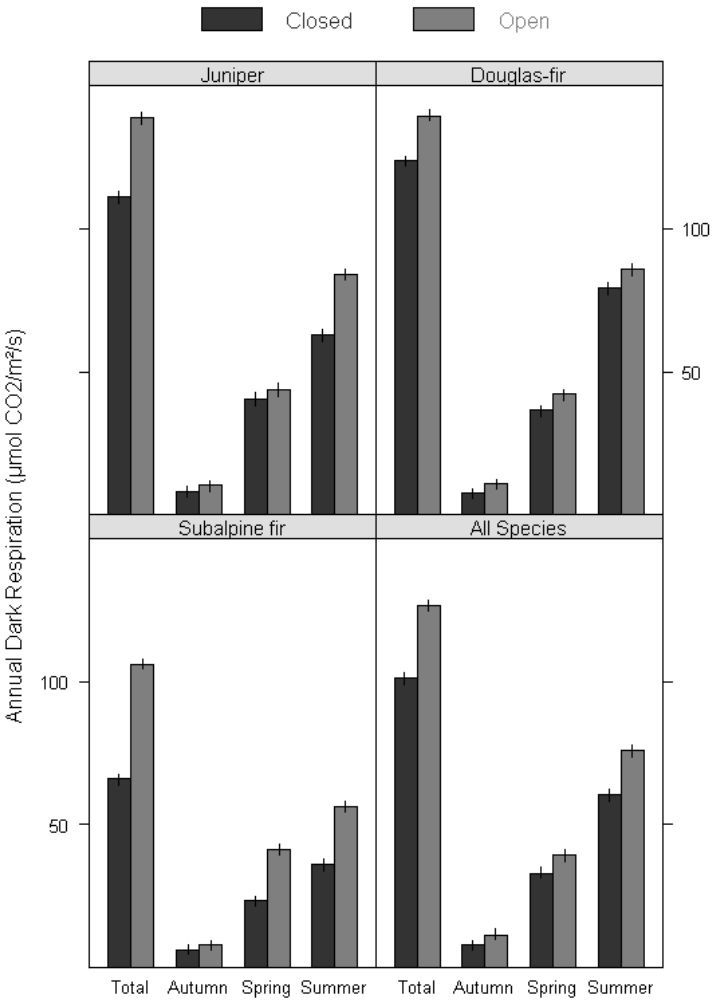

Figure 14. Annual respiration across seasons of three species and all three species pooled.

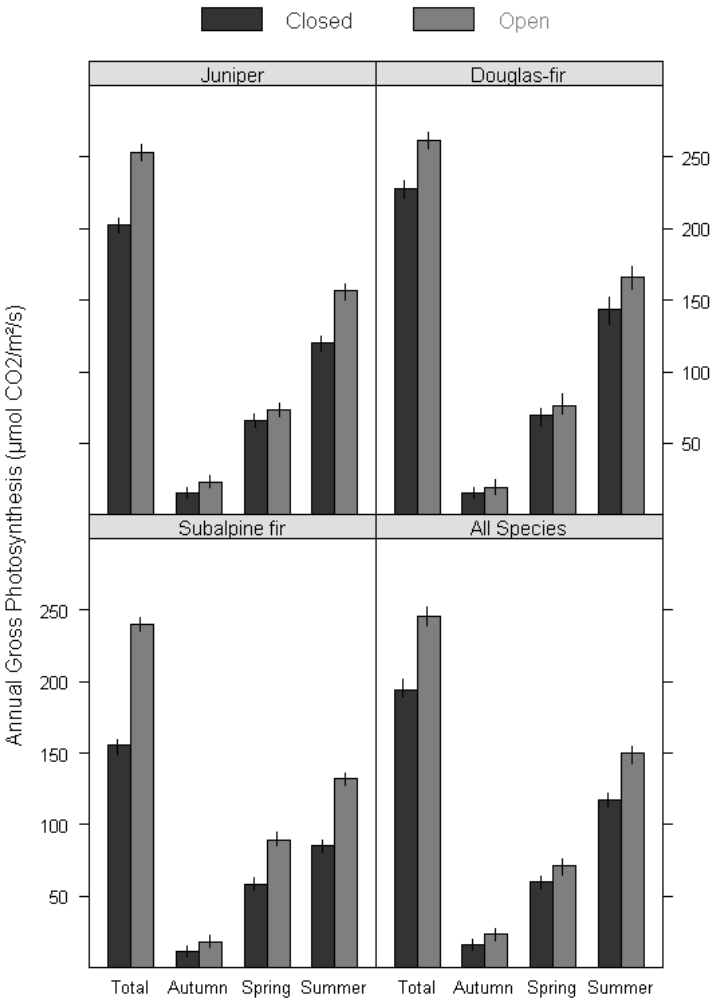

Figure 15. Annual gross photosynthesis across seasons of three species, and all three species pooled. Gross respiration was calculated from combining net photosynthesis and respiration for each season

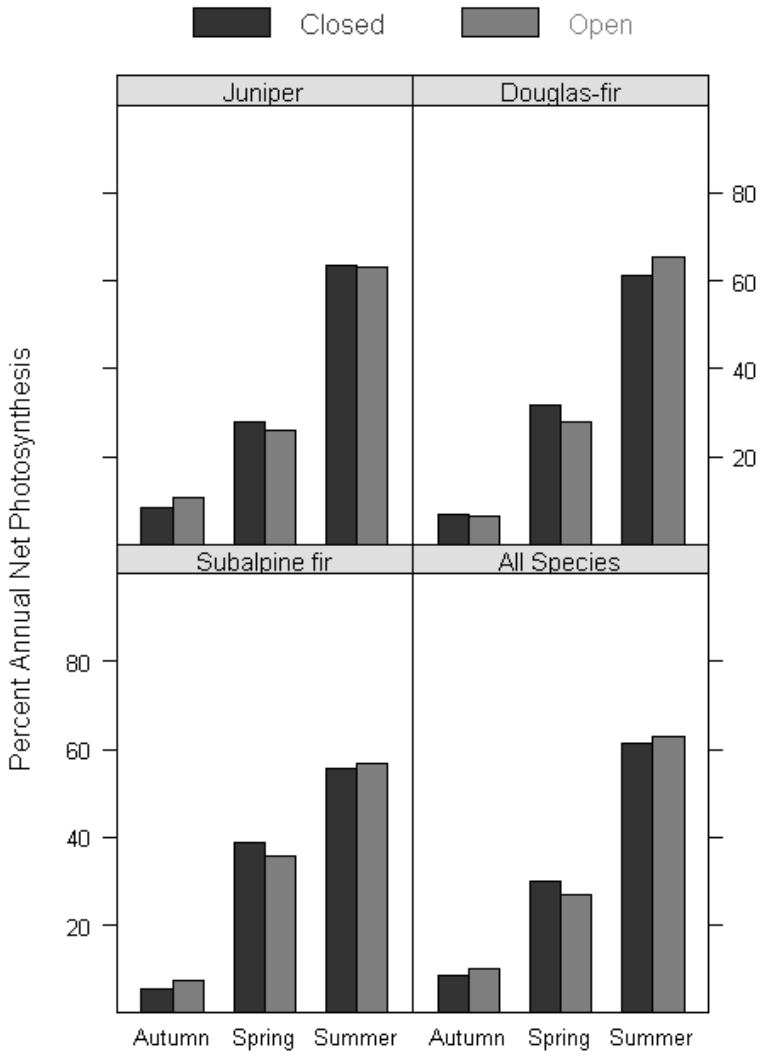

Figure 16. Net photosynthesis as a percent of total annual net photosynthesis of three species, and all three species pooled.

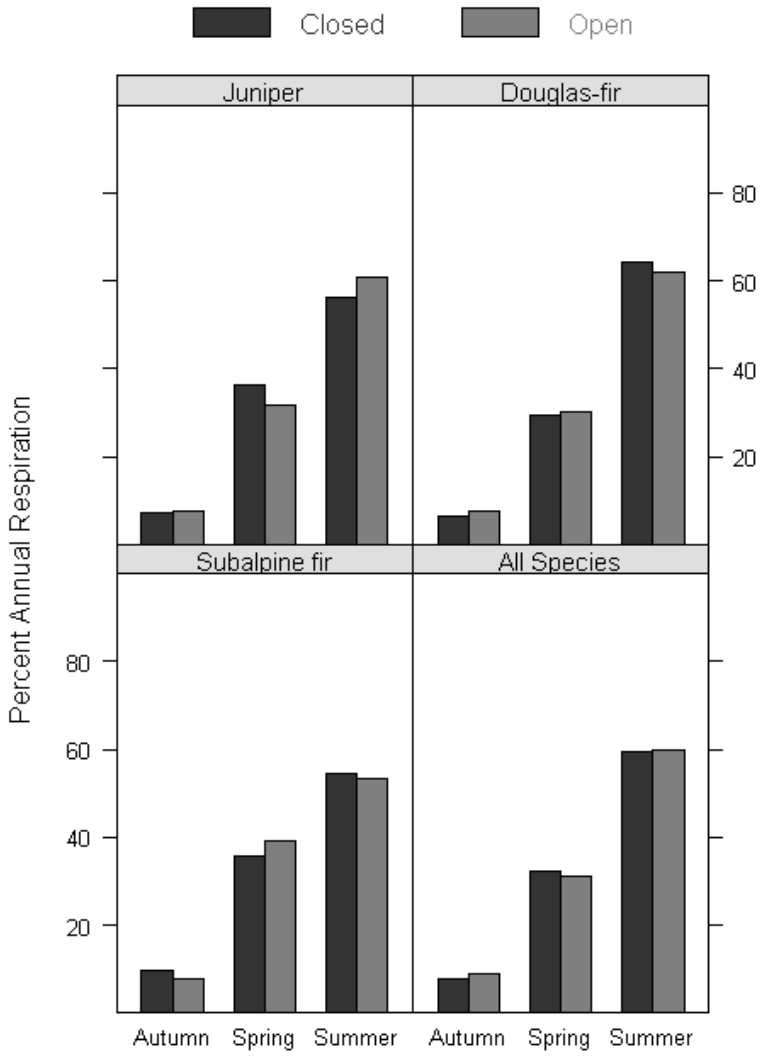

Figure 17. Respiration as a percent of total annual respiration of three species, and all three species pooled.

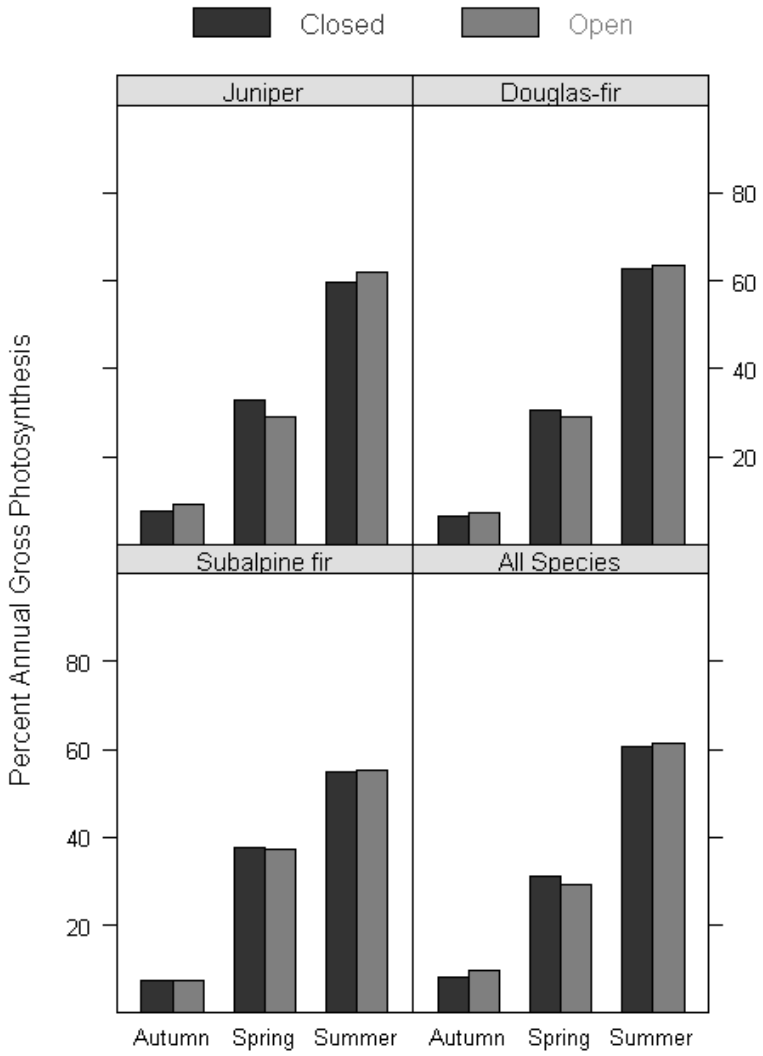

Figure 18. Gross photosynthesis as a percent of total annual gross photosynthesis of three species, and all three species pooled. Gross photosynthesis was calculated from combining net photosynthesis and respiration for each season.

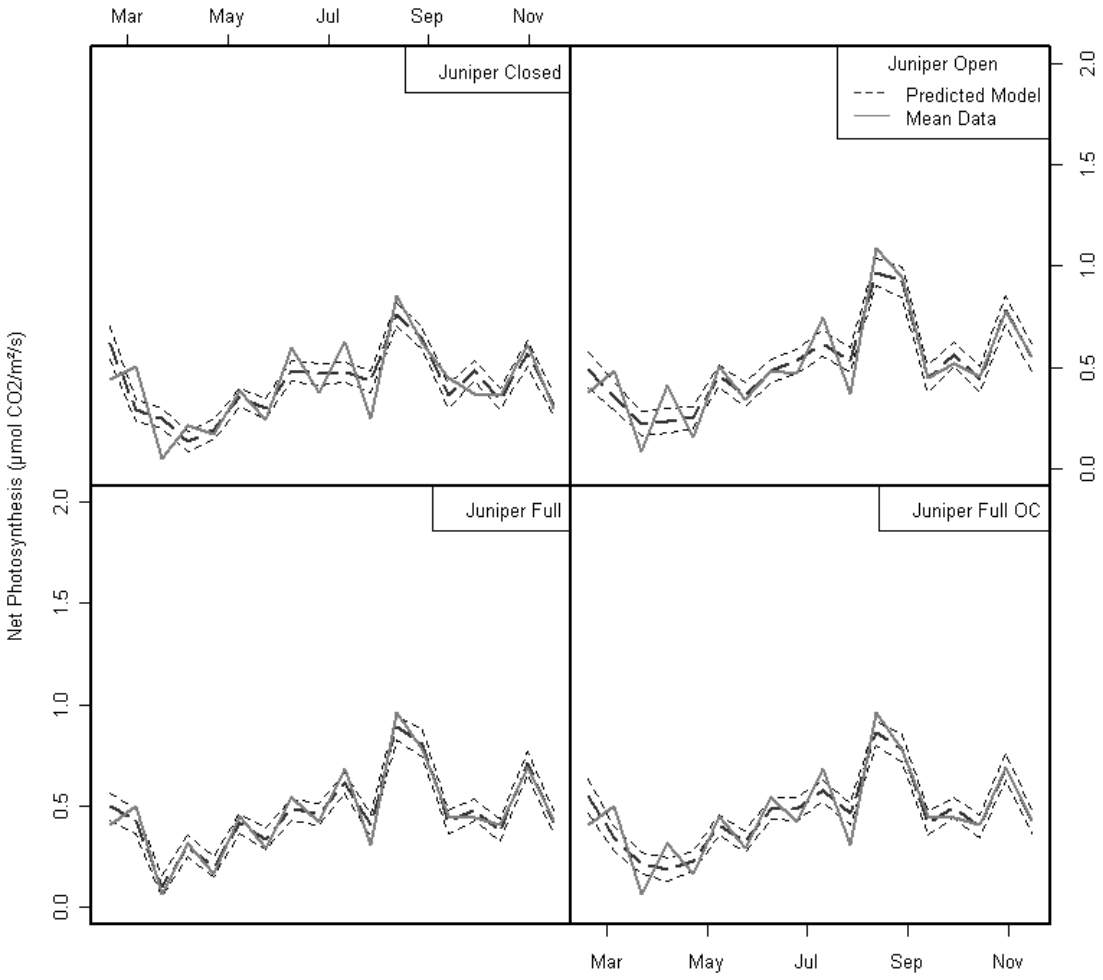

Figure 19. Juniper predicted GAMM photosynthesis a) closed b) open c) full and d) full-oc models compared to mean data over the year

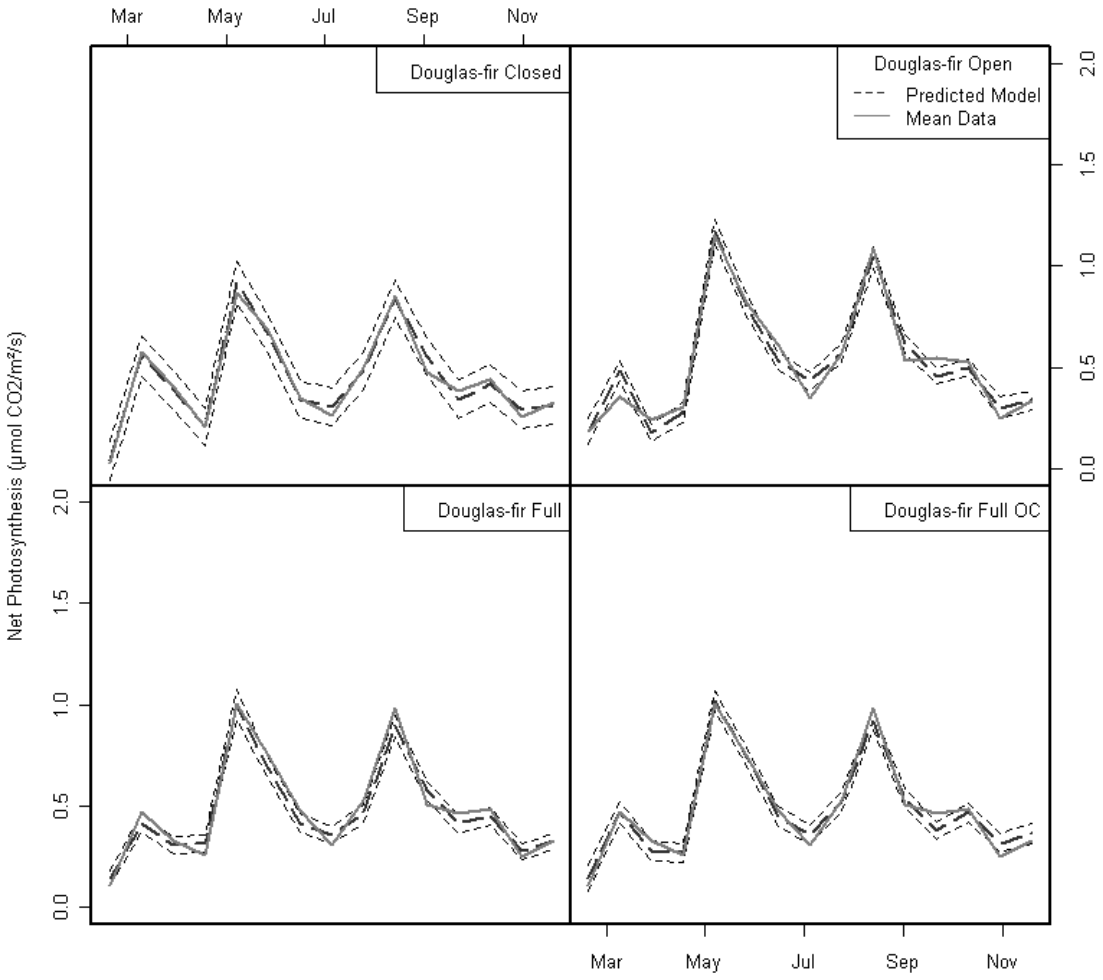

Figure 20. Douglas-fir predicted GAMM photosynthesis a) closed b) open c) full and d) full-oc models compared to mean data over the year

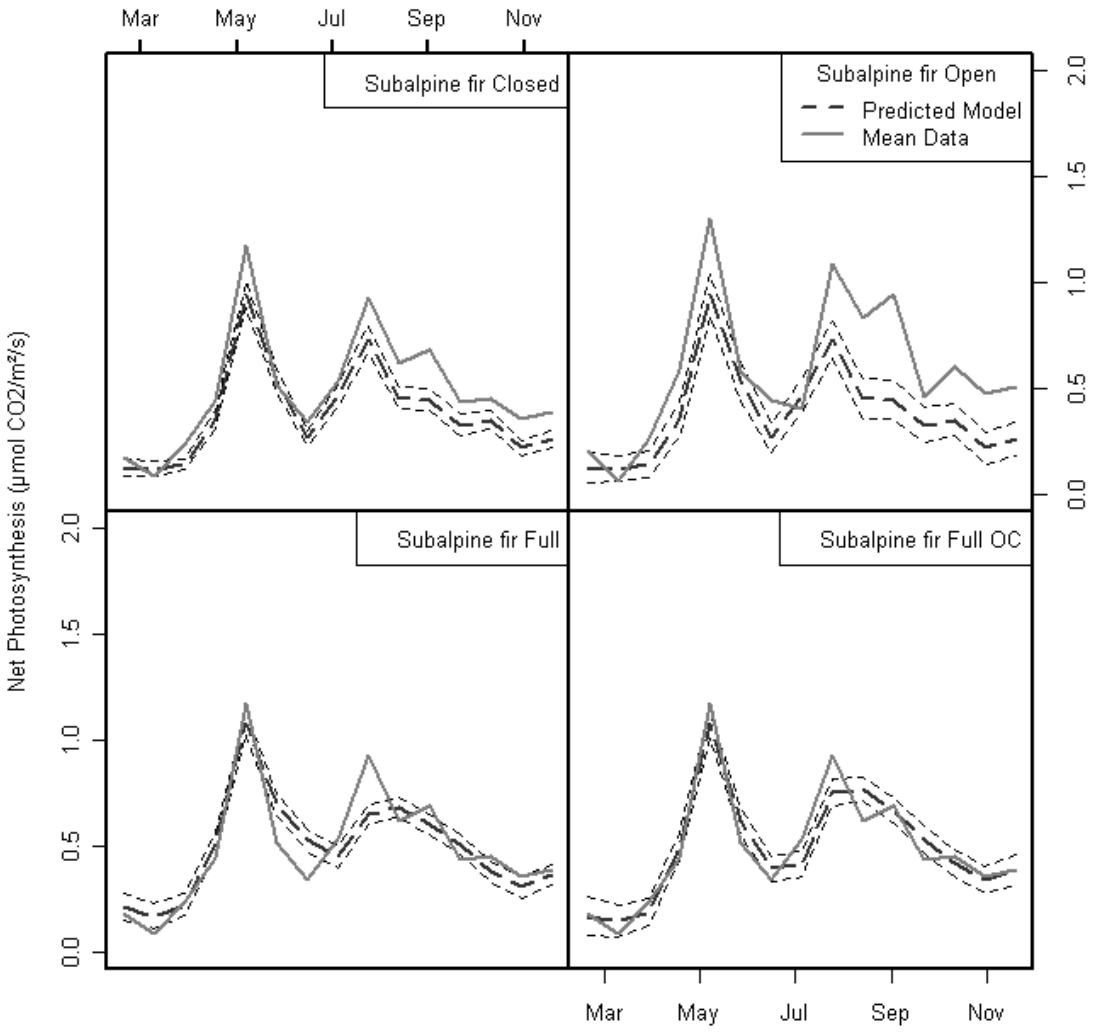

Figure 21. Subalpine fir predicted GAMM photosynthesis a) closed b) open c) full and d) full-oc models compared to mean data over the year

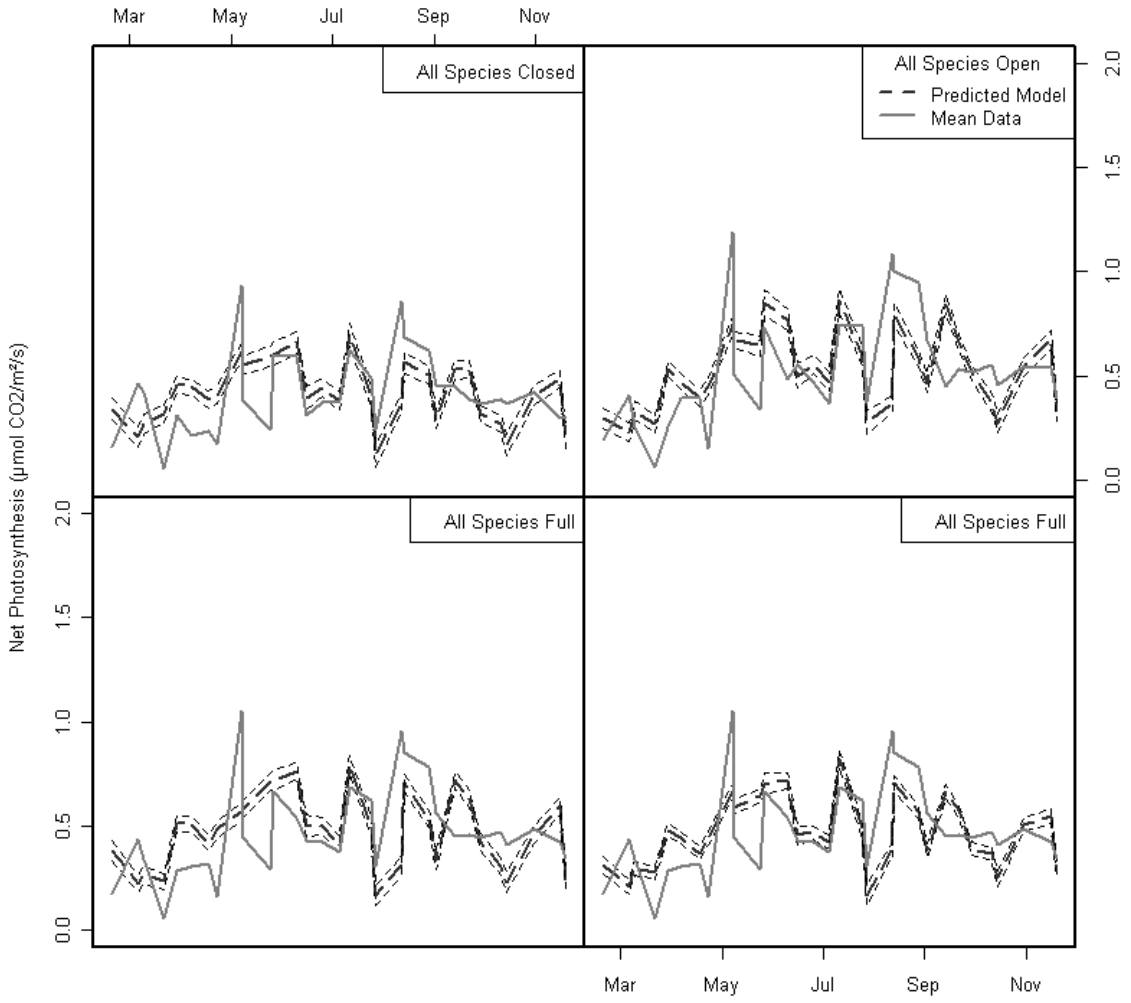

Figure 22. Juniper, Douglas-fir and subalpine fir pooled for full predicted GAMM photosynthesis a) closed b) open c) full and d) full-oc models fit to data

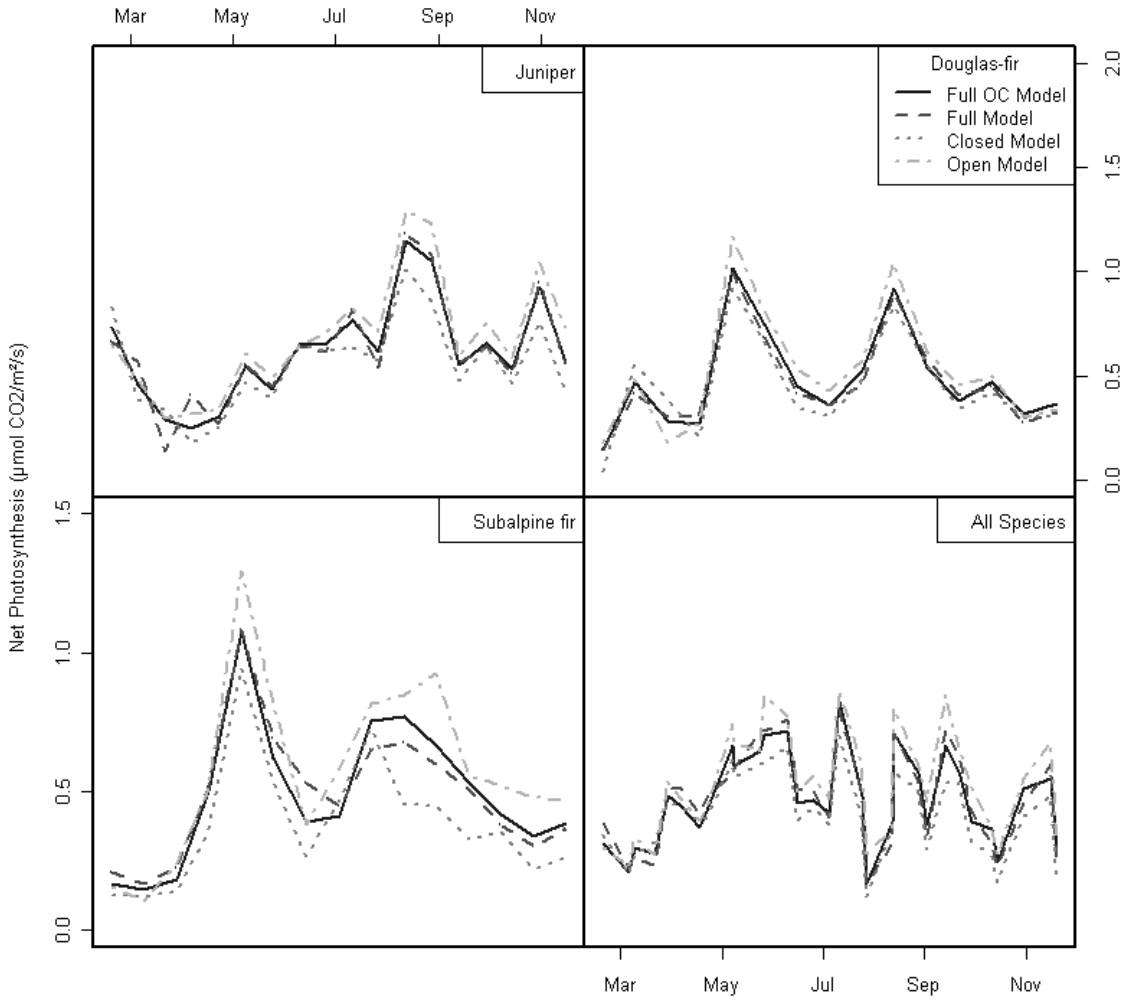

Figure 23. Photosynthesis model comparison of a) juniper b) Douglas-fir c) subalpine fir and d) all species for closed, open, full and full-oc models.

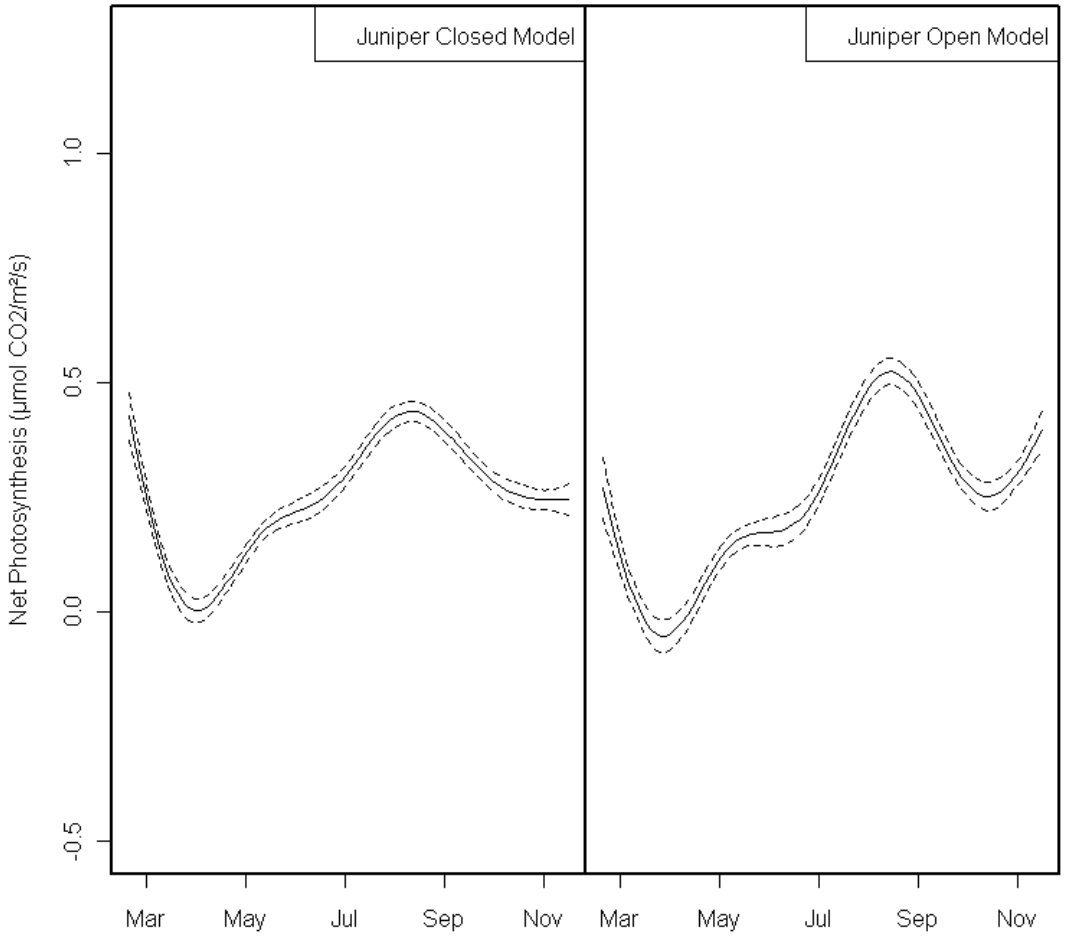

Figure 25. Smoothed photosynthesis curves of closed and open juniper GAMMs.

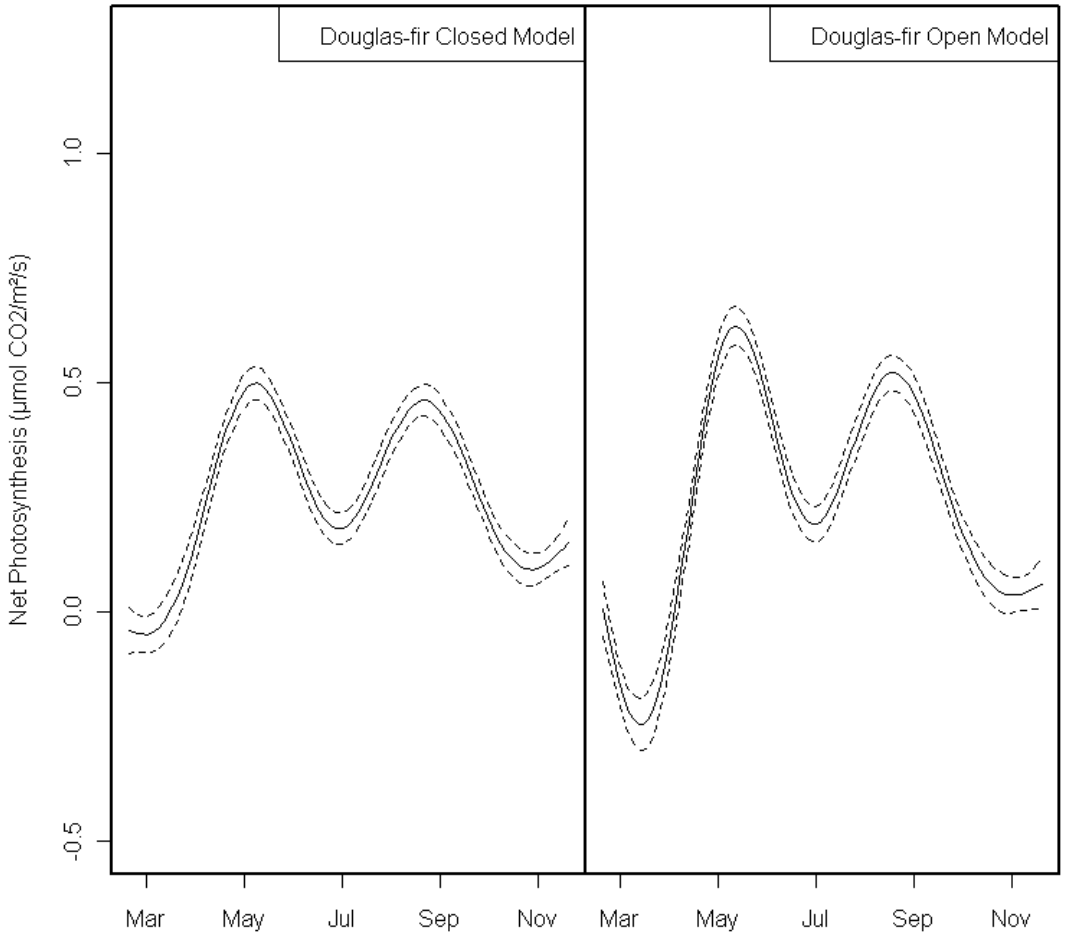

Figure 26. Smoothed photosynthesis curves of closed and open Douglas-fir GAMMs.

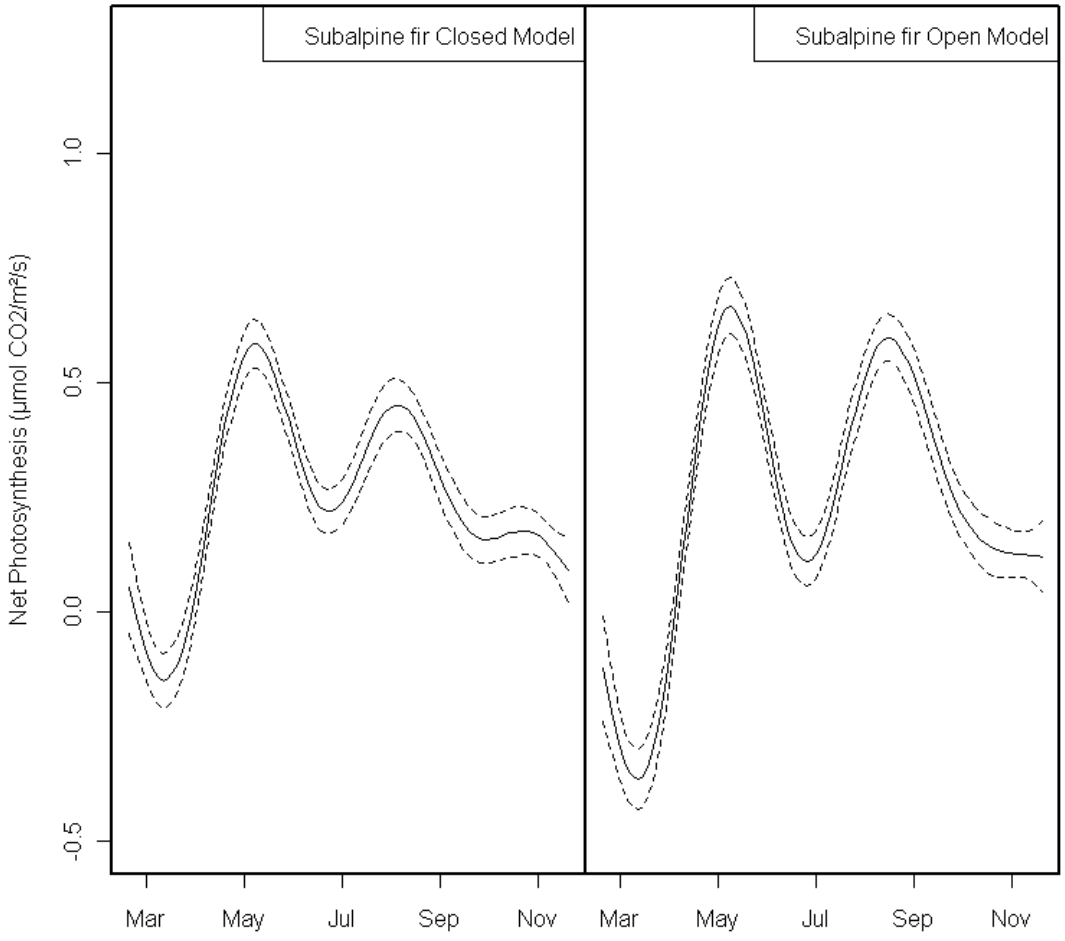

Figure 27. Smoothed photosynthesis curves of closed and open subalpine fir GAMMs.

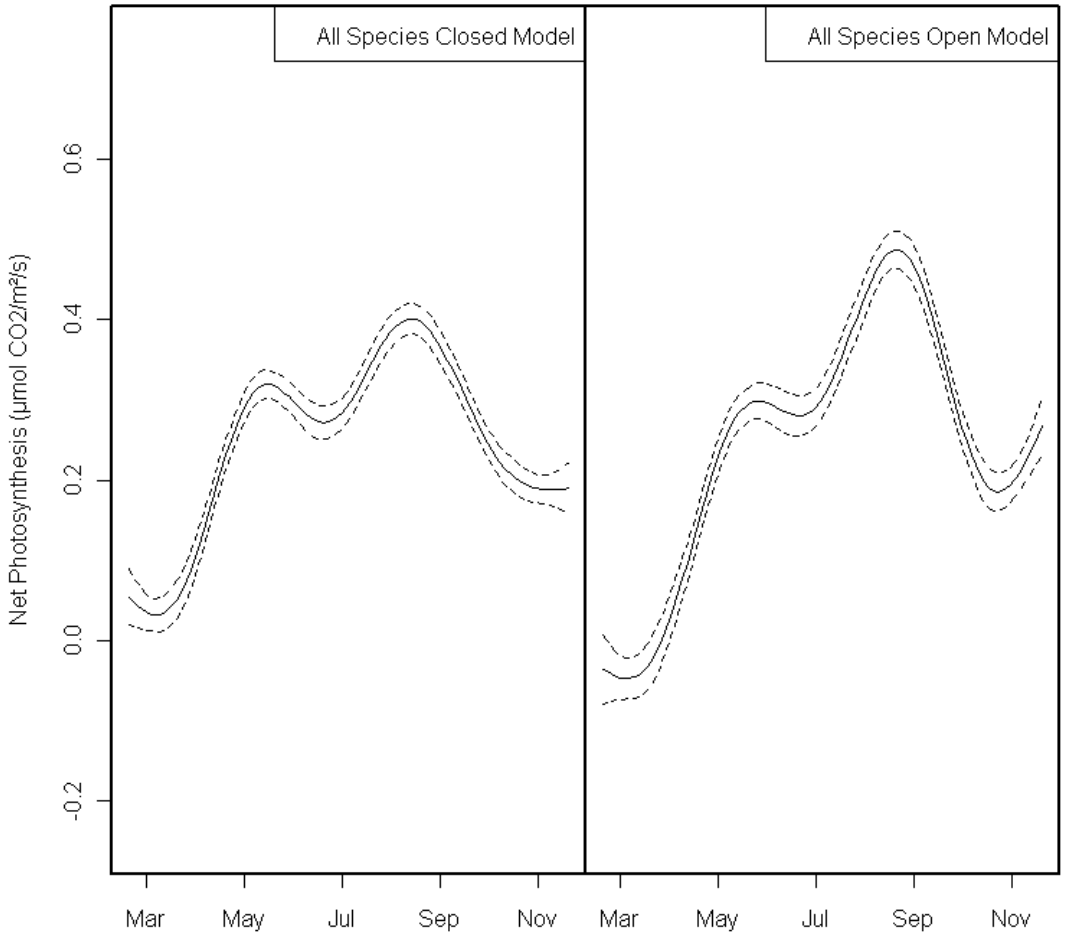

Figure 28. Smoothed photosynthesis curves of closed and open pooled juniper, Douglas-fir and subalpine fir GAMMs.

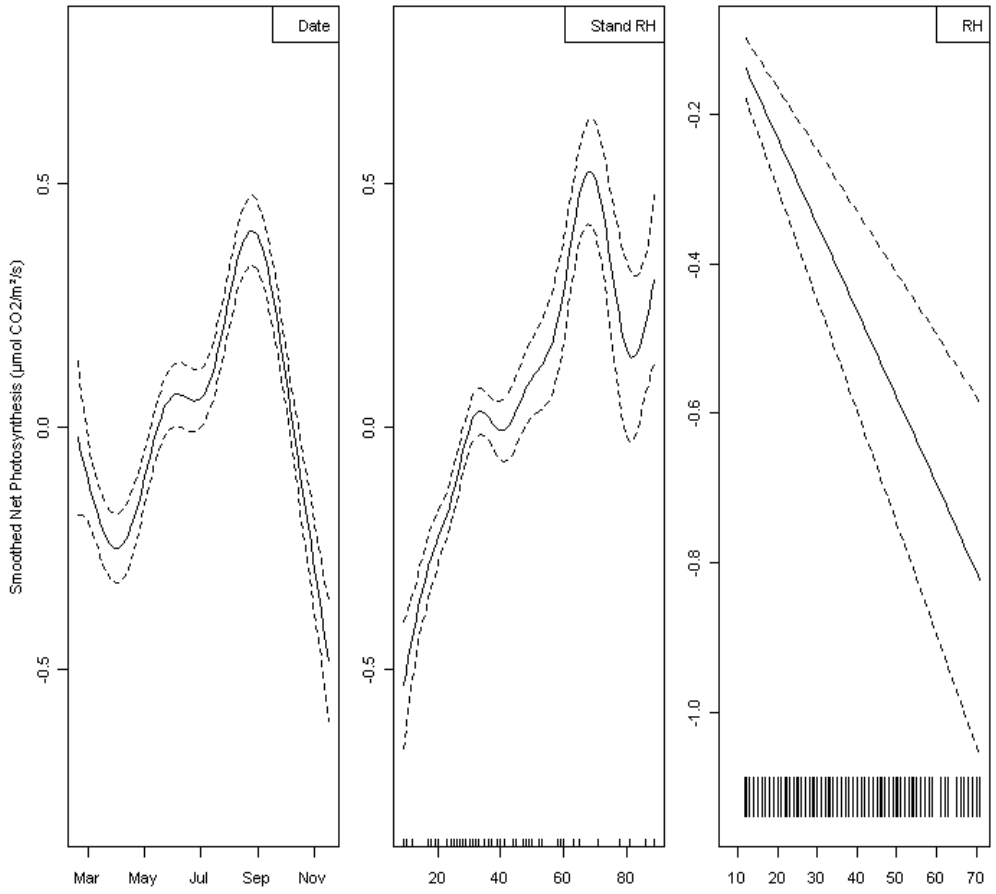

Figure 29. Smoothed photosynthetic response of juniper model of closed stands to a) date b) stand RH c) RH.

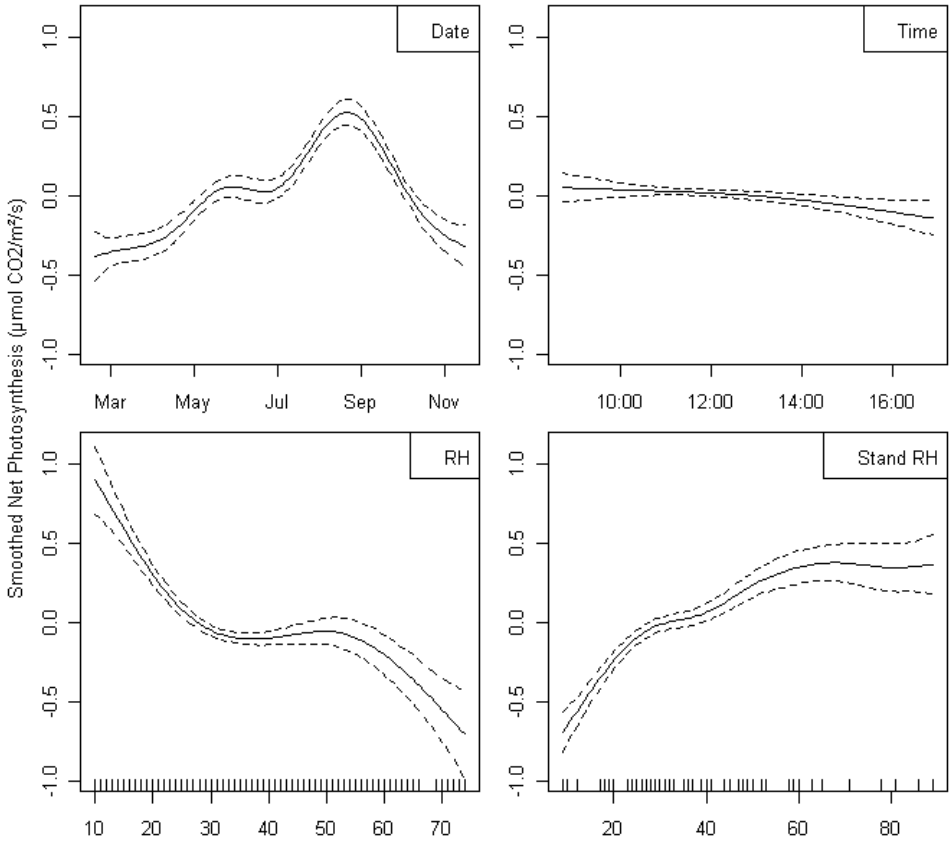

Figure 30. Smoothed photosynthetic response of juniper model of open stands to a) date b) time c) RH d) stand RH.

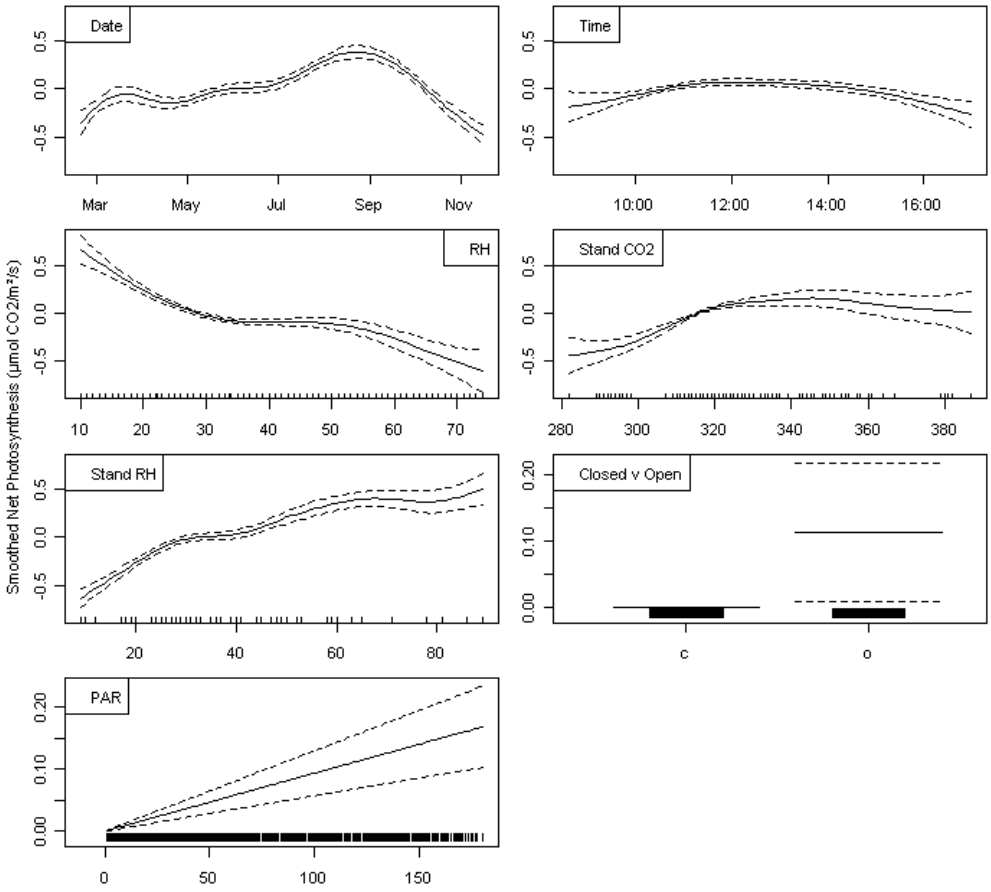

Figure 31. Smoothed photosynthetic response of full juniper model to a) date b) time c) RH d) CO_2 e) stand RH f) open/closed stand g) PAR

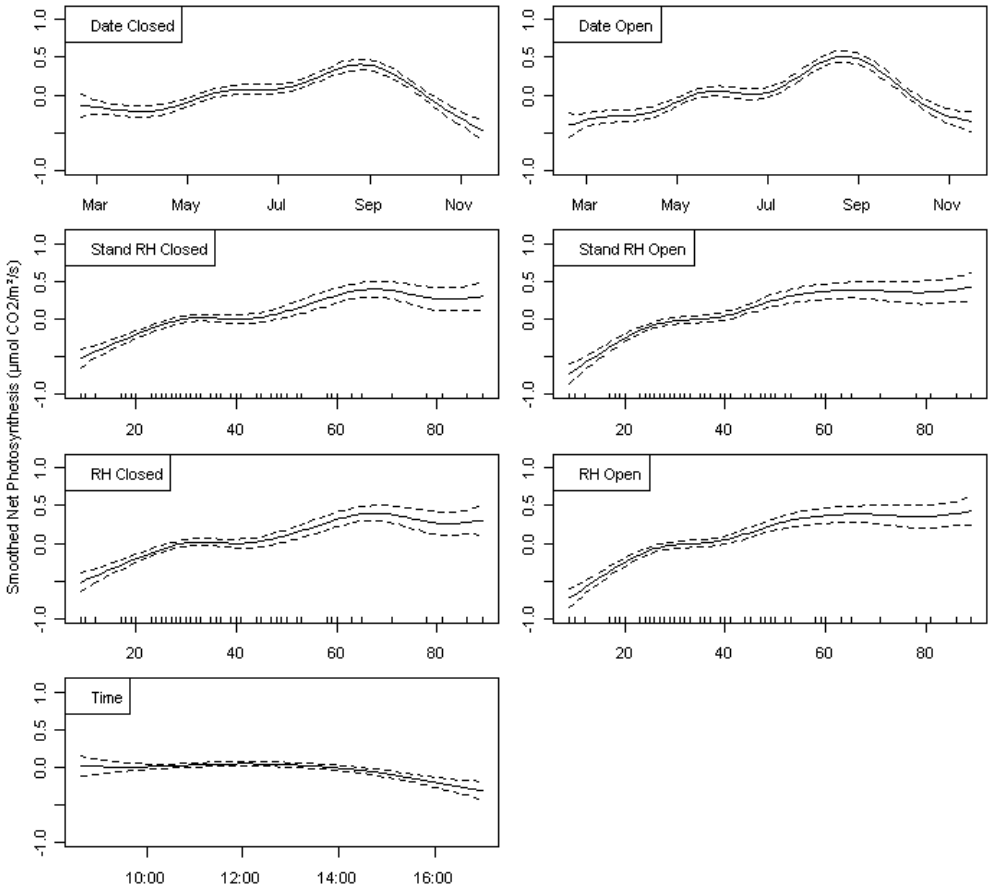

Figure 32. Smoothed photosynthetic response of full-oc juniper model to a) closed tree date b) open tree date c) closed tree stand RH d) open tree stand RH e) closed tree RH f) open tree RH g) time.

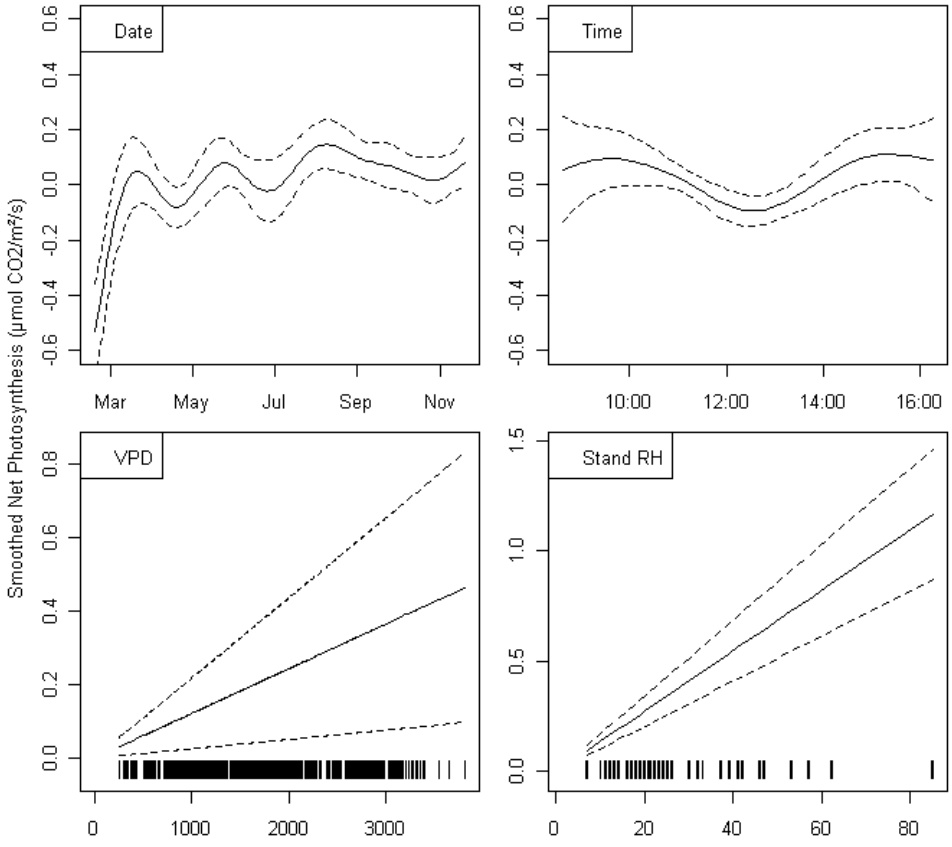

Figure 33. Smoothed photosynthetic response of Douglas-fir model of closed stand to a) date b) stand RH c) temperature d) PAR.

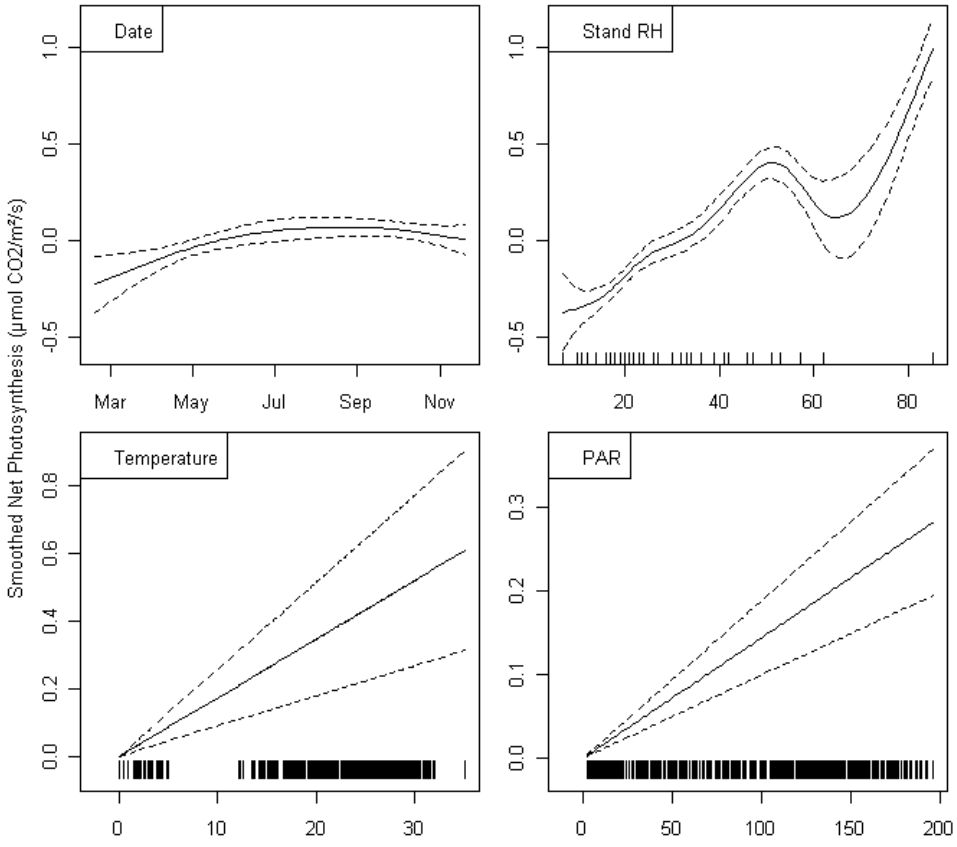

Figure 34. Smoothed photosynthetic response of Douglas-fir model of open stand to a) date b) time c) VPD d) stand VPD.

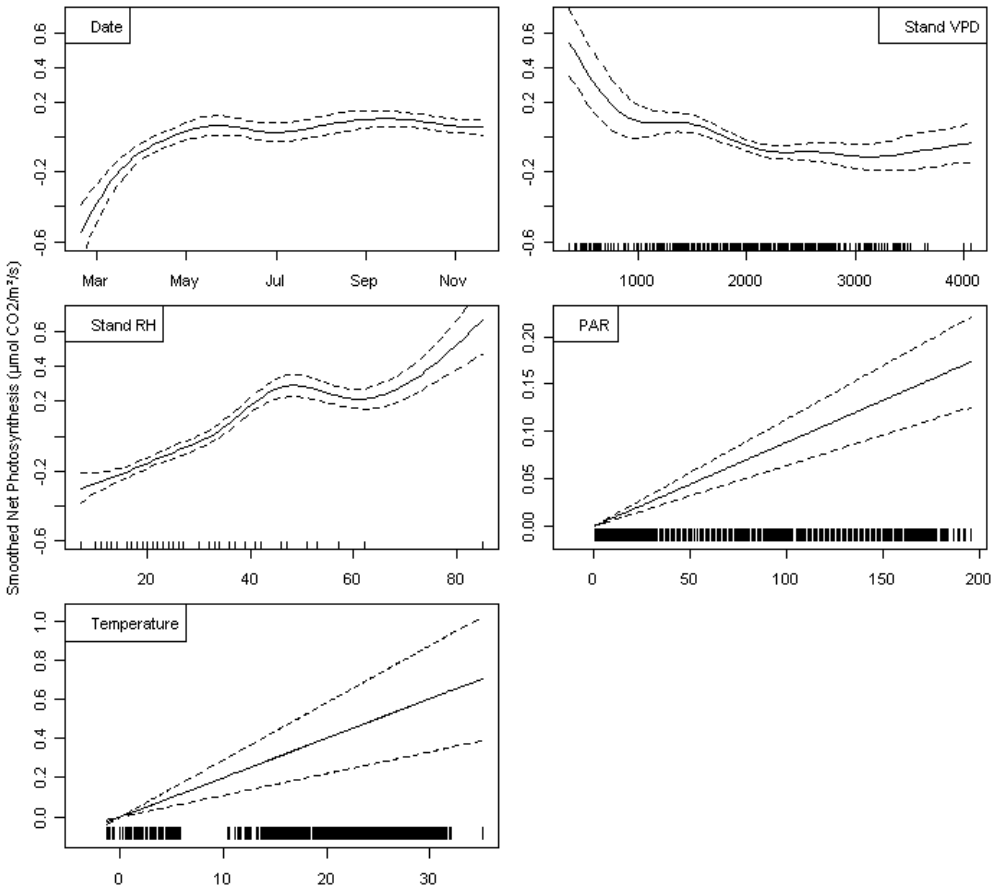

Figure 35. Smoothed photosynthetic response of full Douglas-fir model to a) date b) stand VPD c) stand RH d) PAR e) temperature.

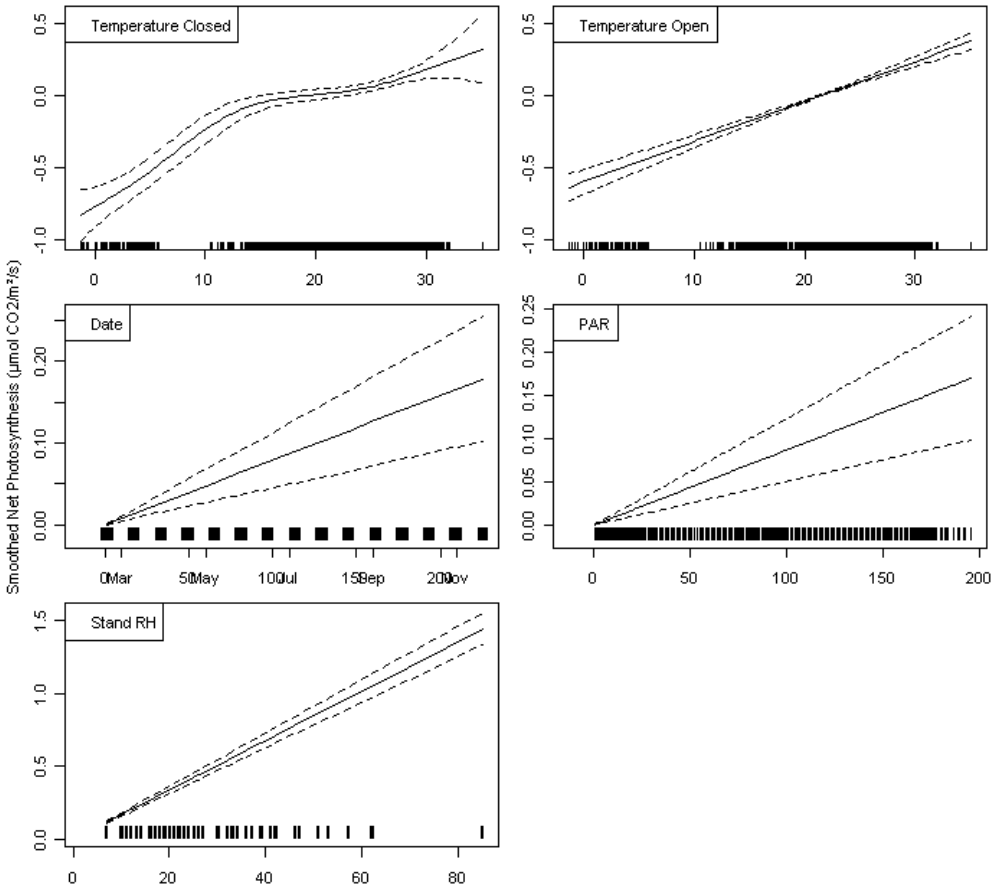

Figure 36. Smoothed photosynthetic response of full-oc Douglas-fir model to a) closed tree temperature b) open tree temperature c) date d) PAR e) stand RH.

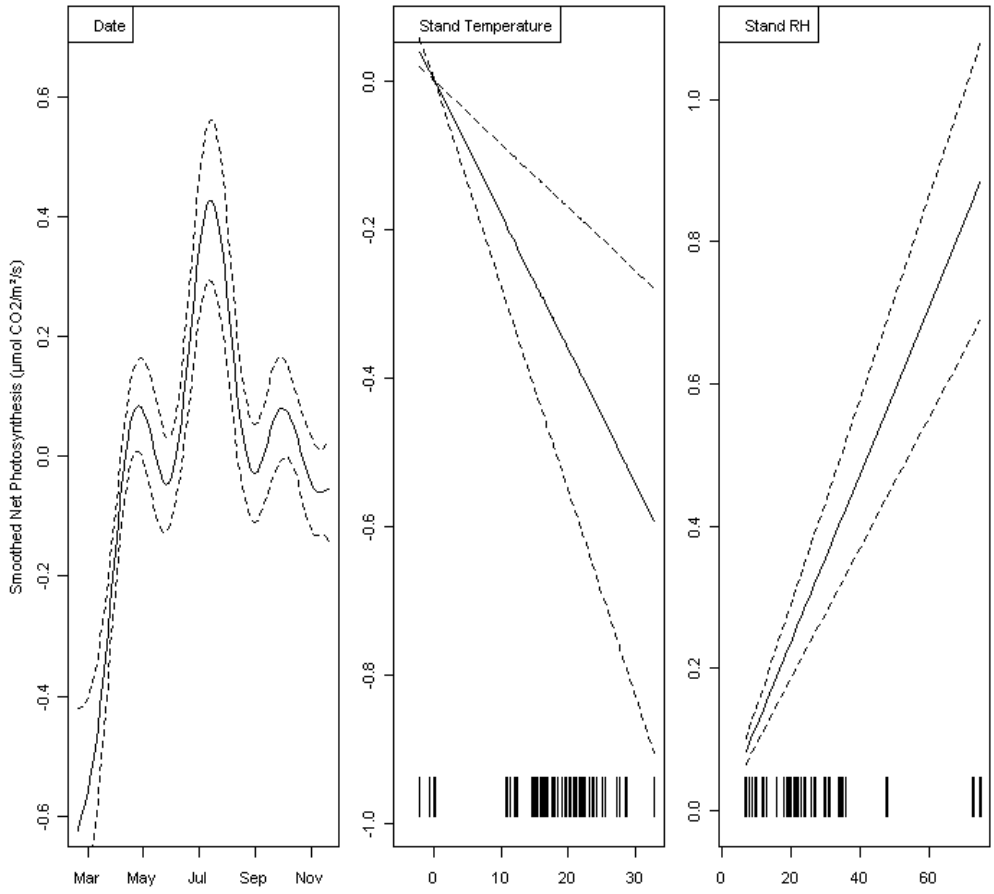

Figure 37. Smoothed photosynthetic response of subalpine fir closed model to a) date b) stand temperature c) stand RH

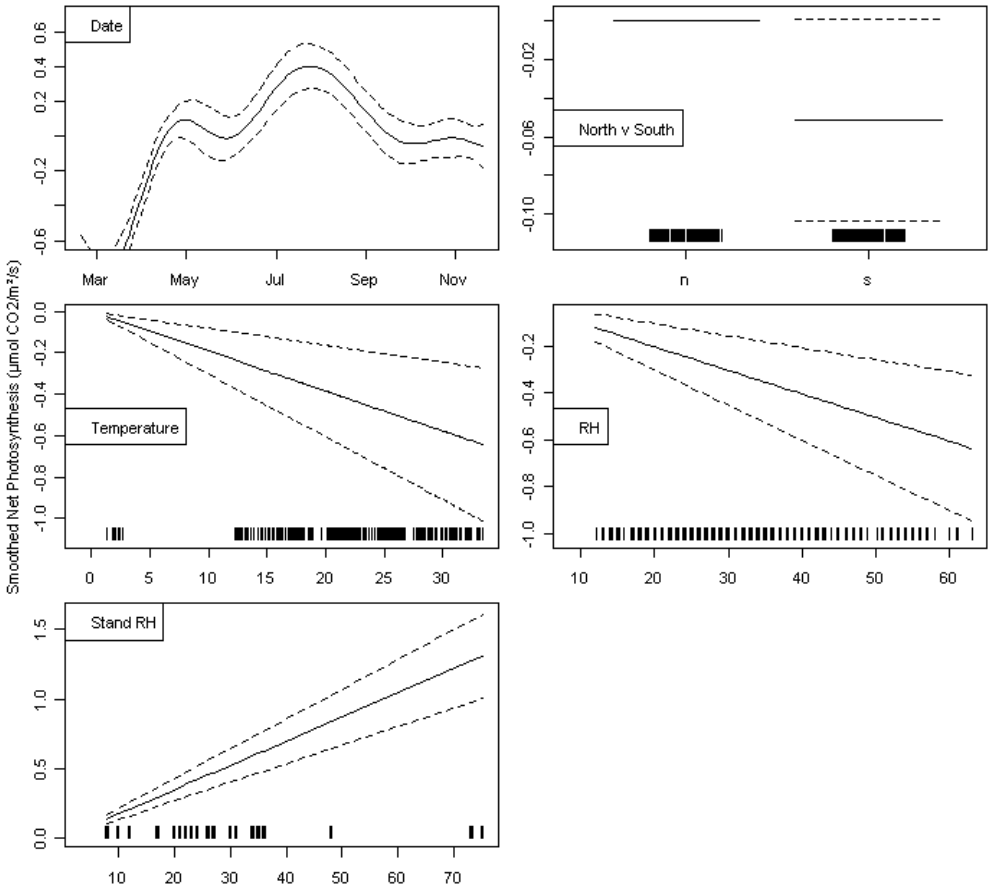

Figure 38. Smoothed photosynthetic response of subalpine fir open model to a) date b) aspect c) RH d) stand RH e) temperature.

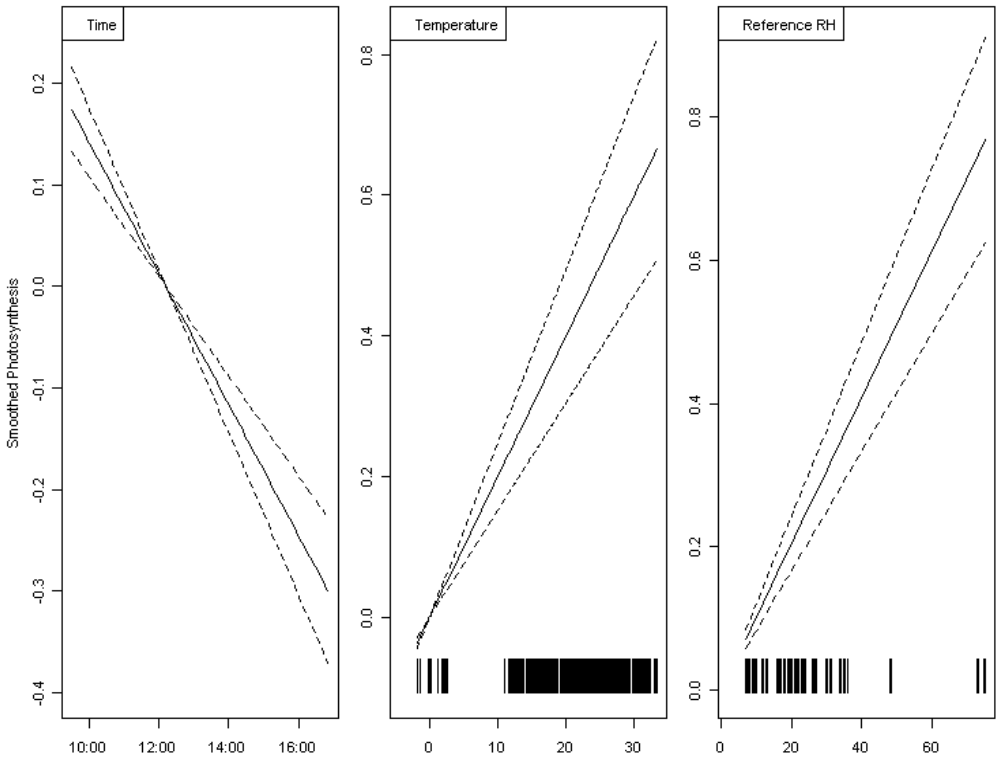

Figure 39. Smoothed photosynthetic response of full subalpine fir model to a) time b) temperature c) stand RH.

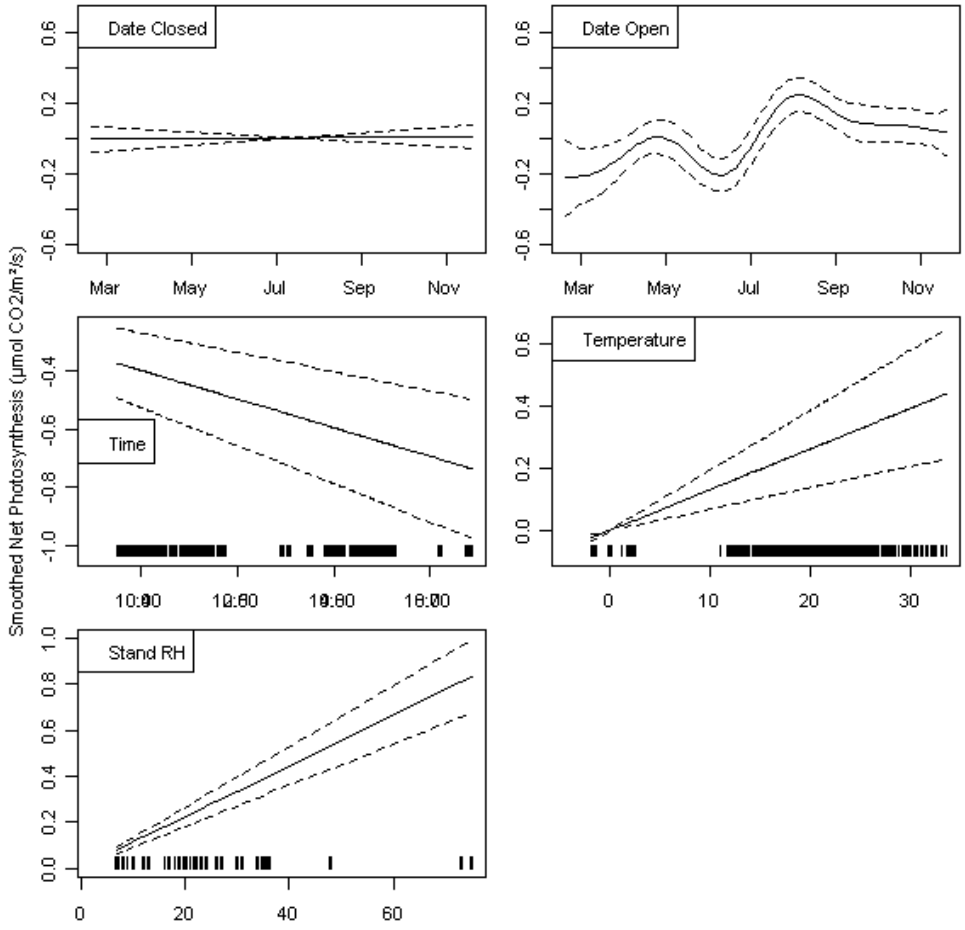

Figure 40. Smoothed photosynthetic response of full-oc subalpine fir model to a) closed tree date b) open tree date c) time d) temperature e) stand RH.

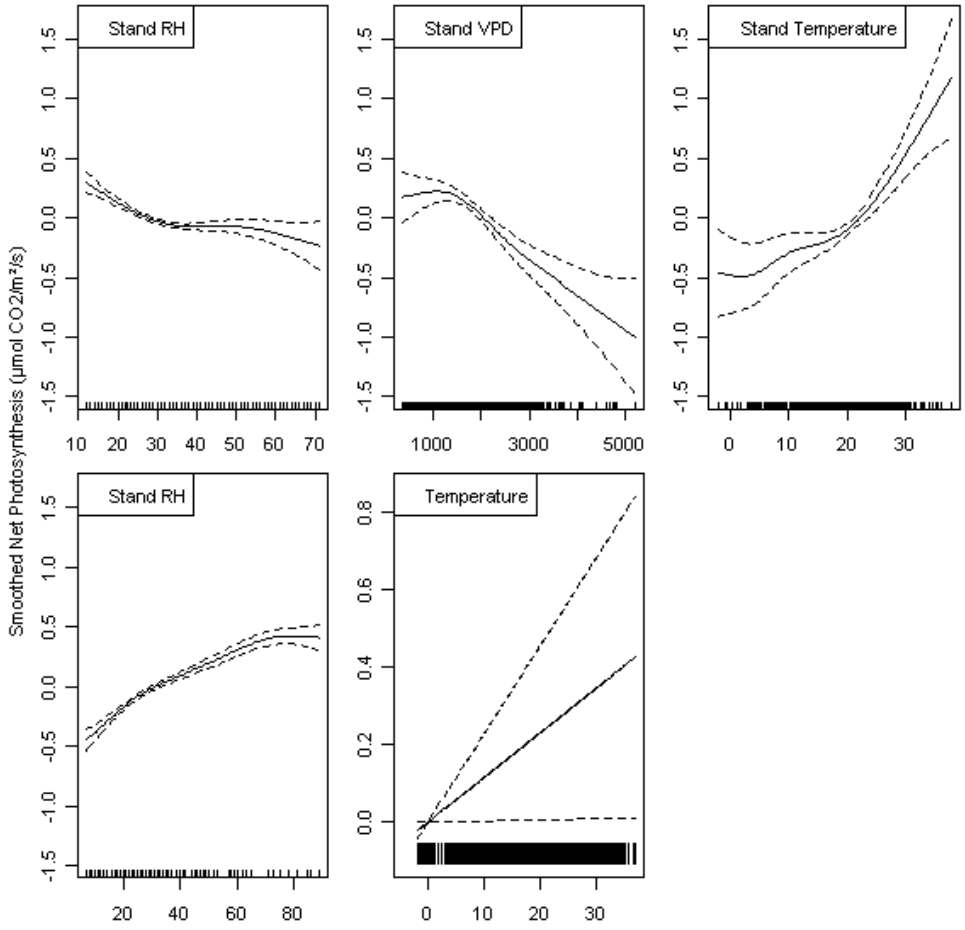

Figure 41. Smoothed photosynthetic response of all species closed model to a) RH b) stand RH c) stand VPD d) temperature e) stand temperature.

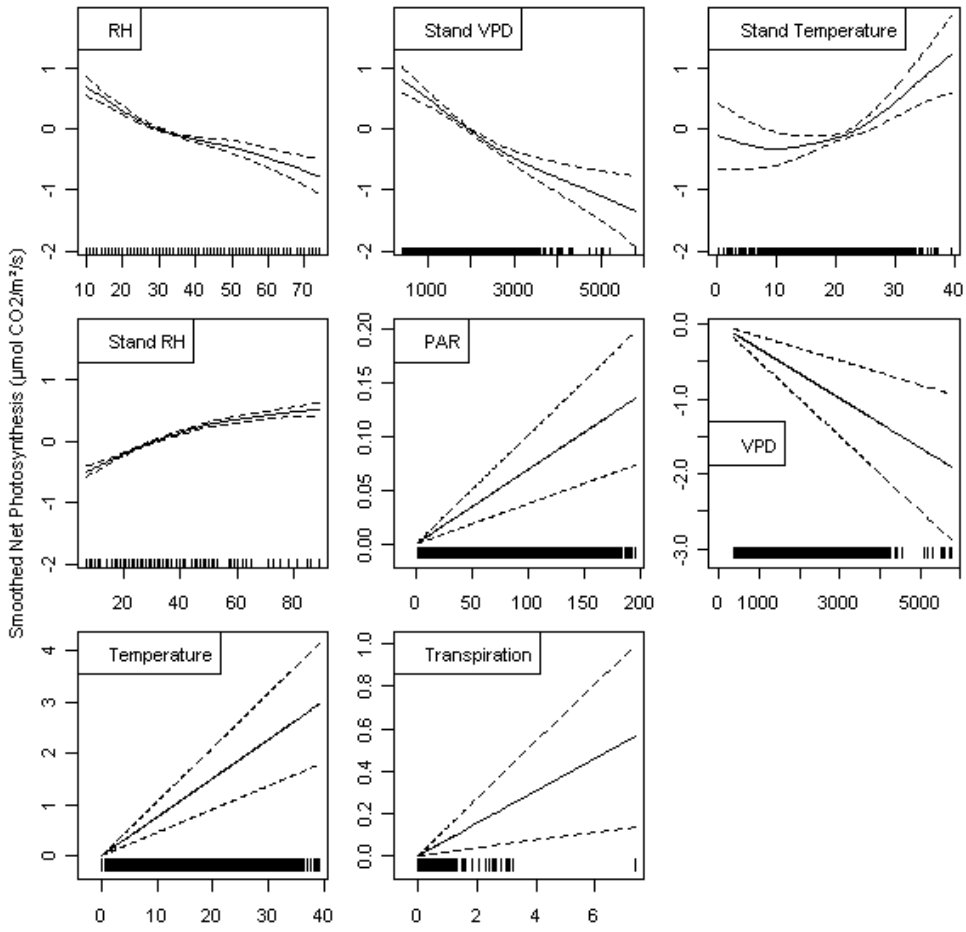

Figure 42. Smoothed photosynthetic response of all species open model to a) RH b) stand VPD c) stand temperature d) stand RH e) PAR f) VPD g) temperature h) transpiration.

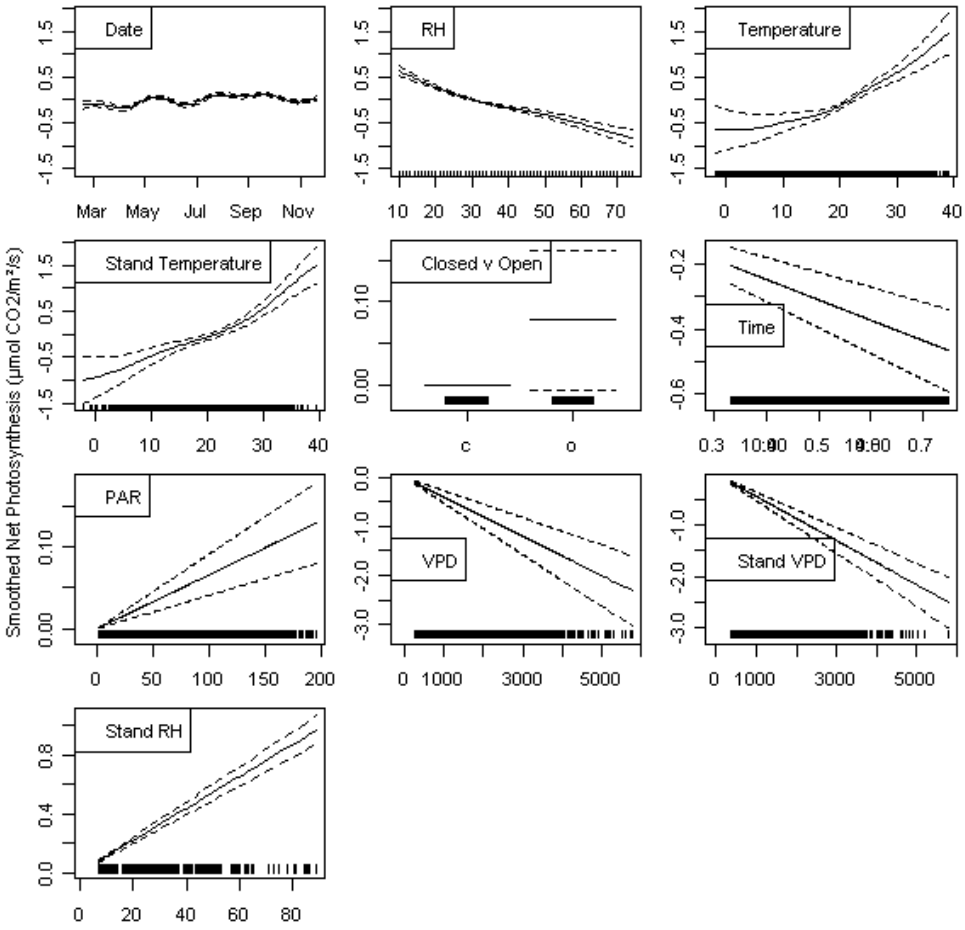

Figure 43. Smoothed photosynthetic response of full all species model to a) date b) RH c) temperature d) closed/open e) time f) PAR g) VPD h) stand VPD I) stand RH.

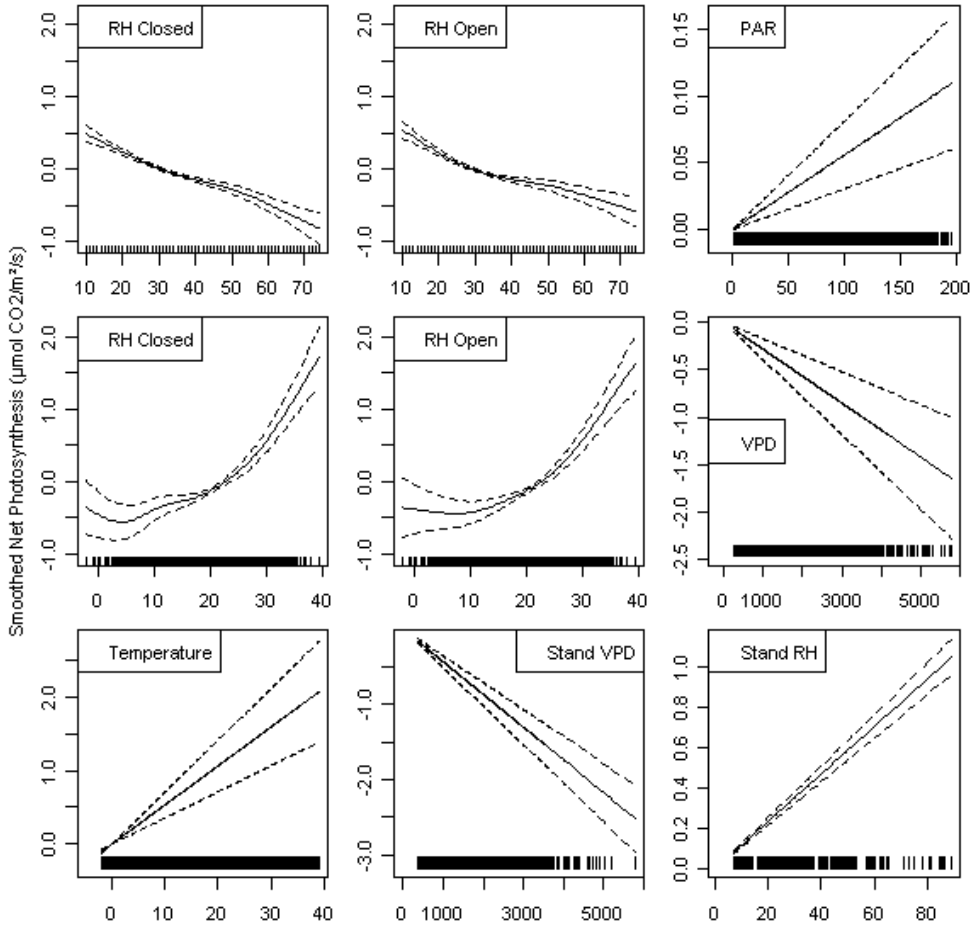

Figure 44. Smoothed photosynthetic response of full-oc all species model to a) closed tree RH b) open tree RH c) PAR d) closed tree stand temperature e) open tree stand temperature f) temperature g) VPD f) stand VPD h) stand RH.

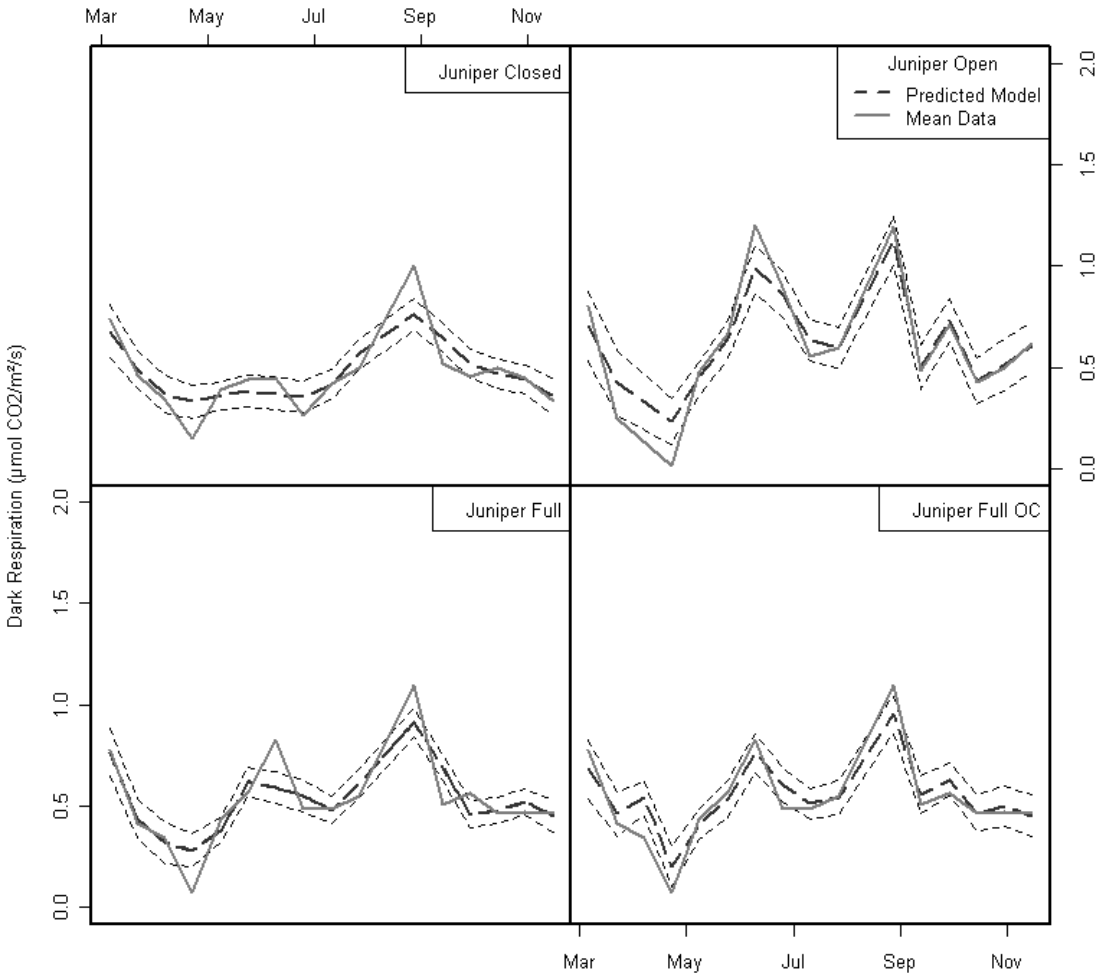

Figure 45. Juniper predicted GAMM respiration a) closed b) open c) full and d) full-oc models fit to data

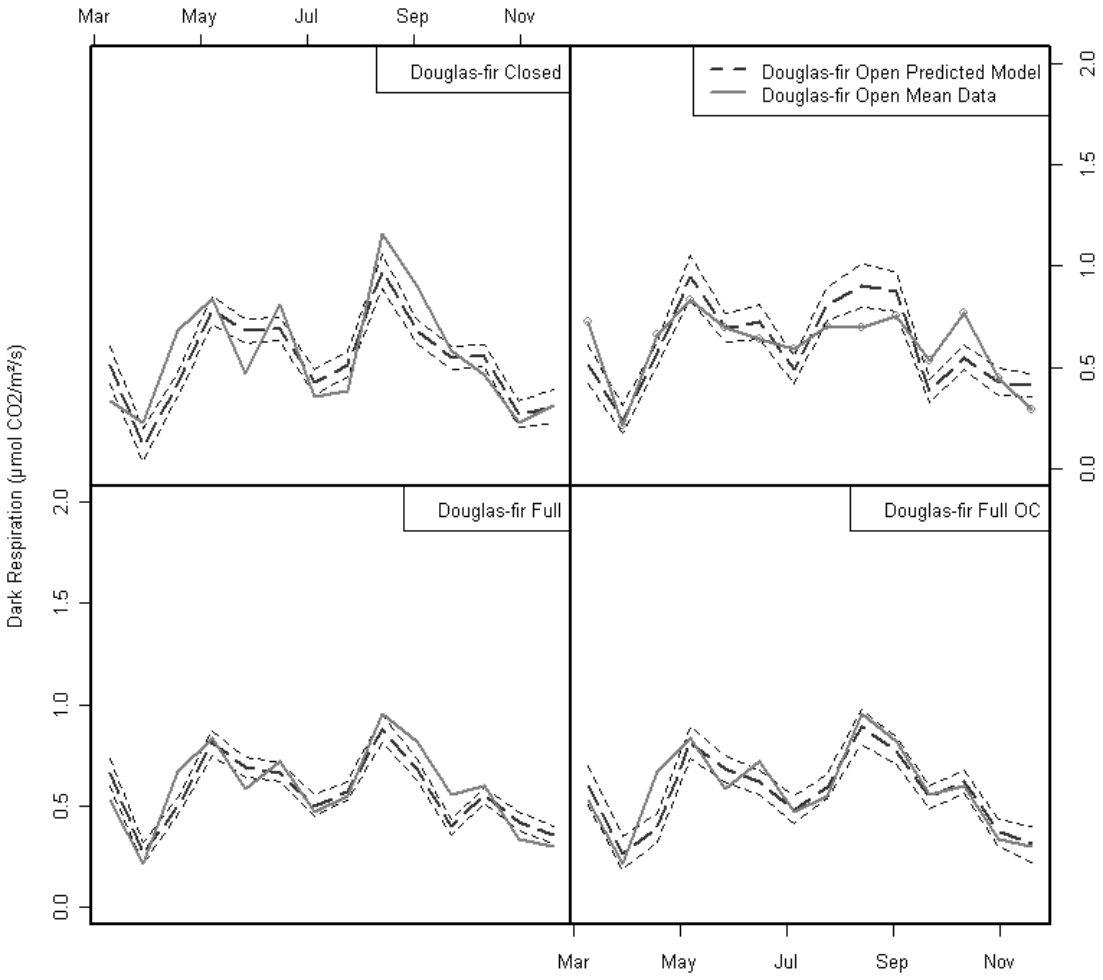

Figure 46. Douglas-fir predicted GAMM respiration a) closed b) open c) full and d) full-oc models fit to data

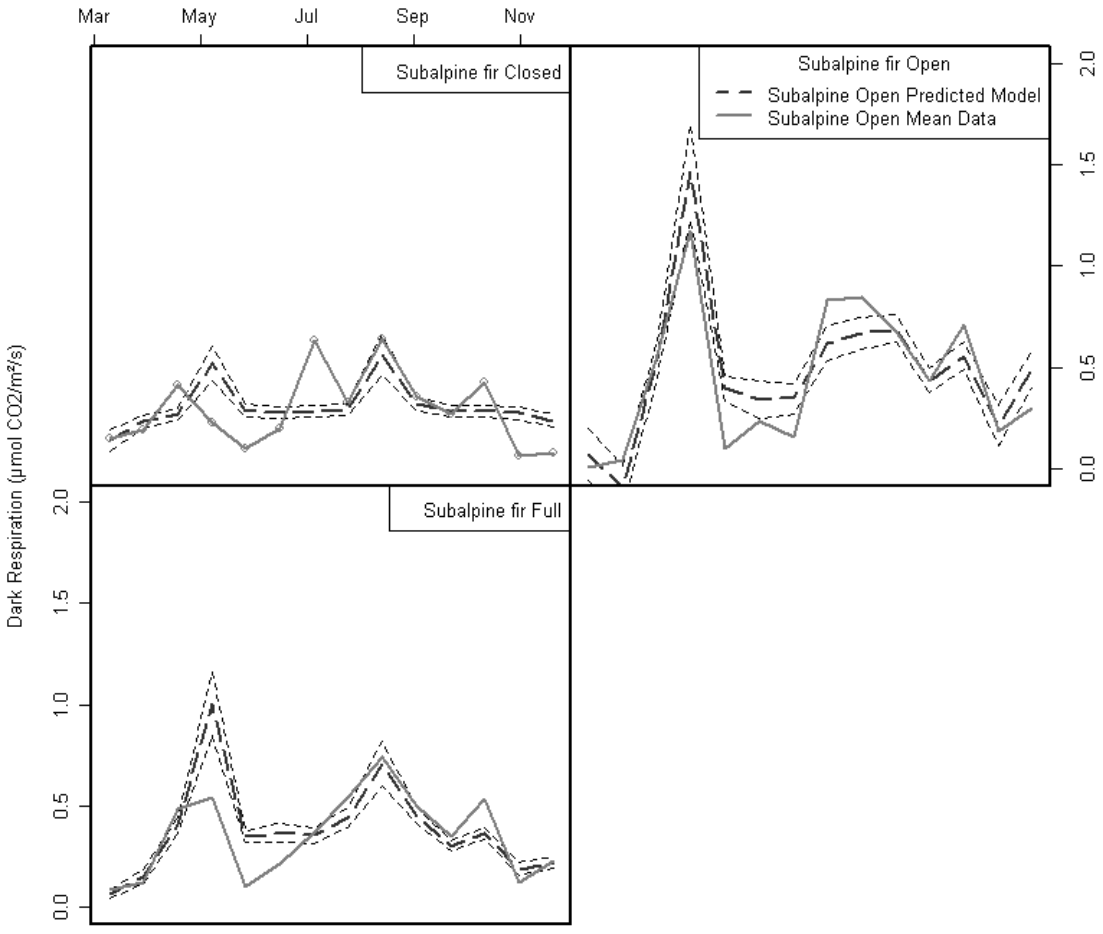

Figure 47. Subalpine fir predicted GAMM respiration a) closed b) open c) full and d) full-oc models fit to data.

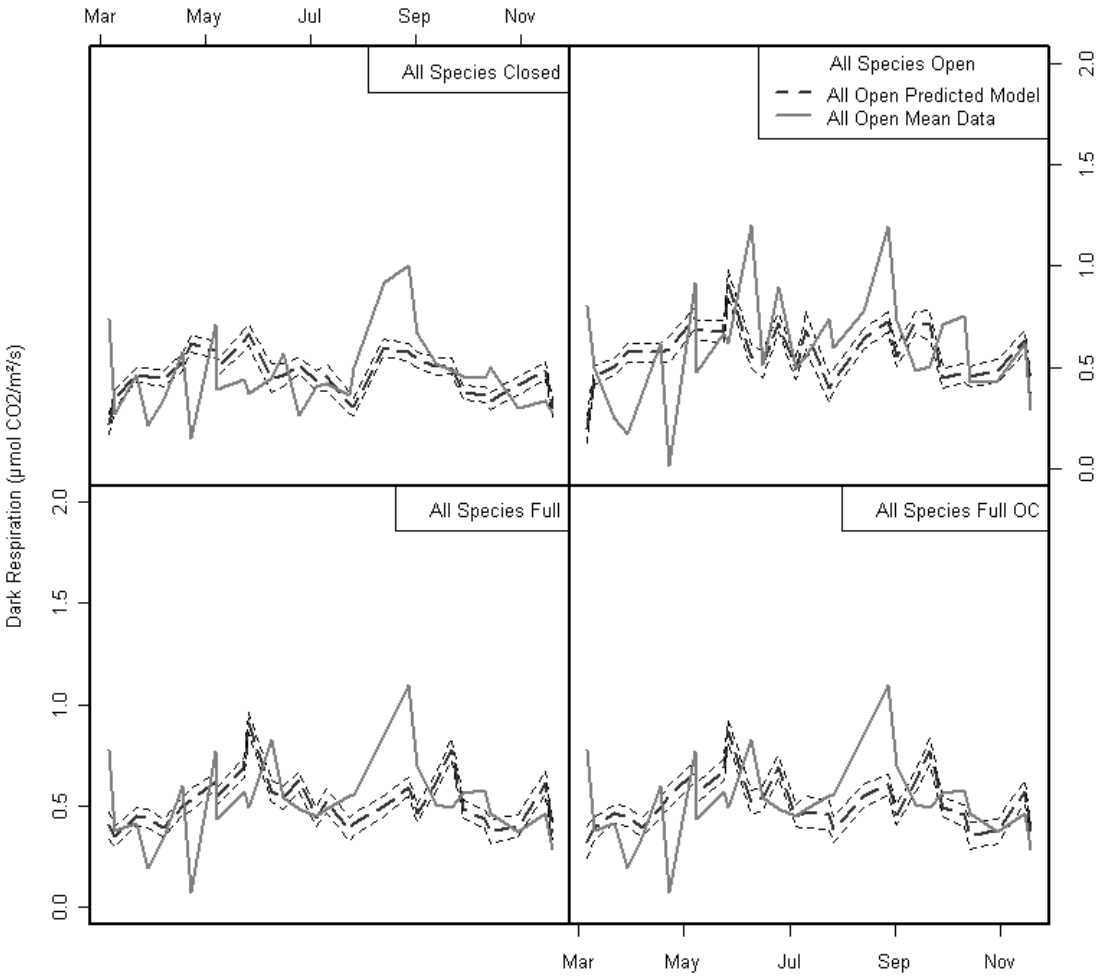

Figure 48. All species predicted GAMM respiration a) closed b) open c) full and d) full-oc models fit to data

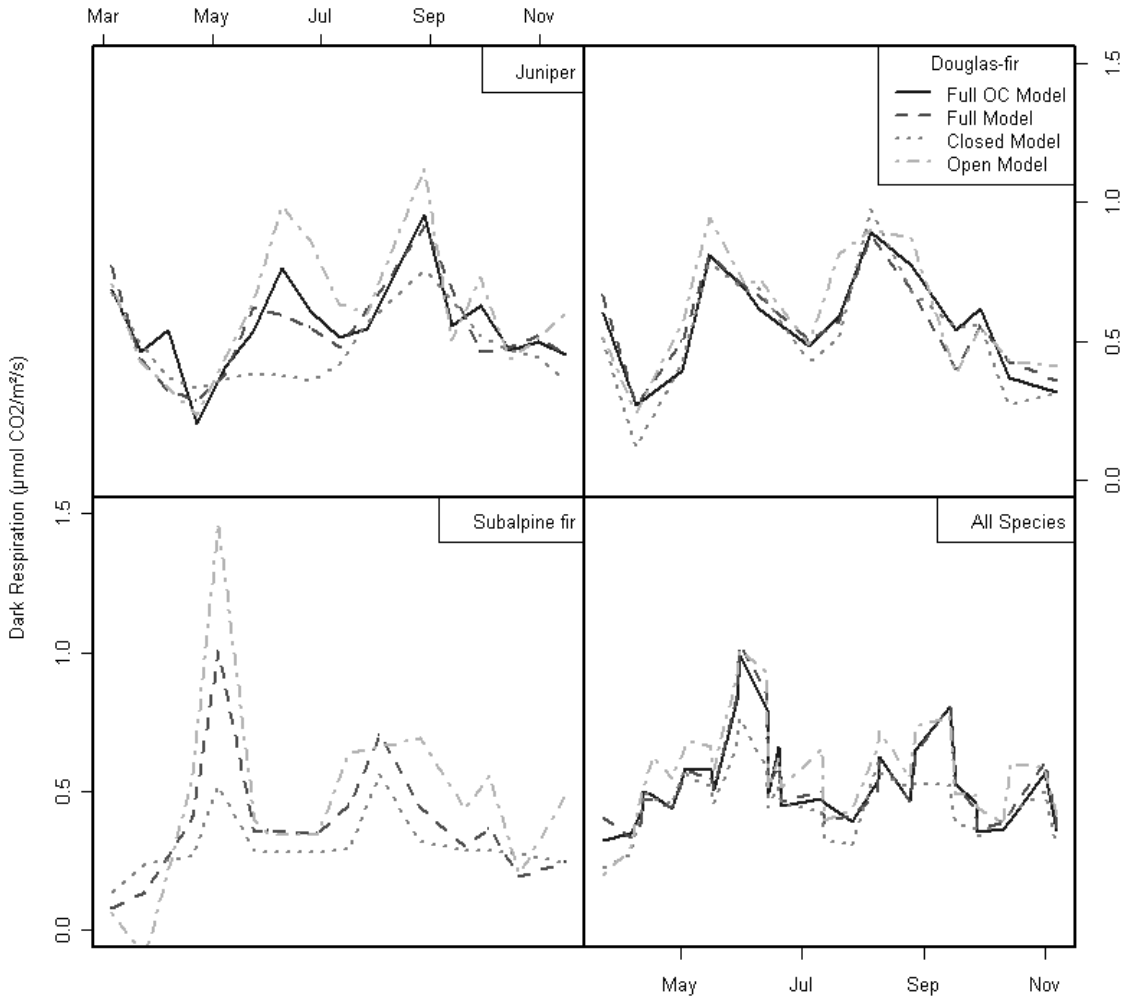

Figure 49. Respiration model comparison of a) juniper b) Douglas-fir c) subalpine fir and d) all species for closed, open, full and full-oc models.

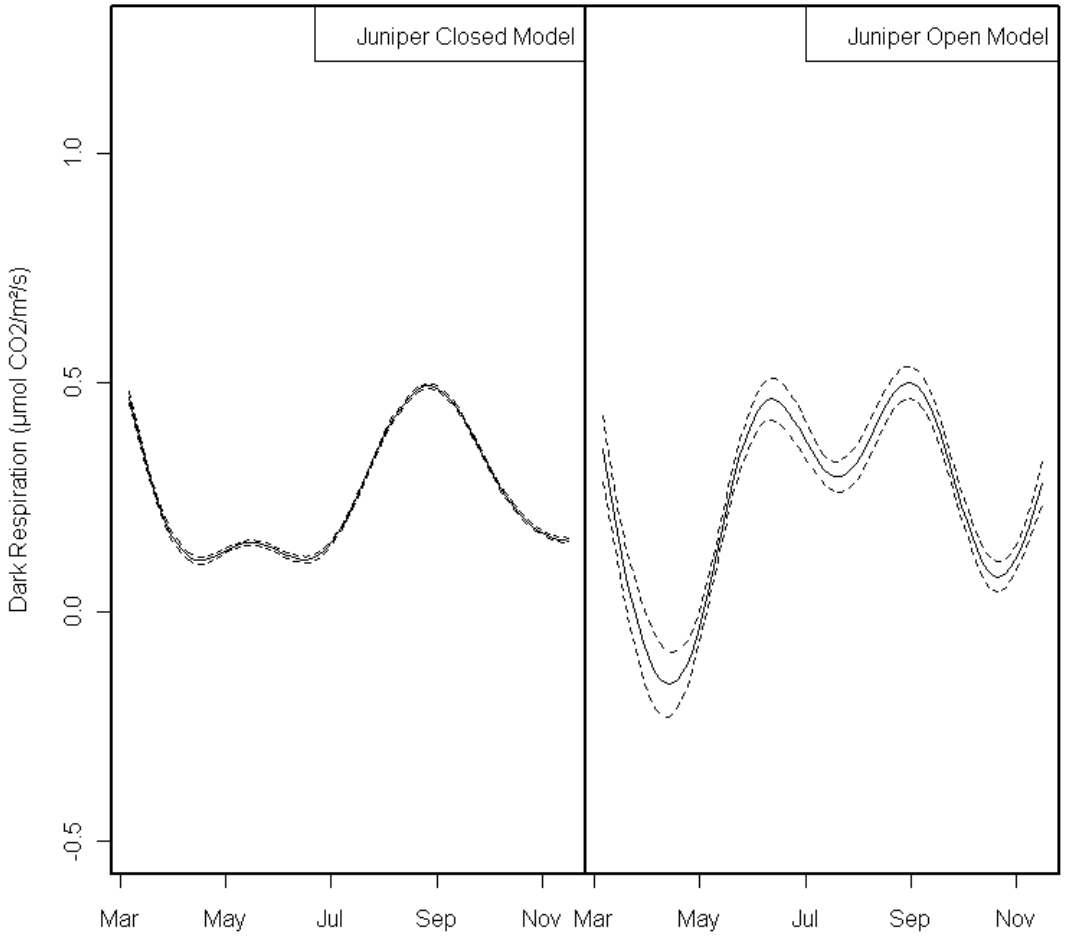

Figure 50. Smoothed respiration curves of closed and open juniper GAMMs.

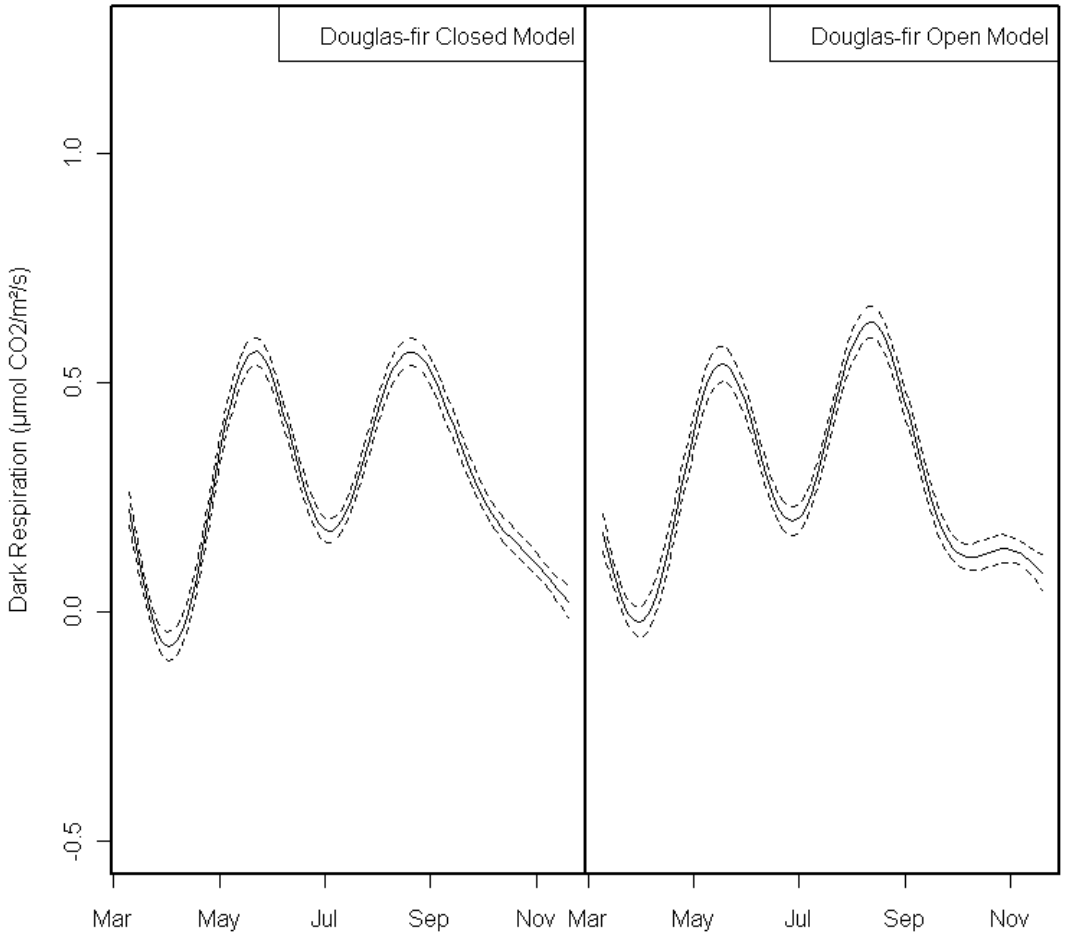

Figure 51. Smoothed respiration curves of closed and open Douglas-fir GAMMs.

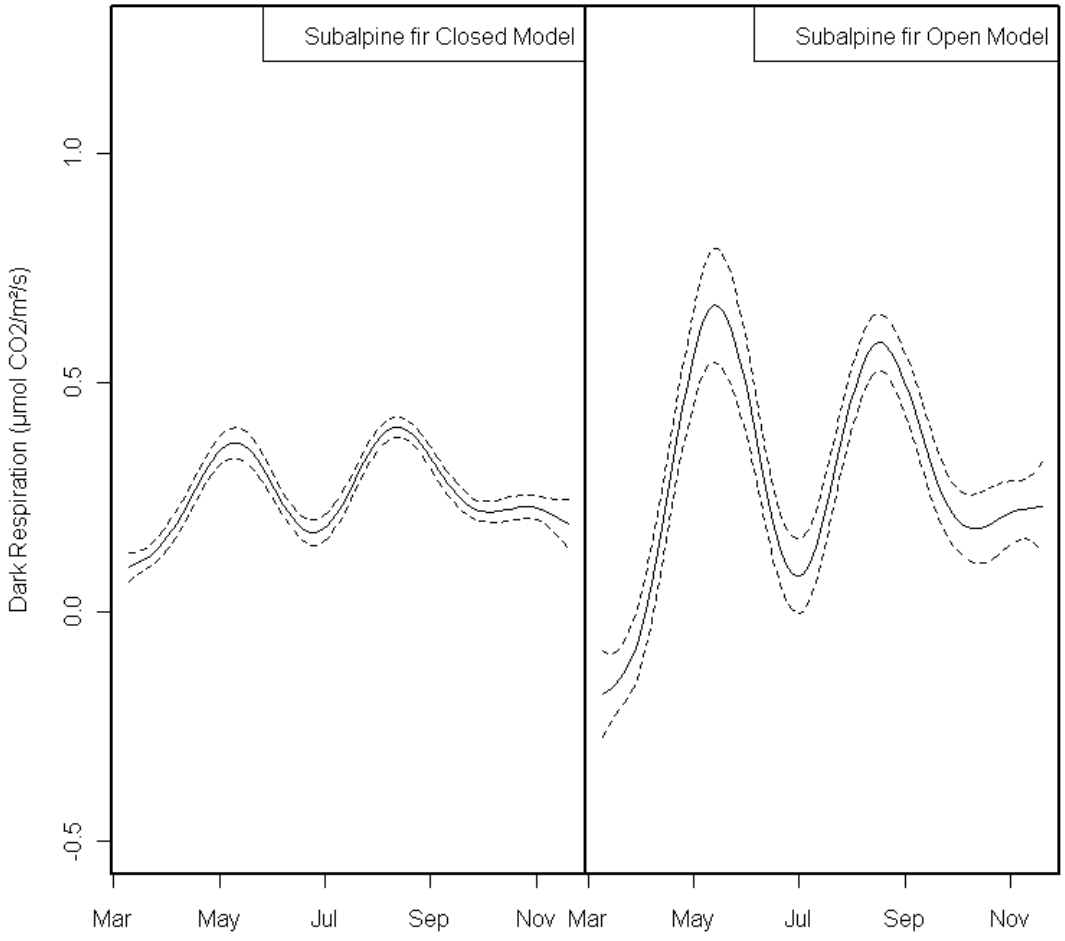

Figure 52. Smoothed respiration curves of closed and open subalpine fir GAMMs.

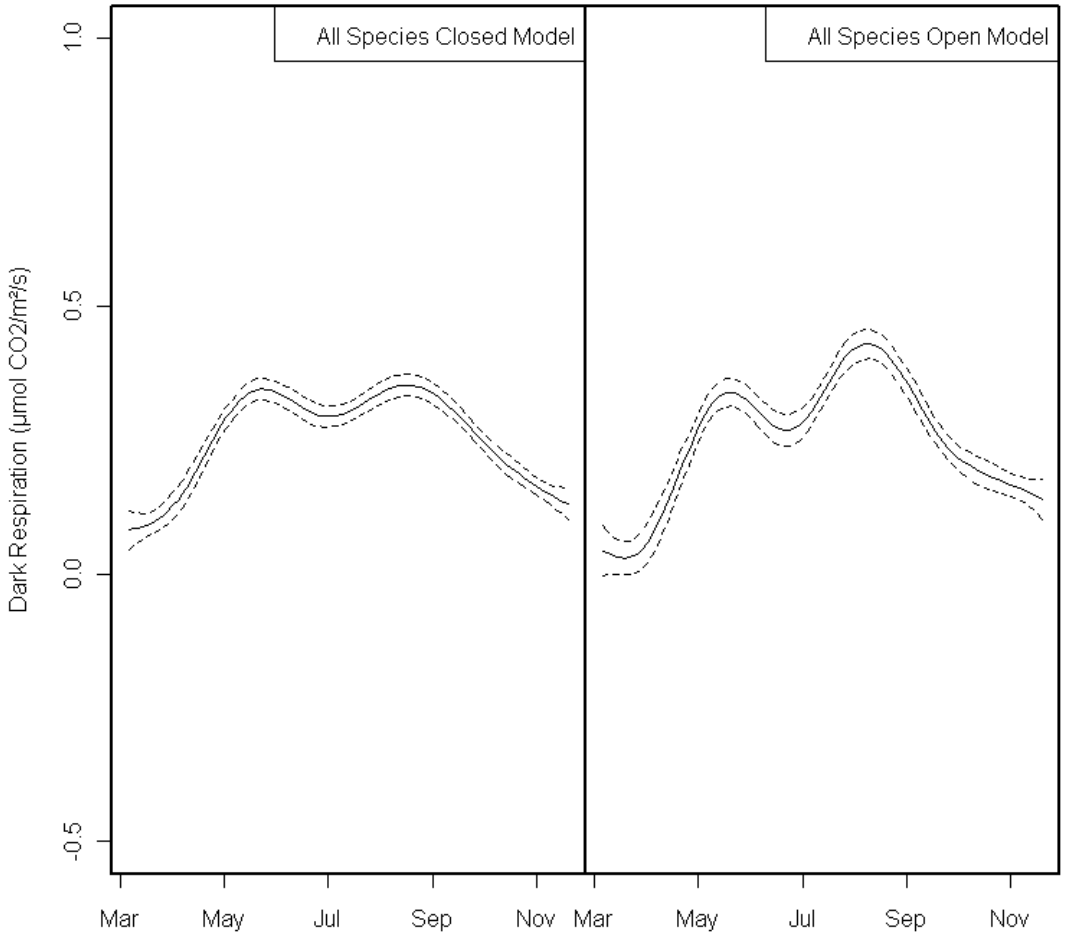

Figure 53. Smoothed respiration curves of closed and open all species GAMMs.

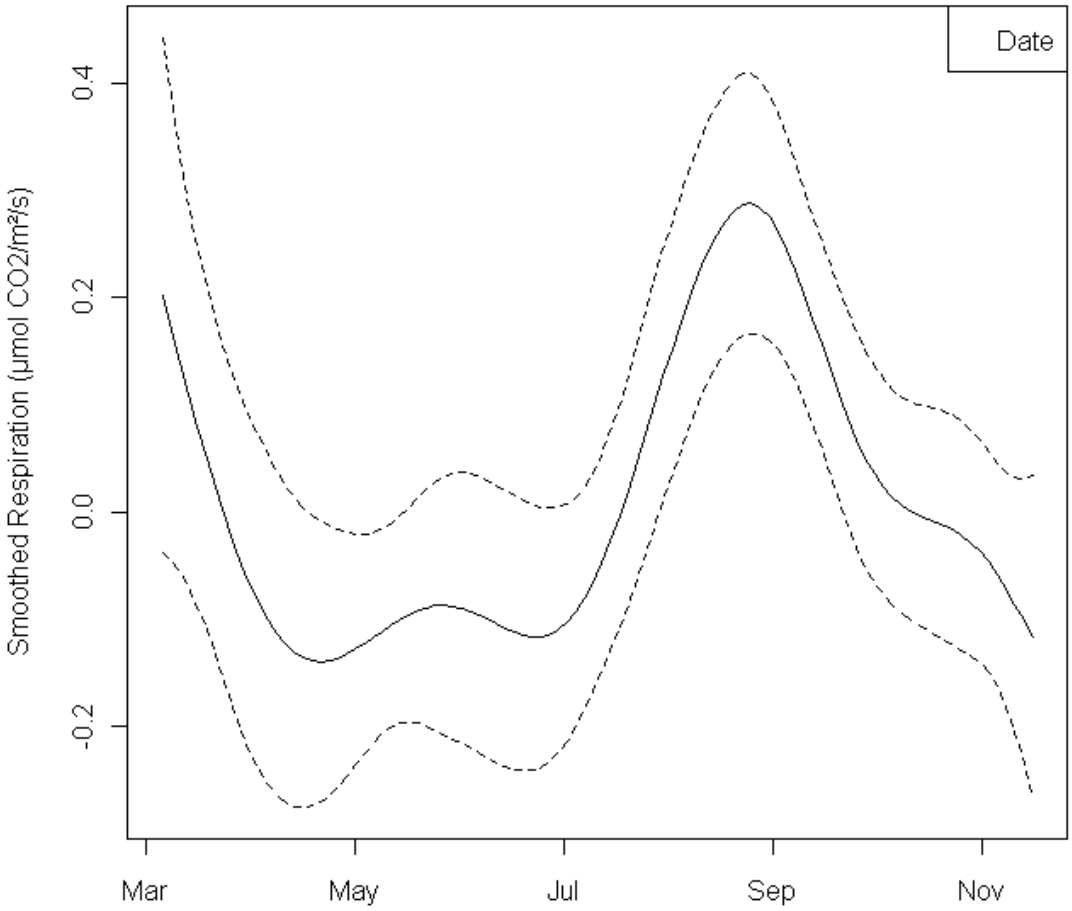

Figure 54. Smoothed respiration response of juniper closed model to date.

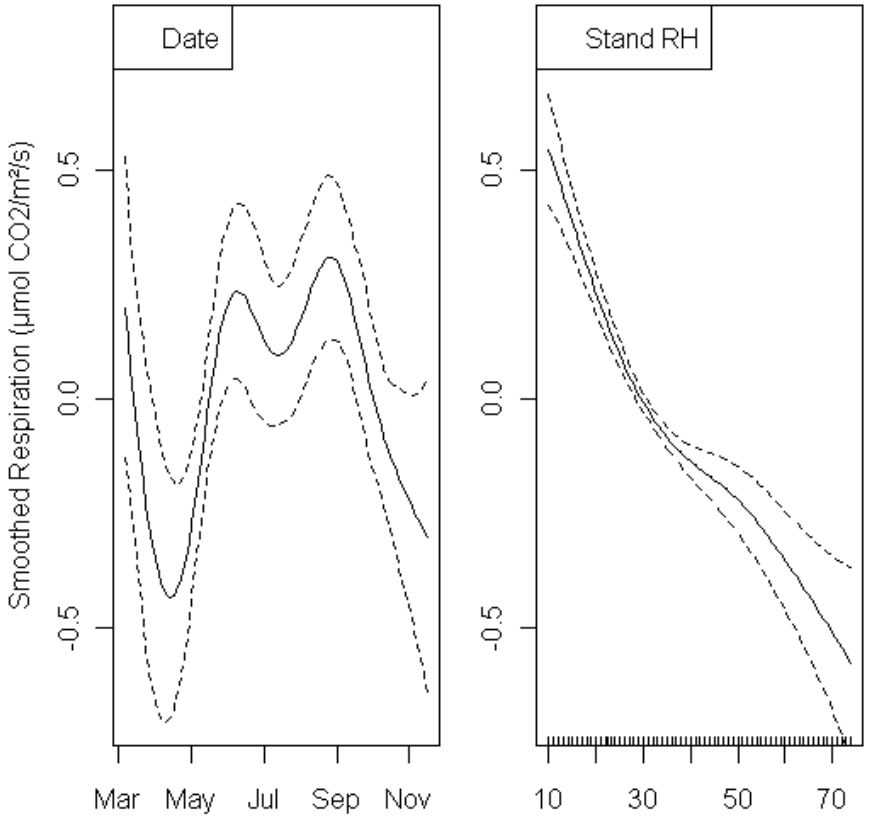

Figure 55. Smoothed respiration response of juniper closed model to a) date b) stand RH.

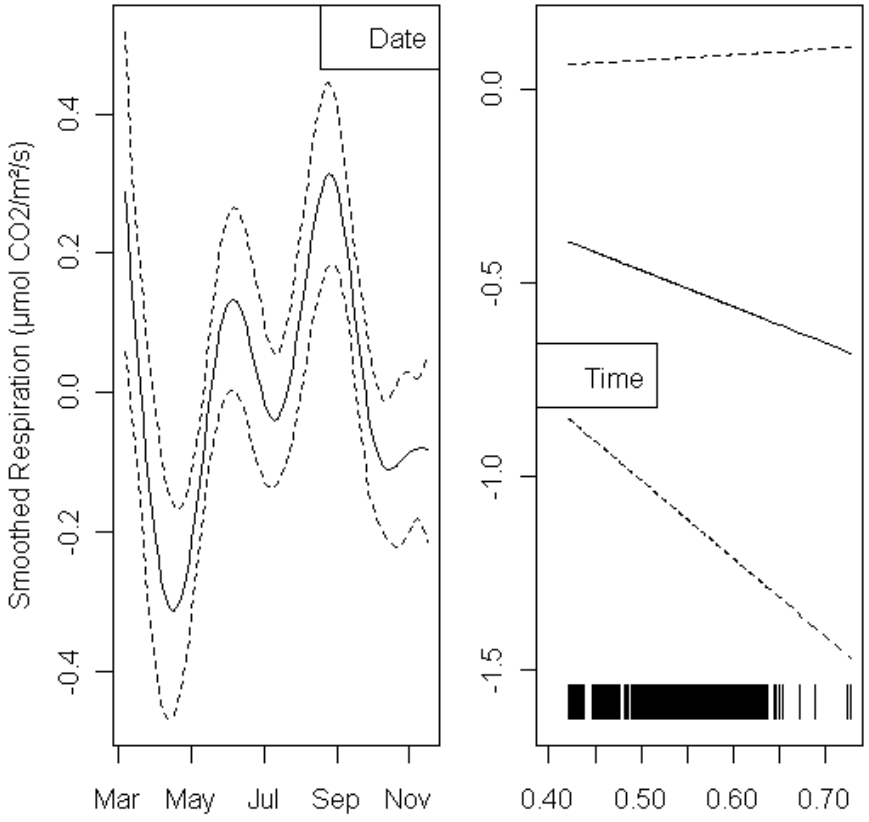

Figure 56. Smoothed respiration response of full juniper model to a) date b) time

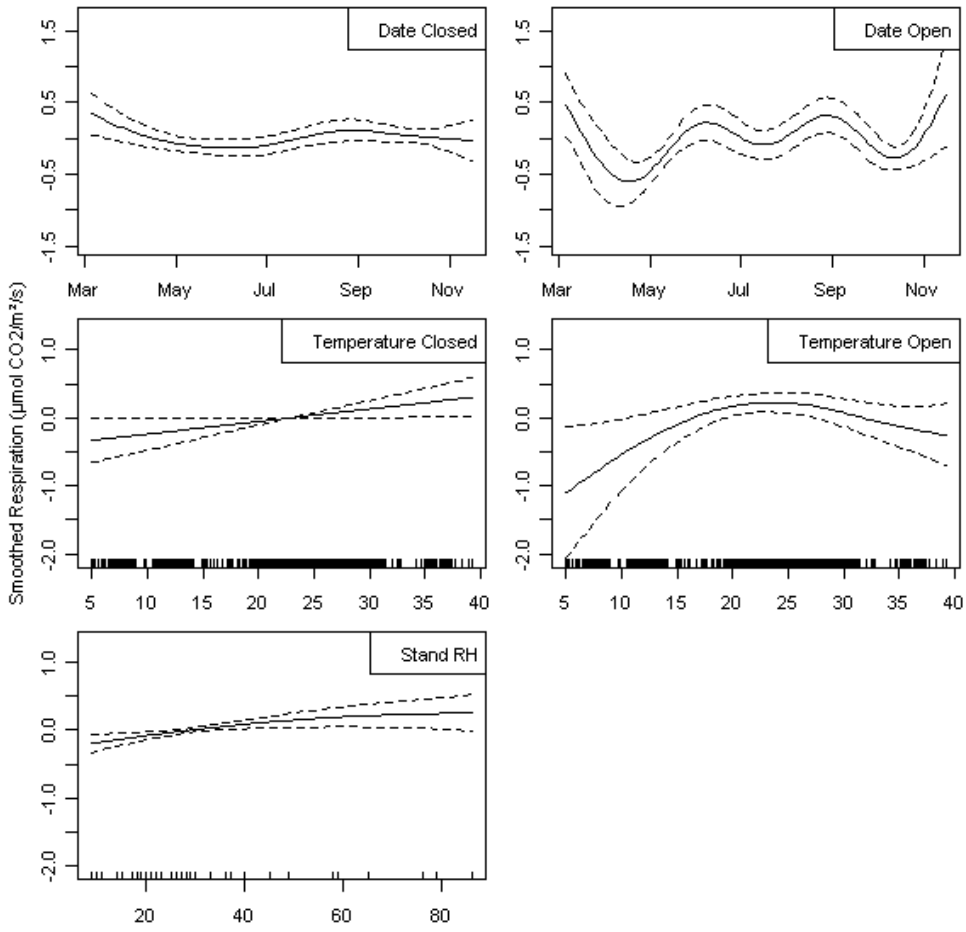

Figure 57. Smoothed respiration response of full-oc juniper model to a) closed tree date b) open tree date c) closed tree temperature d) open tree temperature e) stand RH.

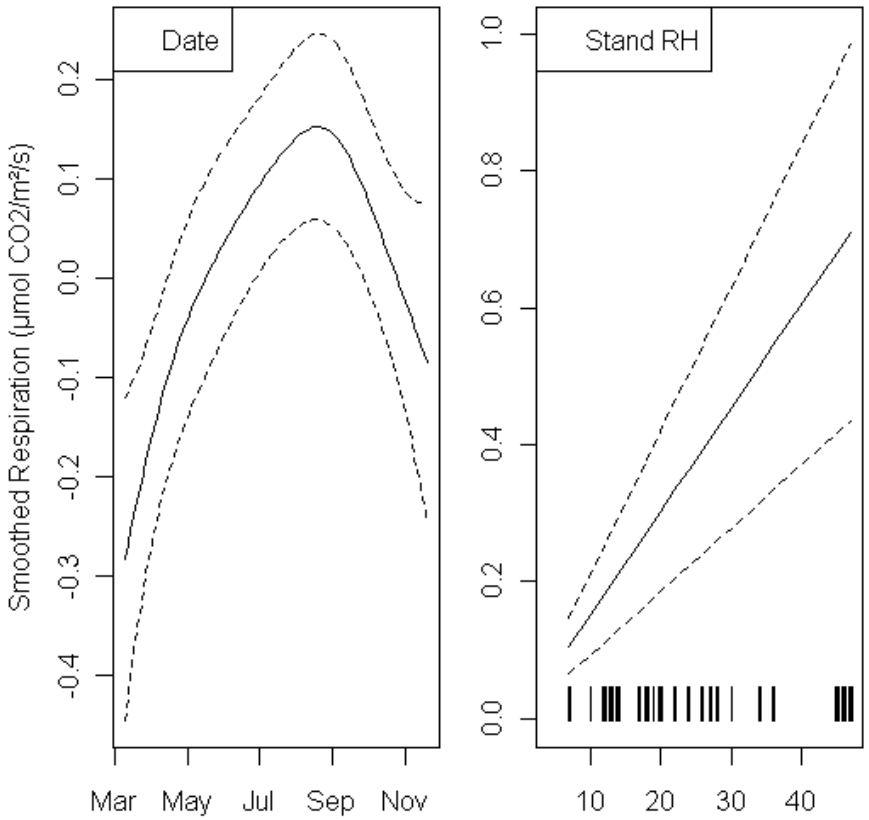

Figure 58. Smoothed respiration response of Douglas-fir closed model to a) date b) stand RH.

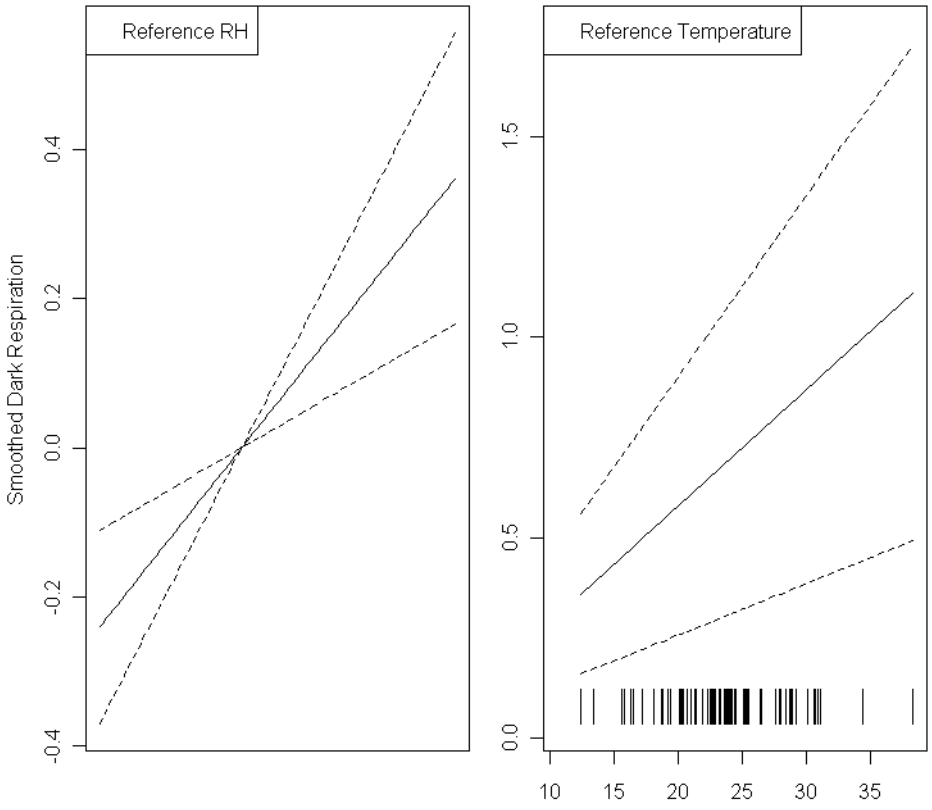

Figure 59. Smoothed respiration response of Douglas-fir open model to a) stand RH b) stand temperature.

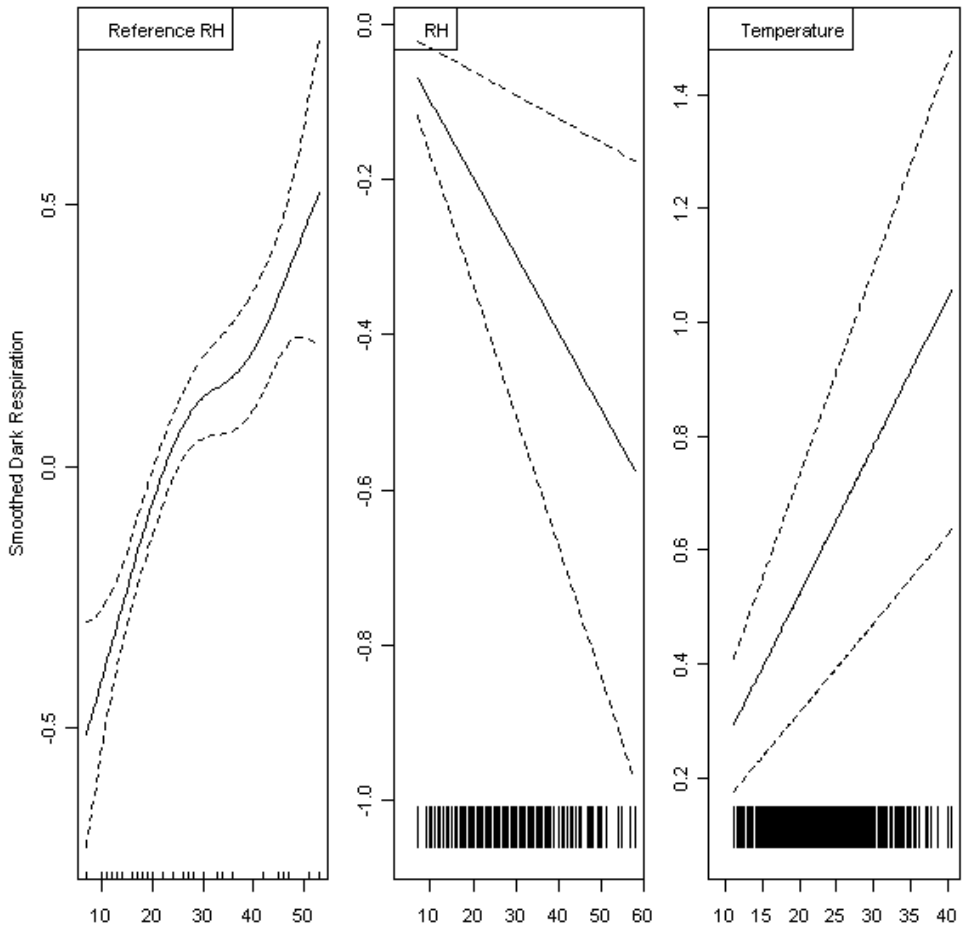

Figure 60. Smoothed respiration response of full Douglas-fir model to a) stand RH b) RH c) temperature.

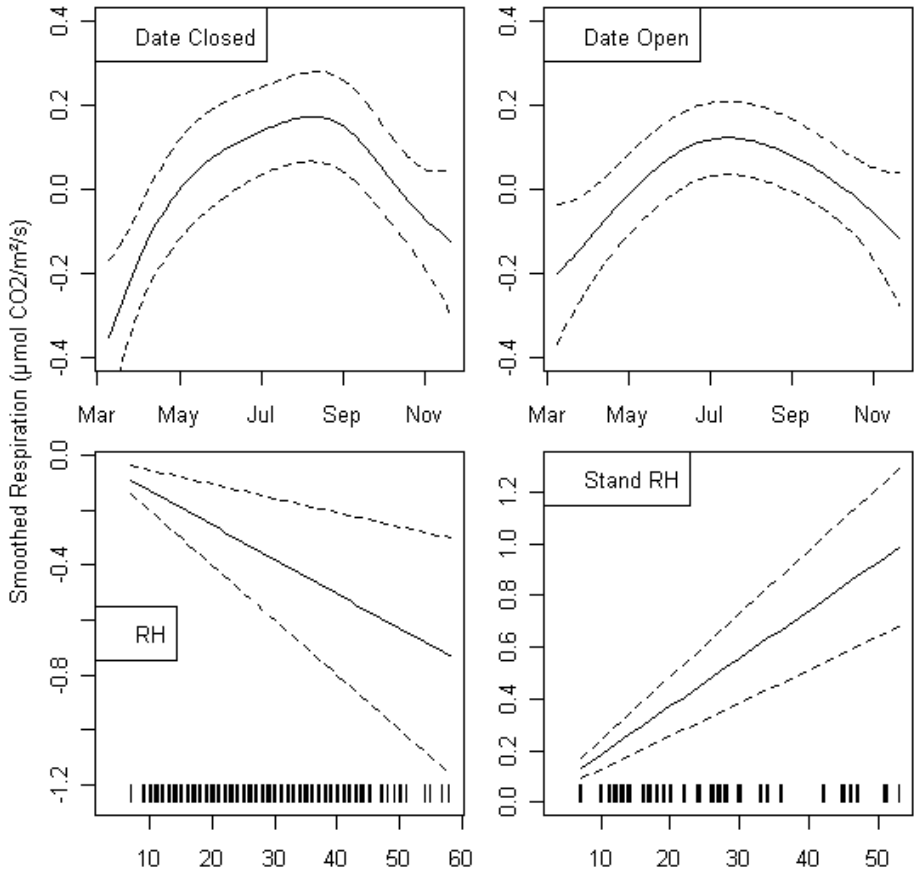

Figure 61. Smoothed respiration response of full-oc Douglas-fir to a) closed tree date b) open tree date c) RH d) stand RH.

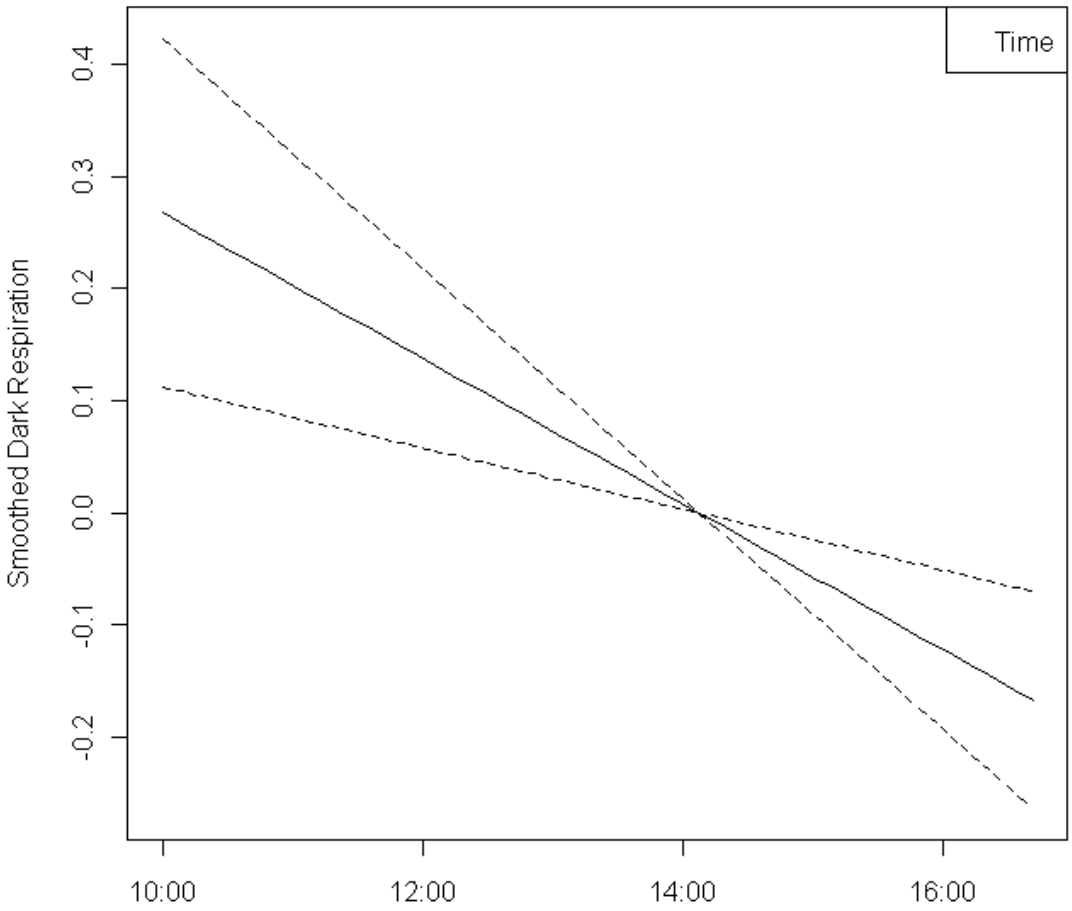

Figure 62. Smoothed respiration response of subalpine fir closed model to time.

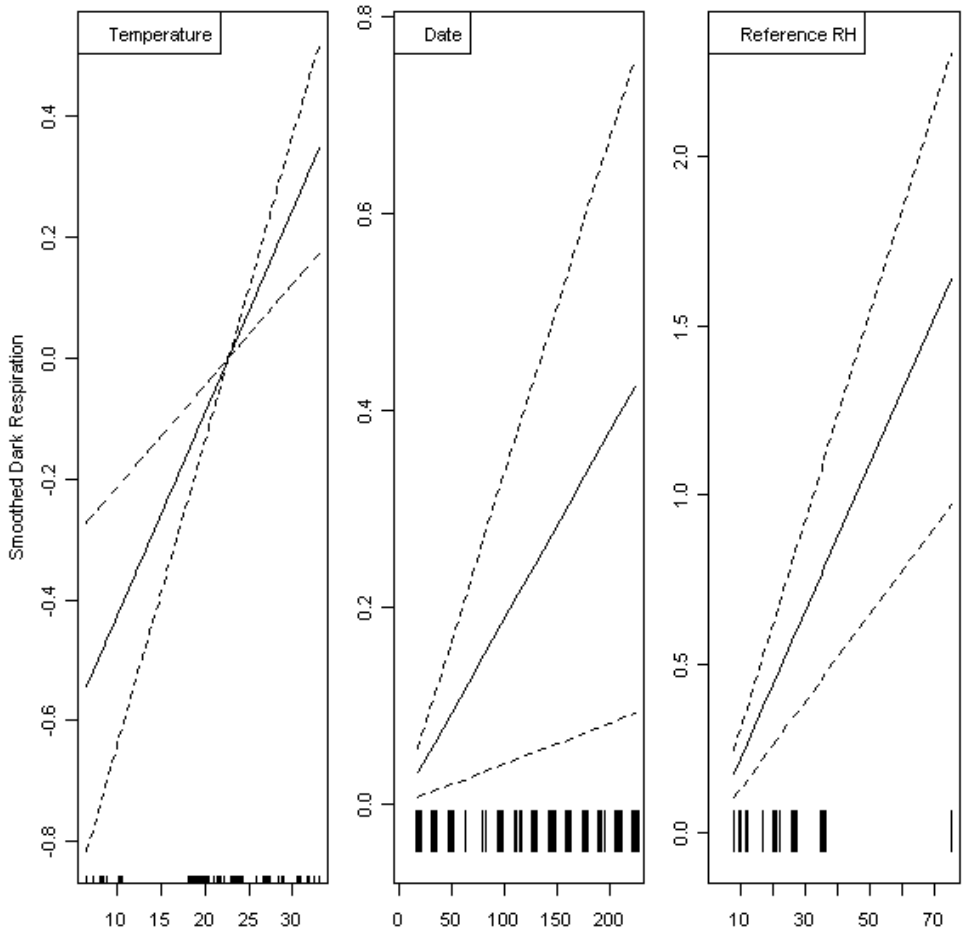

Figure 63. Smoothed respiration response of subalpine fir open model to a) temperature b) date c) stand RH.

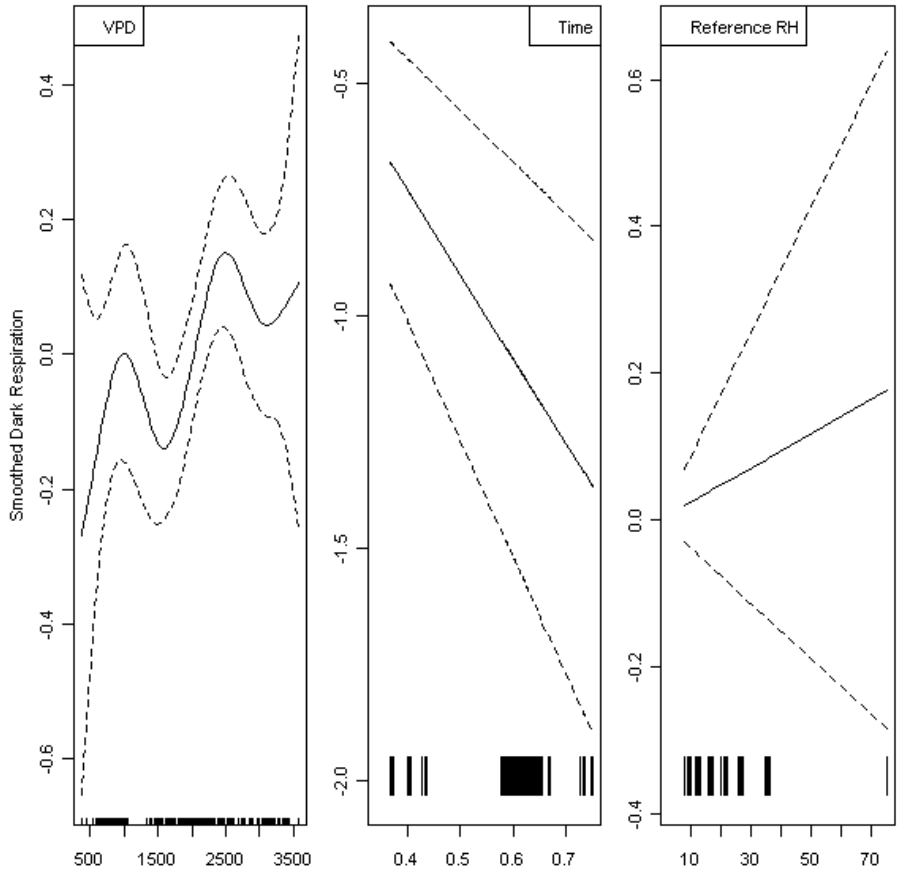

Figure 64. Smoothed respiration response of full subalpine fir model to a) VPD b) time c) stand RH.

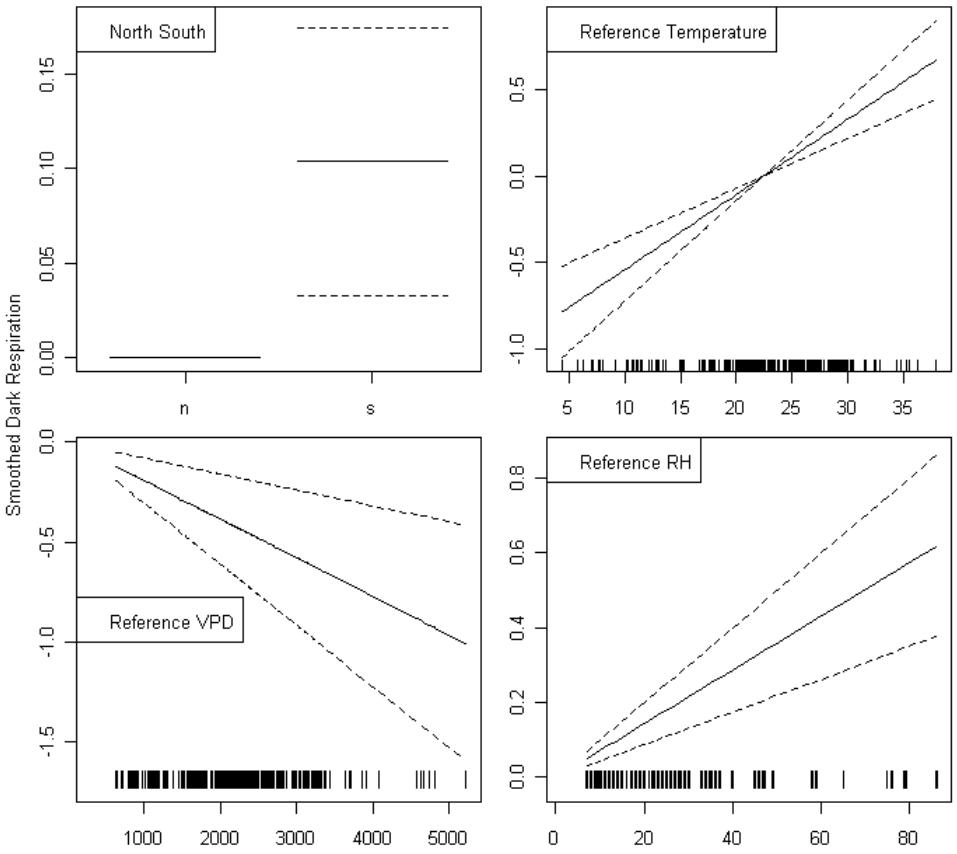

Figure 65. Smoothed respiration response of all species closed model to a) aspect b) stand temperature c) stand VPD d) stand RH.

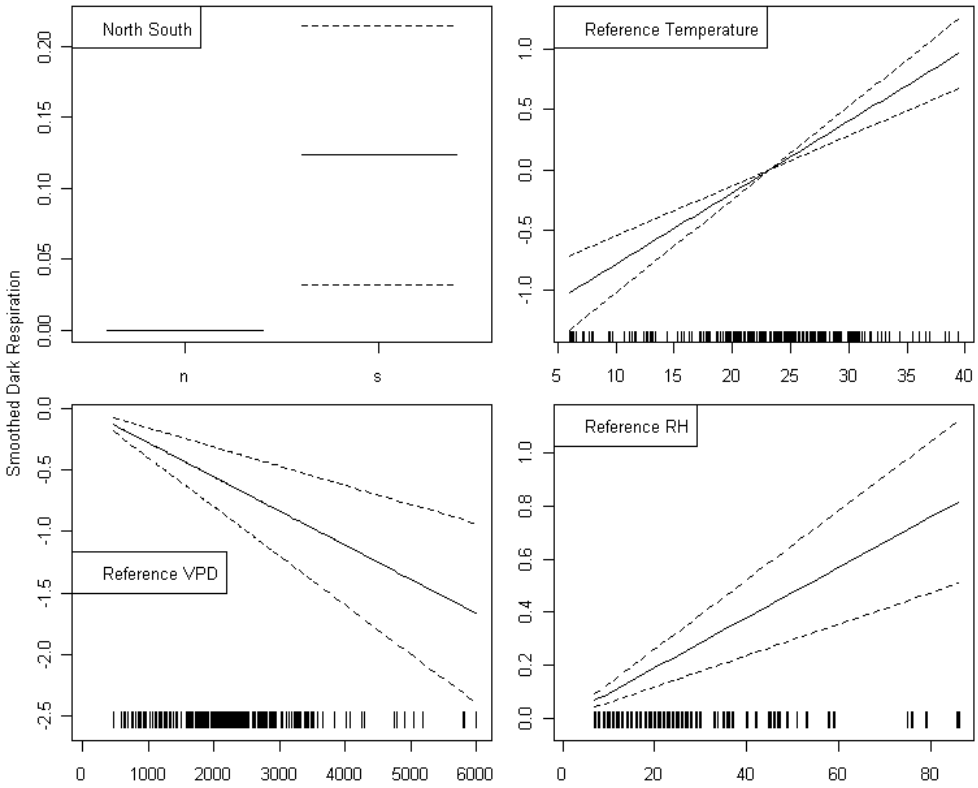

Figure 66. Smoothed respiration response of all species open model to a) aspect b) stand temperature c) stand VPD d) stand RH.

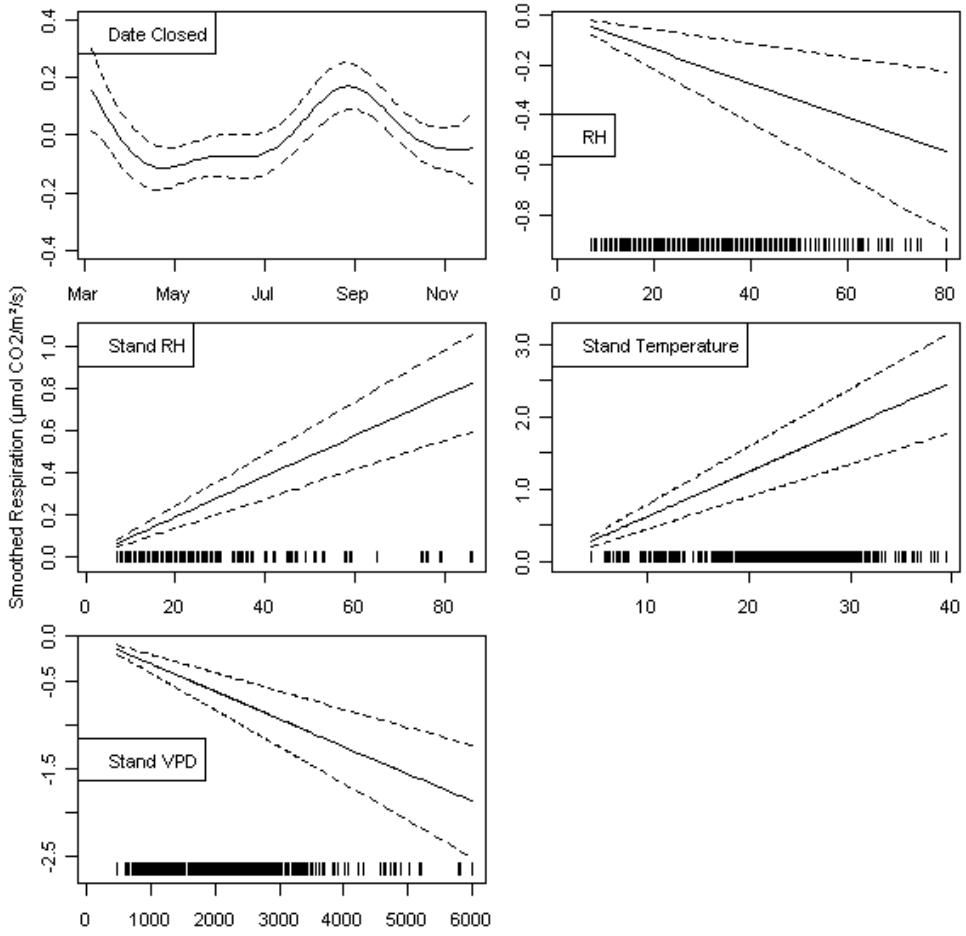

Figure 67. Smoothed respiration response of all species full model to a) date b) RH c) stand RH d) stand temperature e) stand VPD.

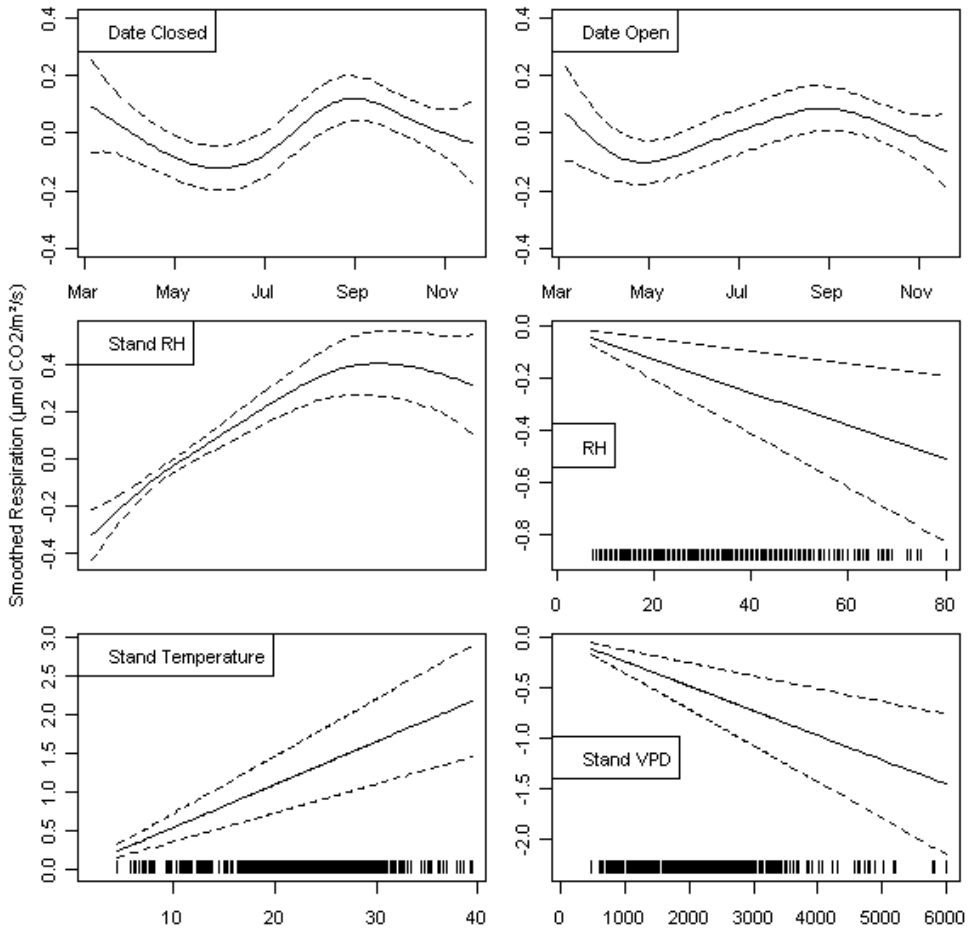

Figure 68. Smoothed respiration response of all species full-oc model to a) closed stand date b) open stand date c) stand RH d) RH e) stand temperature f) stand VPD.