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Abstract: Solar irradiance and precipitation are the most likely drivers of the seasonal variation of net primary productivity (*NPP*) in tropical forests. Since their roles remain poorly understood, we use litter traps, dendrometer bands and census data collected from one hectare permanent plots to quantify the seasonality of above-ground *NPP* components and weather parameters in 13 sites distributed along a 2800-m altitudinal gradient ranging from lowland Amazonia to the high Andes. We combine canopy leaf area index and litterfall data to describe the seasonality of canopy production. We hypothesize that solar irradiance is the primary driver of canopy phenology in wetter sites, whereas precipitation drives phenology in drier systems. The seasonal rhythm of canopy *NPP* components is in synchrony with solar irradiance at all altitudes. Leaf litterfall peaks in the late dry season, both in lowland (averaging 0.54 ± 0.08 Mg C ha y^{-1}, n = 5) and montane forests (averaging 0.29 ± 0.04 Mg C ha y^{-1}, n = 8). Peaks in above-ground coarse woody *NPP* appears to be triggered by the onset of rainfall in seasonal lowland rain forests (averaging 0.26 ± 0.04 Mg C ha y^{-1}, n = 5, in November), but not in montane cloud forests.

Key Words: carbon dynamics, ecophysiology, litterfall, net primary productivity, seasonality, soil water content, solar irradiance, temperature, tropical montane cloud forest

INTRODUCTION

Altitudinal gradients in the tropics can provide an excellent natural laboratory for examining the long-term interactions between forest ecosystems and environmental parameters, and for understanding ecosystem responses to environmental change (Malhi *et al.* 2010). It has long been observed that forest above-ground biomass tends to decrease with altitude in the tropics (Crews *et al.* 1995, Delaney *et al.* 1997, Herbert & Fownes 1999, Leuschner *et al.* 2007), and more recently a number of studies have demonstrated that above-ground net primary productivity (*NPP*, the rate of growth of

wood and canopy biomass) also tends to decrease with altitude (Girardin *et al.* 2010, 2014; Huaraca Huasco *et al.* 2014, Kitayama & Aiba 2002, Moser *et al.* 2008, Raich 1997, Röderstein *et al.* 2005, Soethe *et al.* 2008, Tanner 1980). The reason for this decline remains the subject of a long-standing debate, with suggested drivers being temperature effects on plant metabolism or on nutrient cycling, low light levels in tropical montane cloud forests (TMCF) and soil waterlogging (Bruijnzeel & Veneklaas 1998, Bruijnzeel *et al.* 1993, Grubb 1977, Kitayama & Aiba 2002, Schuur & Matson 2001, Tanner *et al.* 1998, Vitousek & Sanford 1986).

Although the absolute value of mean annual *NPP* has now been quantified for a number of tropical lowland and montane sites, no study to date has examined the patterns of *NPP* seasonality across multiple sites, and

in particular along environmental gradients. Describing and quantifying such patterns can help understand the nature and importance of seasonality in tropical forest ecosystems.

The effects of long-term changes in the seasonality of temperature, rainfall and cloud cover on tropical lowland and montane forests are potentially very significant, but remain poorly understood (Collins *et al.* 2013, Huaraca Huasco *et al.* 2014, Rapp & Silman 2012). Recent field and remote-sensing studies in lowland Amazonian forests suggest that the *NPP* of humid Amazonian forests may synchronize to seasonal variation in solar irradiance, whereas *NPP* of drier Amazonian forests synchronizes to seasonal variation in water supply (Chave *et al.* 2010, Myneni *et al.* 2007, Rapp & Silman 2012, Wright & van Schaik 1994).

In this paper we present the first detailed study (to our knowledge) of how the seasonality of the components of above-ground NPP varies with elevation, along a 2800-m altitudinal gradient in the Peruvian Andes. We hypothesize that solar irradiance is the primary driver of canopy phenology in cloudier high-elevation sites, whereas precipitation drives phenology in drier systems. We address the following specific hypothesis: (1) the amplitude and phase of seasonal variation of solar irradiance and precipitation vary along the altitudinal gradient; (2) the partitioning of above-ground NPP between wood, leaves, flowers and fruit shows no variation with altitude; (3) the seasonal variation of above-ground NPP is synchronized with the seasonality of solar irradiance in cloudier sites, and synchronized with precipitation in sites that experience a dry season.

MATERIALS AND METHODS

Site description

Our study region is the focus of the interdisciplinary Andes Biodiversity and Ecosystem Research Group (Malhi *et al.* 2010). Eight experimental sites were established in 2006 from 1527 m to 3045 m asl on the eastern slope of the Andes, in the Kosñipata valley, Province of Paucartambo, Department of Cusco, Southern Peruvian Andes, one site was established at 1000 m in an adjacent valley (Tono valley), a further two lowland Amazonian sites (215 m and 223 m asl) were established in the Tambopata reserve, Tambopata Province, Department of Madre de Dios, Peru, approximately 244 km east of the main transect, and two lowland Amazonian sites (120 m and 150 m asl) were established in the Maynas Province, Department of Loreto, Peru, within the Allpahuayo-Mishana National Reserve. All sites were monitored according to the same protocol. Four plots were continuously monitored from 2006 to 2011, five were monitored from 2006 to 2008

and a further two plots were established in 2008 and monitored until 2011 (Appendix 1).

Girardin *et al.* (2010) reported annual *NPP* estimates for a number of these sites. More recently, Girardin *et al.* (2014), Huaraca Huasco *et al.* (2014), Malhi *et al.* (2014) and del Aguila-Pasquel *et al.* (2014) provided comprehensive descriptions of the carbon cycle for eight of these sites.

As geological substrate and topographic position can have a significant influence on forest dynamics (Takyu *et al.* 2002), all the TCMF plots were established along a ridge-top on umbrisols, with a thick humic layer increasing in depth from 5 to 30 cm along the altitudinal gradient (B. Quesada, pers. comm.). The montane forest plots are situated on a bedrock of Palaeozoic slates and shales, with the exception of TU-07 and TU-08, situated on a late-Permian granite intrusion bedrock. Plots at 1000 m and below were situated on clay-rich sediments formed from alluvial deposition (though all are now above river flood levels). Total soil nitrogen and available phosphorus in the TMCF sites were above the range typically reported for lowland rain forests (B. Quesada, pers. comm.). Soil carbon, nitrogen and phosphorus stocks in the top 50 cm were highest in the 2000–3045-m band, where there was a build-up of a thick layer of humic material (typically 20–30 cm thick) above carbon-rich topsoil (Girardin *et al.* 2014).

All plots along the altitudinal transect were selected in areas with relatively homogeneous stand structure, and with no sign of significant human influence. All had closed canopies without any large gaps, although lowland forests have less gaps and a more even canopy than TMCF forests. Forest composition changed with altitude: the most common families in the lowland plots were Clusiaceae, Bixaceae, Urticaceae, Moraceae and Fabaceae; lower montane plots were dominated by the families Sapotaceae, Moraceae, Clusiaceae, Urticaceae, Euphorbiaceae and Anacardiaceae, and the highest altitudinal plots were dominated by Clusiaceae, Cunoniaceae, Sabiaceae, Rosaceae and Lauraceae (Appendix 1). Species composition varied considerably between neighbouring plots, with likely impacts on productivity. At highest altitudes, the 3045-m stand (Wayqecha) was dominated by *Weinmannia crassifolia* and a number of successsional species (e.g. *Pentacalia* spp., *Ageratina* spp. and *Hesperomeles ferruginea*).

Weather data

Time series for solar irradiance (W m^{-2}), air temperature (°C), relative humidity (%) and precipitation (mm mo^{-1}) were collected from Automatic Weather Stations (AWS, Campbell Scientific) located *c.* 1 km from the 3045-, 1527- and 215-m stands (Halladay *et al.* 2012). The original

data were measured with at least 30-min resolution for the period July 2005 to December 2010. These data were quality controlled to remove outliers, and monthly time series were gap-filled as described in Girardin *et al.* (2014).

The transition from lower to upper montane forest often coincides with more persistent dry-season cloud condensation (Bruijnzeel 2004, Edwards & Grubb 1977, Hamilton *et al.* 1995). We do not have sufficient meteorological data to determine the altitudinal limits of the cloud immersion zone in the Kosñipata valley. Nonetheless, based on forest composition (e.g. large increase in vascular epiphyte and bryophyte biomass, Horwath 2011), soil properties (Zimmermann *et al.* 2009) and the ecophysiology (Girardin *et al.* 2010) of forests along the Kosñipata Valley, we estimate that the base of the cloud zone forms between 1527 and 1800 m asl (J. Rapp, pers. comm.). The cloud-forest zone extends to the tree line at approximately 3400 m asl, above which puna grasslands dominate (Halladay *et al.* 2012).

Net primary productivity

Above-ground coarse woody net primary productivity. We determined plot-level NPP_{ACW} using multiple censuses (2003, 2007, 2011) of the forest plots and three-monthly dendrometer band measurements (November 2006–September 2011). We completed tree censuses to determine the growth rate of existing surviving trees and the rate of recruitment of new trees. Data on dbh (diameter tape) and tree height (clinometer when possible, or visual estimate) were recorded for all trees ≥ 10 cm dbh. Mortality in any year was estimated for each site by calculating the biomass of trees that were measured alive in the previous annual census and were dead in the latest census. ACW biomass was calculated using the allometric equation of Chave *et al.* (2005) for tropical moist forests, employing data on diameter, height and wood density.

$$AGB = 0.0509 \times (\rho \times dbh \times H) \qquad (1)$$

where AGB is above-ground biomass (kg), ρ is density of wood (g cm^{-3}), dbh is diameter at breast height (cm) and H is height (m). Wood density was estimated for each species from a global database of tropical forest wood density (Chave *et al.* 2009), ideally assigned to species, but to genus or family level where species identity or species-level wood-density data were not available. To convert biomass values into carbon, we assumed that dry ACW biomass is 47.3% carbon, based on recent studies in lowland forests in Panama that included volatile carbon compounds not recorded by conventional dry assessment (Martin & Thomas 2011). For the few trees where height data were not available we estimated height by employing a plot-specific polynomial regression between dbh and height. Tree fern incidence ranged from 0% in the lowlands to 21% at 2020 m, peaking between 1885 m and 2758 m asl. Palm tree incidence varied from 0% (3045 m) to 27% in one plot in the Tambopata lowlands. The biomass was then summed over all trees > 10 cm dbh to estimate total above-ground biomass. Above-ground woody production was calculated as the sum of biomass increase of individual surviving trees between census intervals.

To determine seasonal variation in woody growth rates, we installed dendrometer bands in January 2007 or 2009 (Appendix 1) on approximately 200 randomly selected trees in each plot (all trees in Tambopata lowland plots). The 200 dendrometer bands were measured every 3 mo with callipers. The dendrometer data were scaled up to 1 ha by using the annual full census data to determine the ratio of wood net primary productivity (NPP_{ACW}) of all trees over NPP_{ACW} of dendrometer trees. This ratio provided a scaling factor that we applied to the dendrometer data, to estimate seasonal NPP_{ACW} for the entire plot (i.e. to include trees that had no dendrometers), with the implicit assumption that the productivity of the dendrometer trees is representative of the wider population. The effects of seasonal moisture expansion on tree growth data were estimated to be negligible, based on examination of seasonal diameter variation of slow-growing trees (Girardin *et al.* 2014, Huaraca Huasco *et al.* 2014, Malhi *et al.* 2014). As the census interval was small (1 y) we did not apply a correction for trees that grow and die between census intervals without being recorded (Malhi *et al.* 2004). We did not account for the wood productivity of lianas in Tambopata, although their leaf productivity is recorded by litterfall traps.

Litterfall. Canopy litterfall was collected in 25 0.25-m^2 (50 × 50 cm) litter traps installed 1 m above the ground on each plot. There were only five litter traps at 2020 m asl due to topographic constraints. Litterfall was collected every 15 d over a period of 18 or 24 mo between 2006 and 2011 (Appendix 1), split into different components (leaves, fruits, flowers, seeds, woody tissue, bromeliads, other epiphytes (non-vascular epiphytes, mosses and liverworts) and unidentified fine debris), oven dried at 80 °C, and weighed. Seasonal variation of large palm leaf litter was not accounted for in the lowland plots, implying an underestimation of litterfall at 215 m and at 223 m asl. Malhi *et al.* (2014) estimate that palm leaf litterfall accounts for 5.46% ± 0.12% (TAM-05) and 75.7% ± 0.11% (TAM-06) of total leaf litterfall in the two lowland plots.

Litterfall is a good estimator of canopy productivity on annual or larger timescales. However, it represents

the timing of canopy biomass loss, not biomass gain, and hence cannot record seasonal variation in canopy productivity. We combined datasets of litterfall, canopy Leaf Area Index, LAI (del Aguila-Pasquel *et al.* 2014, Girardin *et al.* 2014, Huaraca Huasco *et al.* 2014, Malhi *et al.* 2014) and Specific Leaf Area, SLA (Salinas *et al.* 2011) to estimate the seasonal cycle of canopy net primary productivity (NPP_{canopy}) at low ($\sim$200 m), mid- ($\sim$1527 m) and high ($\sim$3000 m) altitudes (Doughty & Goulden 2008):

$$NPP_{canopy} = (\Delta LAI/SLA) + \text{litterfall} \qquad (2)$$

where ΔLAI is the change in LAI between months (m^2 m^{-2}), SLA is the mean specific leaf area (m^2 g^{-1}) and litterfall is total litterfall (g m^{-2}). We estimate SLA by taking a subsample of fresh leaf litterfall, scanning each leaf to determine fresh leaf area, and then drying at 80 °C and weighing the leaf to determine dry mass. SLA is fresh leaf area divided by dry leaf mass. Leaf area was calculated using image analysis software, Image J freeware (http://rsb.info.nih.gov/ij/). NPP_{canopy} is estimated in g m^{-2}.

Above-ground net primary productivity. NPP_{AG} can be estimated as the sum of NPP_{ACW}, NPP_{canopy}, branch turnover ($NPP_{branch\ turnover}$) and volatile organic compound production (NPP_{VOC}).

$$NPP_{AG} = NPP_{ACW} + NPP_{canopy}$$
$$+ NPP_{branch\ turnover} + NPP_{VOC} \qquad (3)$$

We obtained seasonal NPP_{ACW} estimates from the dendrometer band growth, and NPP_{canopy} values through the seasonal litterfall measurements coupled with seasonal variation in Leaf Area Index. Branch turnover productivity is hard to estimate at seasonal resolution (Girardin *et al.* 2014, Huaraca-Huasco *et al.* 2014), hence for the purpose of this paper, we concentrate on NPP_{ACW} and NPP_{canopy} seasonality. Finally, we did not estimate the contribution of volatile organic carbon emission from vegetation, which was found to be a very minor contribution in lowland tropical forest ecosystems (Malhi *et al.* 2009).

Analytical techniques. We used these data to describe the seasonal variation of NPP_{ACW} and litterfall along the Kosñipata altitudinal gradient. All uncertainty estimates are given as the standard error of the mean. Linear regression analyses were conducted to identify significant altitudinal trends in ecosystem allocation to above-ground components of productivity and the relationships between components. We used stepwise regression to explore the correlations between abiotic parameters and NPP_{ACW}. We explored the seasonal amplitude of each

abiotic and biotic parameter. Seasonal amplitude was estimated by subtracting the minimum 3-mo moving average from the maximum moving average recorded. Repeated-measures ANOVA was used to assess the significance of seasonal increases in productivity. All error estimates are provided as ± SE. All statistical analyses were performed with the R version 2.9.0 statistical package (Chambers 2008).

RESULTS

How do the amplitude and phase of seasonal variation of solar irradiance and precipitation vary along the altitudinal gradient?

Annual means. Over the study period, mean annual air temperatures ranged from 24.9 °C ± 1.06 °C (223 m asl) to 10.9 °C ± 0.44 °C (3045 m asl). A linear regression against altitude explained 97% of the variation in mean air temperature (P < 0.0001), with an air temperature lapse rate of 4.69 °C km^{-1} along the transect (Figure 1). Mean annual rainfall varied between 5302 mm y^{-1} below the cloud base (1527–1776 m asl) and 1560 mm y^{-1} at the highest altitude (3045 m asl), this may be lower than long-term means as the region experienced droughts during the study period, in 2005 and 2010. Neither water shortage nor prolonged water logging were recorded in the TMCF sites. Mean annual shortwave irradiance decreased significantly as cloud amount increased with altitude, from 4.8 GJ m^{-2} y^{-1} at 215 m asl to 3.51 GJ m^{-2} y^{-1} at 3045 m asl.

Seasonality in solar irradiance. In the lowlands, light availability was fairly constant throughout the year, as lower sun angles offset the lower cloudiness of the dry season (austral winter). Seasonality of solar irradiance was most pronounced at TMCF sites: low sun angles, short days and a lower cloud base (resulting in more frequent cloud immersion) resulted in a decrease in solar irradiance during the austral winter. At all altitudes, solar irradiance increased towards the end of the dry season, reaching a peak between September and November, just before the dry-to-wet transition period. Although we did not obtain sufficient data to estimate the full seasonal cycle of solar irradiance at each altitude, the data we obtained from low-, mid- and high-altitude sites allowed us to record the seasonality of solar irradiance across the gradient (Figure 2a).

Precipitation. All sites showed strong seasonal variation of rainfall, with highest values recorded between December and February (Figure 2b). The dry season
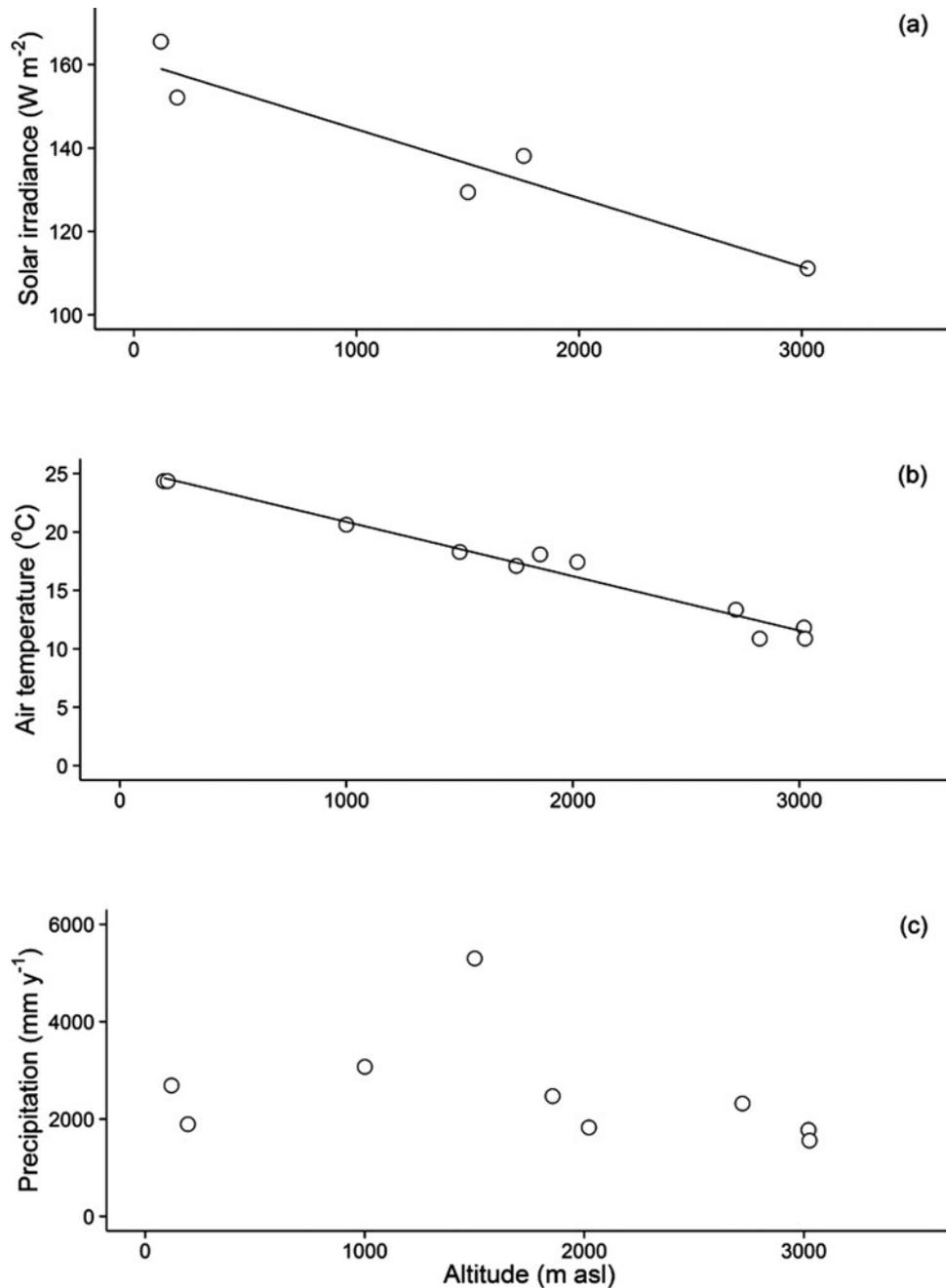
Figure 1. Weather patterns along the Kosñipata altitudinal gradient, Peruvian Andes. Solar irradiance (W m^{-2}, r^2 = 0.94, P < 0.001) (a), mean annual air temperature (°C, SE < 0.05, r^2 = 0.96, P < 0.0001) (b) and mean annual precipitation (c) are reported at each altitude. We provide data from Acjanaco (3950 m asl), a weather station located in the grassland above the treeline, although it is not a plot in this study. Error estimates are provided as ± SE.

caused significant water deficits (precipitation <100 mm mo^{-1}) at the lowland sites, and may also cause seasonal water stress at the top of the transect, near the treeline (although evapotranspiration rates are likely to be lower). The intermediate montane sites showed less seasonality in water availability and soil moisture content, with precipitation remaining fairly high in the dry season (lower montane sites) and/or cloud immersion suppressing water loss through evapotranspiration (upper montane sites). In the lowlands, the Allpahuayo sites (120 m asl and 150 m asl) had less seasonality in rainfall than other lowland Amazonian forests, with rainfall ranging from 100 mm mo^{-1} to 300 mm mo^{-1}, and no dry season.
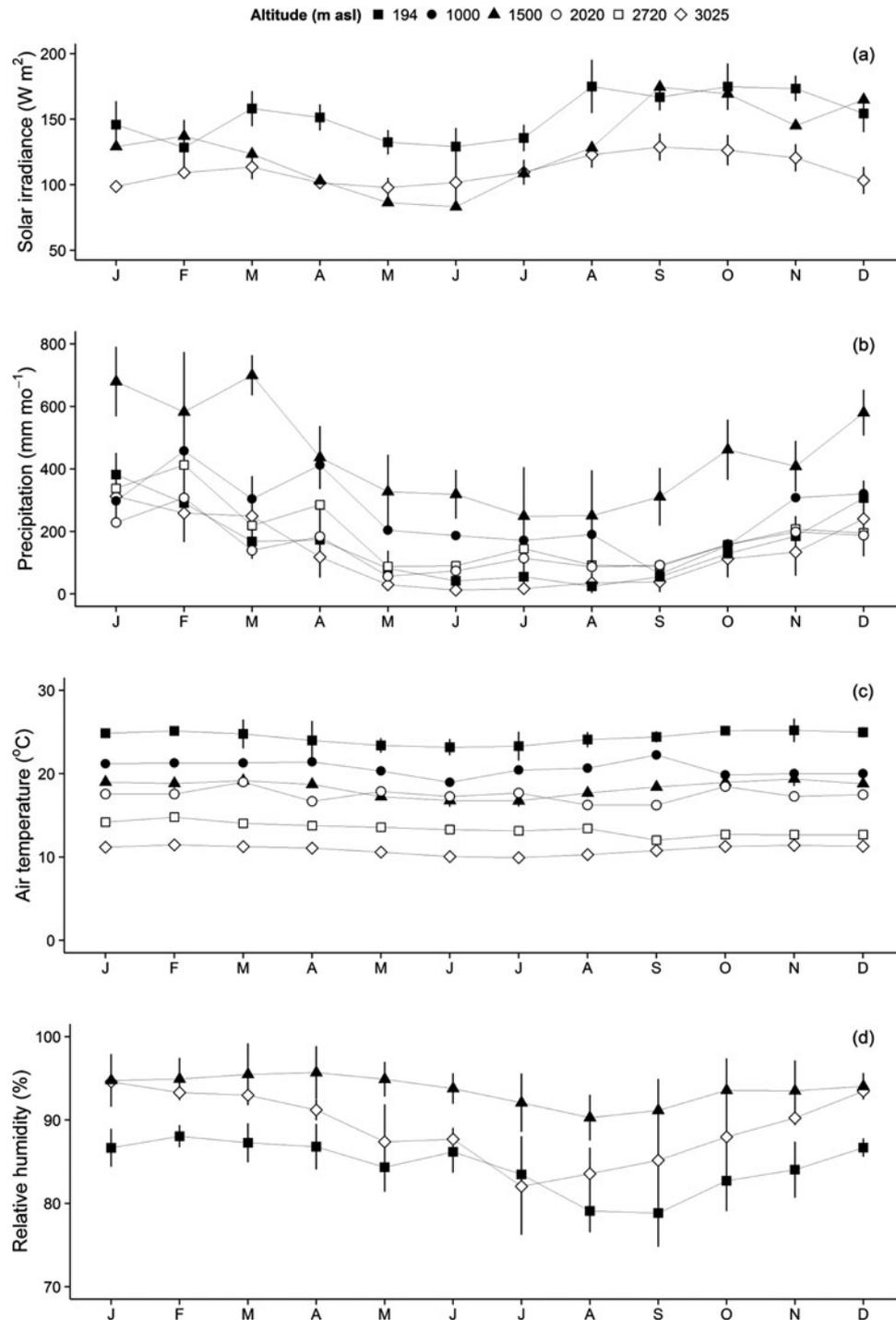
Figure 2. Seasonality of weather components along the Kosñipata altitudinal gradient, Peruvian Andes. Solar irradiance (W m^{-2}) is reported at 3045 m, 1776 m, 1527 m and 215 m (a), precipitation (mm mo^{-1}) at 3045 m, 2758 m, 1885 m, 1776 m, 1527 m and 215 m, air temperature (ºC) at 3045 m, 2758 m, 2020 m, 1885 m, 1776 m, 1527 m and 215 m, and relative humidity (%) at 3045 m, 1527 m and 215 m. Error estimates are provided as ± SE.

Air temperature. We found very little seasonal variation in air temperature along the altitudinal gradient (Figure 2c). Relative humidity shows moderate seasonality at the lowland and upper treeline ends of the transect (Figure 2d) in synchrony with the wet and dry seasons, but little seasonality at the intermediary montane sites, where cloud immersion is frequent in the dry season.

How does the partitioning of the components of NPP_{AG} between wood, leaves, flowers and fruit vary with altitude?

Total NPP_{AG} has previously been shown to decline substantially with altitude for this transect (Girardin *et al.* 2010). Strikingly, the allocation of the components of NPP_{AG} show no trends with altitude. On average, the fraction of total NPP in the canopy is 45% ± 2%, and in above-ground coarse woody material is 23% ± 1%. The mean fraction of canopy NPP in flowers and fruit material is 8% ± 1%, and in fine wood (twig) production is 15% ± 0.5%. Epiphyte litter (probably significantly underestimated because much epiphyte material can decompose in situ) accounts for less than 2% ± 0.5% of litterfall in the montane cloud forests, but makes a negligible contribution to the lowland and submontane forests (Figure 3).

How does the seasonal variation in the components of NPP_{AG} vary with altitude?

Above-ground coarse woody net primary productivity. We recorded seasonal trends of NPP_{ACW} at all altitudes (Figure 4). Forests located below the cloud base showed clear seasonal trends of NPP_{ACW}, with significantly higher growth rates reported during the peak wet season, November–March (0.30 ± 0.03 Mg C ha^{-1} mo^{-1} at 215 m asl, 0.25 ± 0.02 Mg C ha^{-1} mo^{-1} at 223 m asl, 0.43 ± 0.06 Mg C ha^{-1} mo^{-1} at 120 m asl and 0.40 ± 0.06 Mg C ha^{-1} mo^{-1} at 150 m asl) and minimum growth rates during the peak dry season, May–August (0.16 ± 0.02 Mg C ha^{-1} mo^{-1} at 215 m asl, 0.17 ± 0.02 Mg C ha^{-1} mo^{-1} at 223 m asl, 0.20 ± 0.03 Mg C ha^{-1} mo^{-1} at 120 m asl and 0.14 ± 0.02 Mg C ha^{-1} mo^{-1} at 150 m asl). This is true even in the northern Peru Allpahuayo plots, where rainfall remains quite high in the dry season and there is little seasonal water stress. There was a weak inverse seasonality at the highest altitudes (2758 m to 3045 m), with a tendency to increase woody production during the months of lower rainfall.

Canopy net primary productivity. We monitored the seasonal variation in each component of canopy litterfall at each altitude. Within the cloud immersion zone, leaf litterfall showed almost no seasonality, with the notable exception of the cloud-base transition plot at 1500 m which shows a peak in litterfall in the late dry season (August–October), and to a lesser degree the higher transition plot at 1776 m (Figure 5a). Below the cloud base (∼1500 m asl), the forest plots showed a strong peak in leaf litterfall rates (shedding) and synchronous production (replacement) through the mid and late dry season (August–October) (Figures 5b, 6).

For a subset of our plots, we combined our leaf litterfall with monthly collected canopy leaf area data to estimate the seasonality in leaf production and compare with the seasonality of leaf litterfall (Figure 6). These analyses showed that the periods of leaf litterfall (August to November, late dry season and early wet season) synchronize with periods of leaf production, resulting in little seasonal variation in total canopy leaf area. In this study transect, the dominant trees appear to favour shedding and simultaneously renewing their leaves in the dry season, rather than having a period of reduced canopy leaf area. Such shedding and renewal occurs even in sites with little seasonal water stress (e.g. the very wet montane sites at 1500 and 1750 m asl), suggesting that leaf life cycle events are not driven by water stress.

The litterfall of twigs, flowers and fruits (Figure 5) showed a distinct seasonality at most altitudes, with a broad minimum over the austral winter (dry season, low cloud base with frequent cloud immersion in the mountains). In the lowlands and at the 1527-m transition site, flower litterfall peaks in October and November, before the onset of heavy wet-season rains. As most flowers only last for a few weeks before shedding, flower litterfall is likely a good indicator of seasonality in flower production.

In the TMCF, seasonal trends were strongest in the plots located at the lower (1527 m asl) and upper (2758 m asl) limits of the cloud immersion zone, with a bimodal peak mirroring those of solar irradiance. In the lowlands, all plots showed strong seasonality, with a period of increased flower fall at the start of the wet season, indicating a peak in flower production at the end of the dry season, when solar irradiance reaches its maximum values. Only the 215-m plot showed evidence of a bimodal peak in flower fall, at the start and at the end of the wet season.

Fruit litterfall showed no strong seasonality, but there was some evidence of a broad minimum during the dry season (May–July) and a broad maximum over the wet season (Figure 5e, f). This suggests fruit tended to develop in the few months after flowering (mid-late dry season), peaking in development in the early wet season. However, the fruitfall signal is smeared out by differing fruit development cycles between species, and possibly also by frugivory, which explains the less sharp patterns of seasonality in fruit fall.

Seasonal amplitude. The seasonal amplitude of solar irradiance, precipitation and air temperature showed no significant trends along the altitudinal gradient. Of all components of NPP_{AG} monitored, only leaf litterfall showed a significant decrease in seasonal amplitude with increasing altitude. The lowland sites showed more seasonality in leaf production, although this result partially reflected the higher absolute amounts of
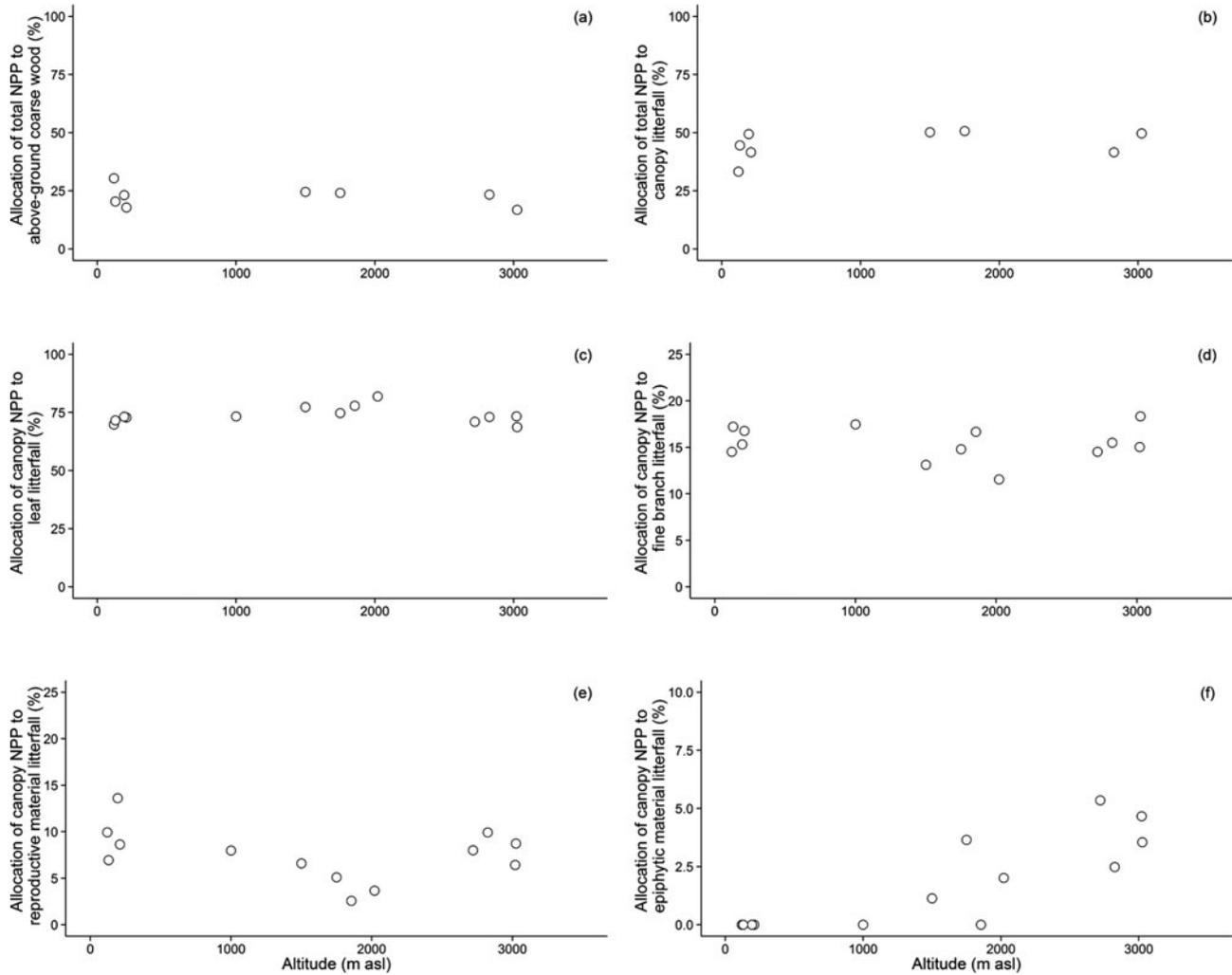
Figure 3. Allocation of total net primary productivity (NPP_{Total}) to above-ground coarse wood (NPP_{ACW}) (a) and canopy (NPP_{canopy}) (b) productivity, and allocation of canopy net primary productivity (NPP_{canopy}) to canopy components along the Kosñipata altitudinal gradient, Peruvian Andes. Annual canopy litterfall data are separated into allocation (%) to leaves (c), fine branch (d), reproductive material (flowers and fruit) (e) and epiphytic material (f) along the altitudinal gradient. Epiphytic material increases significantly with altitude ($r^2 = 0.69$, P < 0.001).

leaf production at these sites. The seasonal amplitude of NPP_{ACW} and of the productivity of reproductive organs (estimated as flower and fruit litterfall) remained remarkably constant over the altitudinal gradient (Figure 7).

Is there any evidence of synchrony between the seasonal variation of productivity and the seasonality of light or precipitation, and does the pattern of synchrony vary with altitude?

NPP_{canopy} and solar irradiance. The seasonality of NPP_{canopy} was in synchrony with the seasonality of solar irradiance at all sites. In most sites, the month of maximum NPP_{canopy} was recorded 1–2 mo before the peak in rainfall, when solar irradiance was at its maximum.

NPP_{ACW} and precipitation. In the lowlands, we recorded an increase in the production of above-ground coarse woody material at the start of the wet season. There was no correlation between NPP_{ACW} and precipitation in TMCF sites.

NPP_{flower}, NPP_{fruit} and solar irradiance. In wet forest sites, flowering patterns were in synchrony with the seasonal trends of solar irradiance. Flower litterfall peaked in October or November, implying that the increase in the production of flowers coincided with the increase in solar irradiance (September–November) at those sites. Two plots (1527 m asl and 2758 m asl) displayed a second peak in flowering that coincided with a secondary peak in solar irradiance (March).
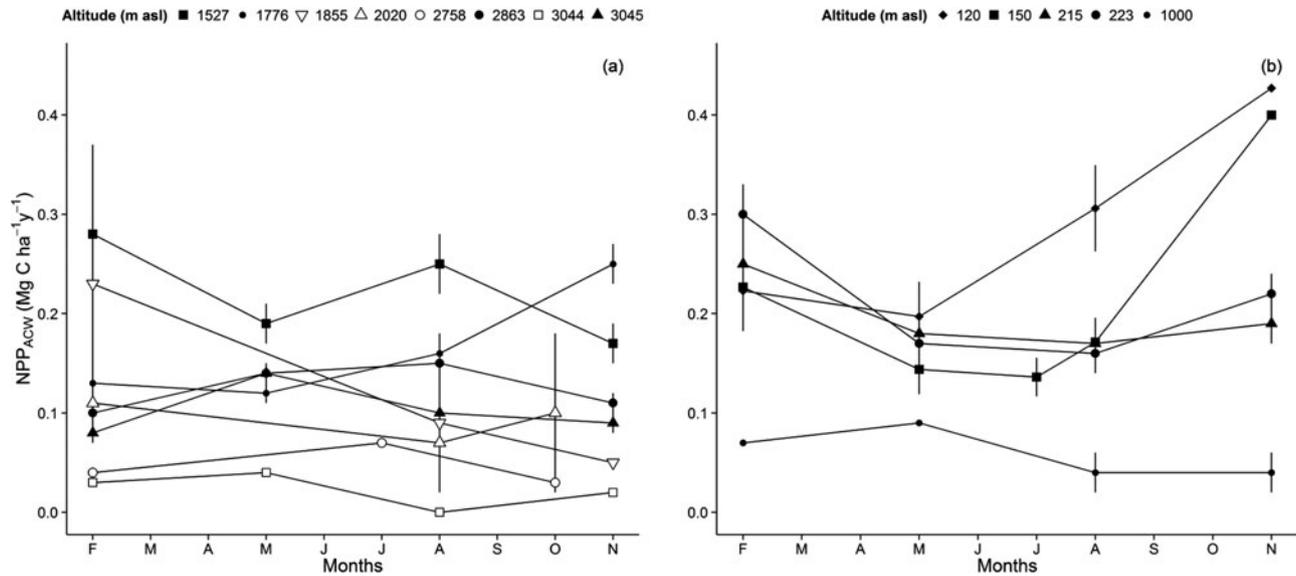
Figure 4. Seasonal variation of above-ground woody productivity (NPP_{ACW}) along the Kosñipata altitudinal gradient, Peruvian Andes. Data provided for Tropical Cloud Montane Forest Plots, at 3045 m, 3044 m, 2863 m, 2758 m, 2020 m, 1885 m, 1776 m, 1527 m (a), and plots located below the cloud base, at 1000 m, 215 m, 223 m, 120 m, 150 m (b). Error estimates are provided as $\pm$ SE.

DISCUSSION

Seasonal trends of above-ground net primary productivity

Drivers of NPP_{canopy} seasonality. The seasonality of NPP_{canopy} appears to be in synchrony with solar irradiance and maintains this pattern even in plots with seasonal water stress, partially confirming hypothesis (3). This may be because trees optimize their resources to boost photosynthetic rates through new leaves at a time of high photosynthetically active radiation (PAR). An alternative hypothesis is that trees invest in building new leaves during the dry season, a period of lower relative humidity and therefore lower pathogen, fungal and insect herbivory pressure (Givnish 1999, Leigh 1999, Wright & van Schaik 1994).

Canopy litterfall as a proxy for NPP_{canopy} seasonality. The data presented in this study are unique in that we were able to track NPP_{canopy} in terms of leaf flush and senescence, rather than relying solely on litterfall as a proxy for productivity. Litterfall is understood to be a reliable estimate of canopy productivity over annual timeframes in ecosystems in equilibrium, however, the relationship between litterfall and leaf production on a seasonal timescale in evergreen tropical forests has only recently been explored (Doughty & Goulden 2008).

We found that seasonality of canopy litterfall closely tracks seasonality of NPP_{canopy} at all sites, except Wayqecha (3045 m asl) (Figure 6). In most forests we monitored, the production of new leaves (leaf flush)

matched the loss of senescent leaves over the seasonal cycle. This suggests that the dominant trees in most of our plots are leaf-exchangers rather than leaf shedders, and that this period of leaf exchange is optimized for the mid- to late dry season. It also suggests that leaf litterfall is a reasonable indicator of seasonality in leaf production, especially in our lower-altitude plots.

The upper montane plots show a distinct peak in NPP_{canopy} in August, contrasting with a slow increase in litterfall. A decoupling of NPP_{canopy} and litterfall patterns suggest that leaf flush exceeds leaf senescence. As a result, we observe an increase in LAI in August, after a peak in solar irradiance. This trend is most notable in Wayquecha. The species composition of Wayqecha, high NPP, low basal area, low incidence of large trees, high density of small-dbh stems and high recruitment rates (Girardin *et al.* 2014, Farfan *et al.* pers. comm. August 2013), led us to speculate that this forest could be recovering from a past disturbance. Hence, Wayqecha has a different species composition to its neighbouring sites. We suggest that the difference in leaf phenology between Wayqecha and Esperanza may be explained by differences in species composition.

The lack of synchrony between NPP_{canopy} and litterfall may also occur in other TMCF sites along the gradient. Of all above-ground NPP components, only leaf litterfall experienced a significant decrease in seasonal amplitude with increasing altitude ($r^2 = 0.64$, P < 0.01) (Figure 7). It is possible that the difference in litterfall seasonality between TMCF and lowland sites reveals a difference in leaf longevity of TMCF dominant species, rather than a lower seasonality in photosynthetic activity of montane
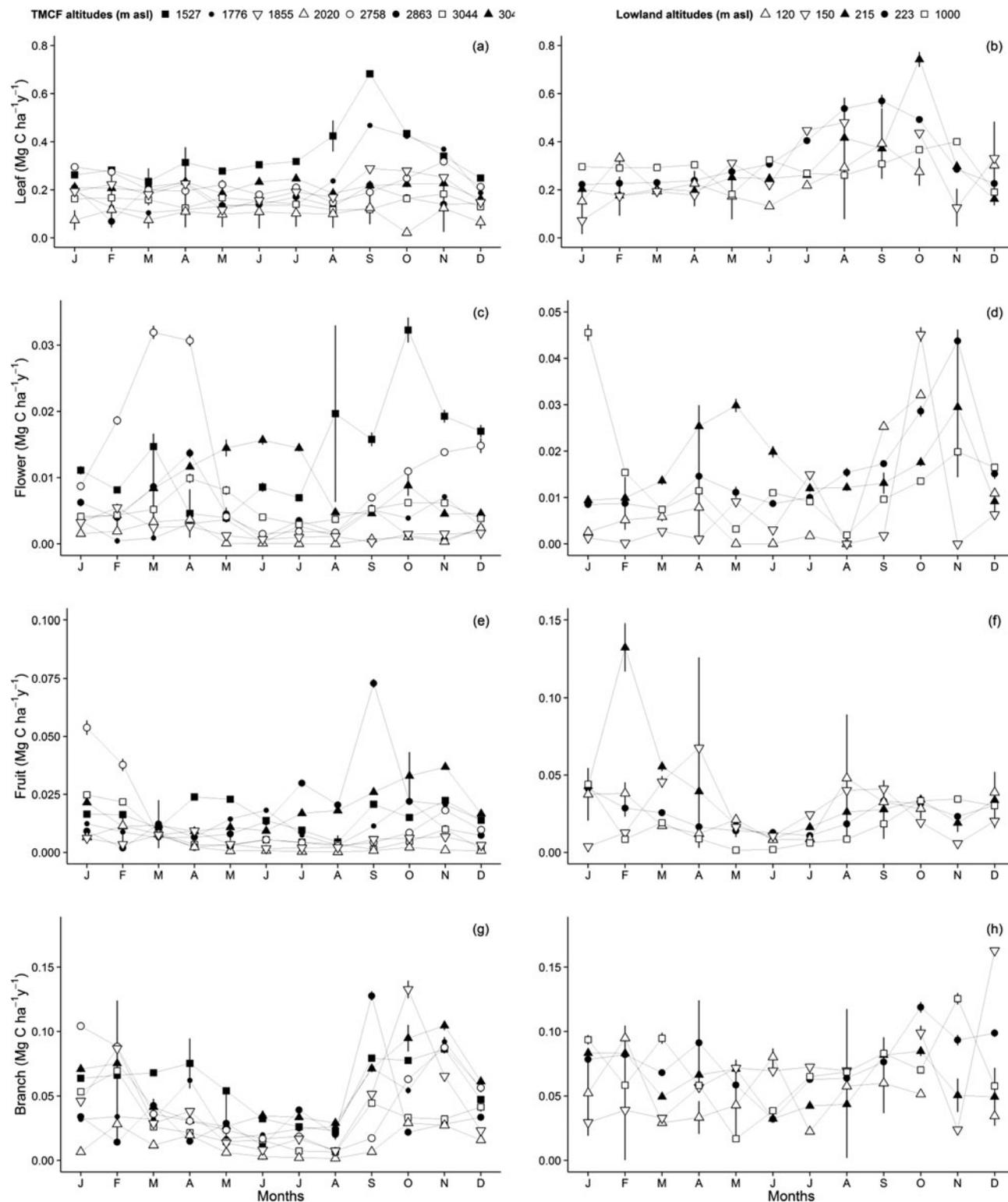
Figure 5. Seasonal variation of canopy litterfall components along the Kosñipata altitudinal gradient, Peruvian Andes. Canopy components were separated into leaf (a, b), flower (c, d), fruit (e, f), and fine branch (g, h). Data provided for Tropical Cloud Montane Forest plots, at 3045 m, 3044 m, 2863 m, 2758 m, 2020 m, 1885 m, 1776 m, 1527 m, and below the cloud base, at 1000 m, 215 m, 223 m, 150 m, and 120 m. Error estimates are provided as ± SE.

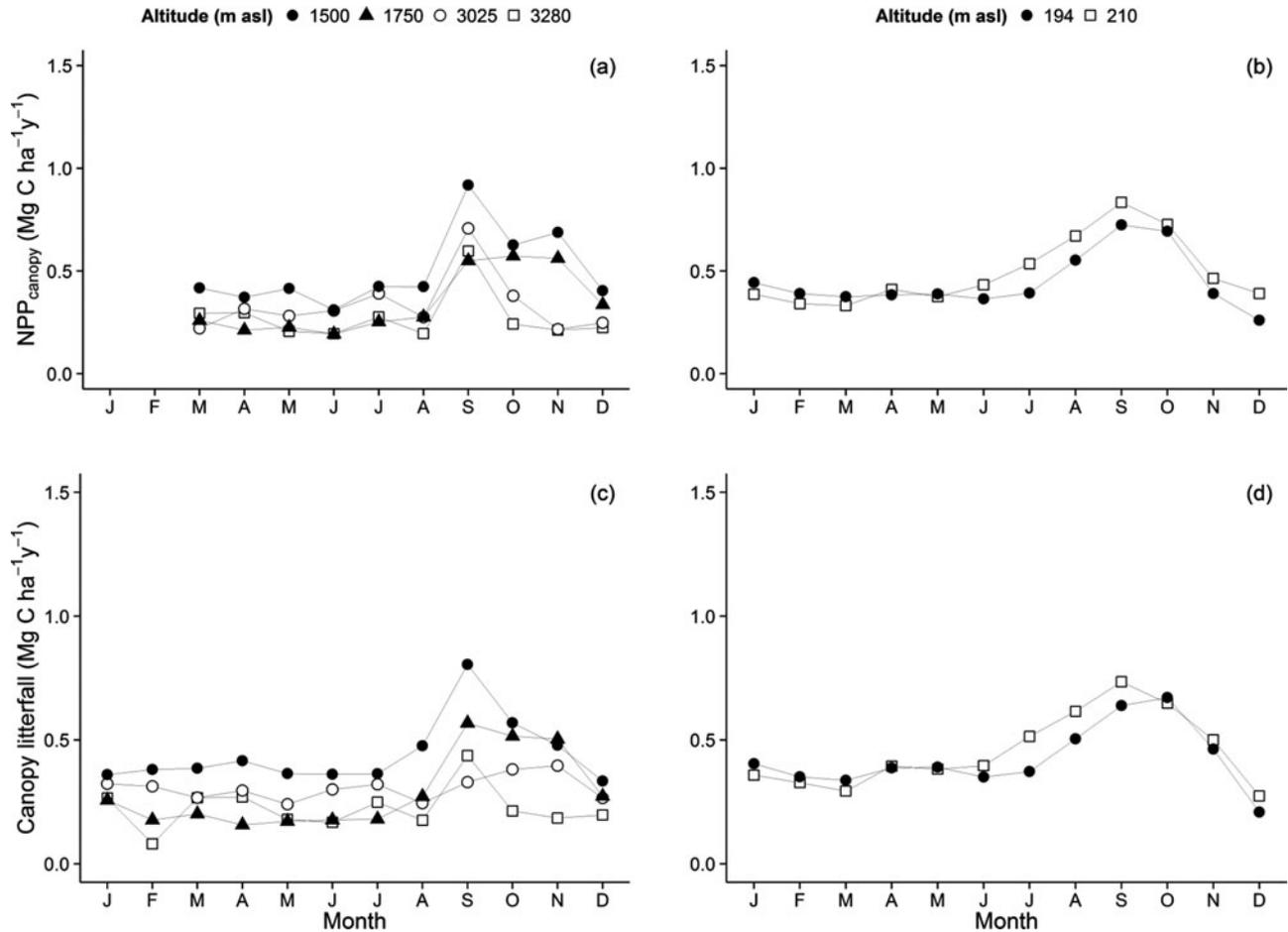**Figure 6.** Seasonal variation of canopy net primary productivity (*NPP*_{canopy}), compared with canopy litterfall along the Kosñipata altitudinal gradient, Peruvian Andes. *NPP*_{canopy} seasonality was separated for plots within the tropical cloud montane forest (TMCF) sites (a) and below the cloud immersion zone (b). Canopy litterfall was also separated into TMCF plots (c) and low-altitude plots (d). TMCF plots were located at 3045 m, 2863 m, and 1776 m, 1527 m, and sites located below the cloud immersion zone were at 215 m and 223 m.

forests. Mostly, TMCF environments appear to create selective pressures favouring leaf longevity (Moser *et al.* 2007, Olivares 1997, Williams *et al.* 1989).

The TMCFs of the Kosñipata gradient are dominated by evergreen species displaying a wide range of leaf longevity. Some leaf-exchanger species (e.g. *Hedyosmum* spp.) exhibit multiple flush patterns throughout the year, maintaining the same leaf area throughout the year. Others, such as *Clusia multiflora*, a dominant species of high-altitude forests, hold leaves for over 2 y (Olivares 1997). This new evidence highlights the importance of understanding the effects of shifts in species composition along the altitudinal gradient (Feeley *et al.* 2011, Rapp *et al.* 2012).

It is worth noting that our estimates will always underestimate *NPP*_{canopy} because we do not have seasonal estimates of *NPP* lost to herbivory (*NPP*_{herbivory}) at our sites. *NPP*_{herbivory}, the fraction of canopy consumed prior to litterfall, is a significant component of leaf productivity (Clark *et al.* 2001). Along the Kosñipata gradient, annual

canopy herbivory rates decrease with increasing altitude, from 0.76 ± 0.05 Mg C ha^{-1} y^{-1} at 223 m to 0.25 ± 0.04 Mg C ha^{-1} y^{-1} at 2863 m (Metcalfe *et al.* 2014).

Drivers of NPP_{ACW} seasonality. In the lowlands, the onset of the first wet-season rains appear to be a direct environmental cue for a shift in allocation of *NPP* from canopy to above-ground coarse woody material. The increase in *NPP*_{ACW} and decrease in *NPP*_{canopy} rates in November suggest a shift in allocation from leaves to wood production at the onset of the rainy season (Figure 4b). This shift in allocation from leaf net primary productivity, assumed to be driven by solar irradiance, to wood production, likely to be triggered by water availability, has been reported throughout lowland Amazonian forests (Doughty *et al.* in press, Rowland *et al.* 2013, Wagner *et al.* 2013). The relationship between the production of leaves and woody material is less clear in the TMCF (Figure 4a). We hypothesize that the allocation of photosynthates to
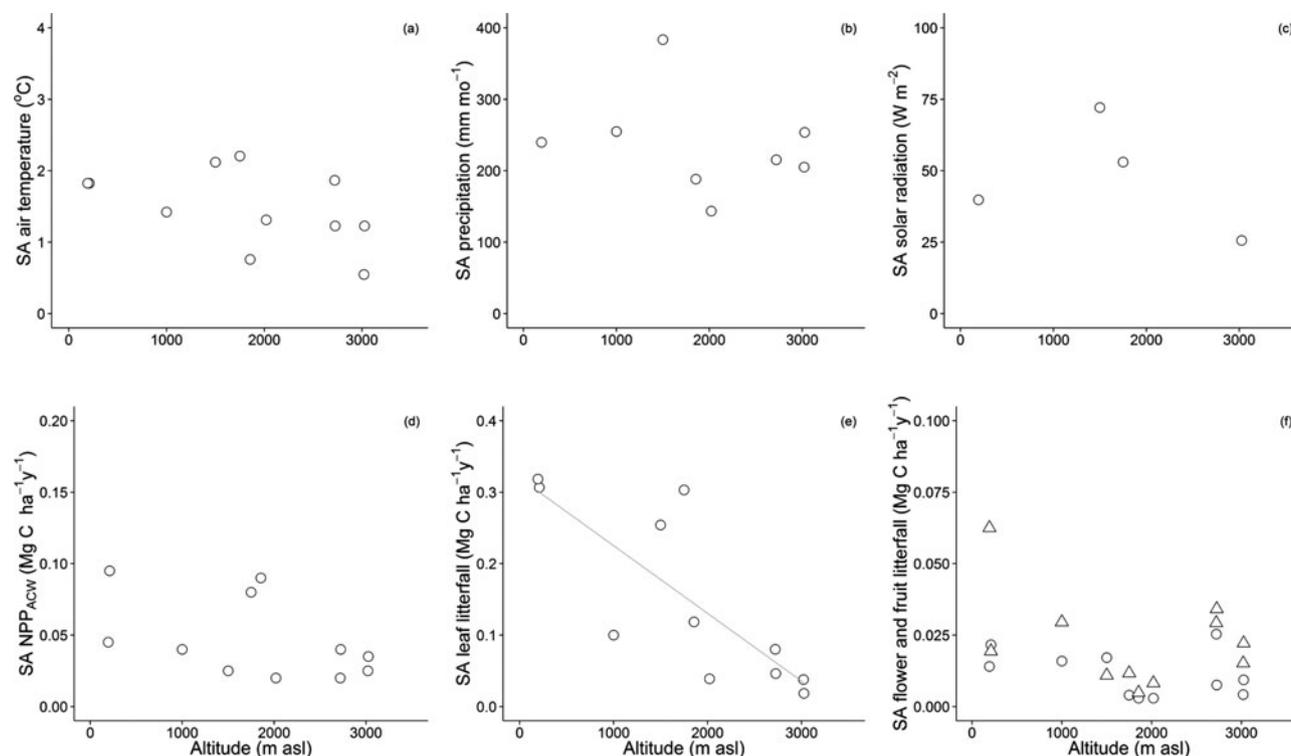
Figure 7. Seasonal Amplitude (SA) of weather components and above-ground components of net primary productivity along the Kosñipata altitudinal gradient, Peruvian Andes. SA of weather components are presented as air temperature (a), monthly precipitation (b) and solar irradiance (c). SA of all metrics or proxies for net primary productivity are provided in Mg C ha^{-1} y^{-1}: above-ground coarse woody material (d), leaf litterfall (e), flower and fruit litterfall (f).

wood is not triggered by seasonal moisture availability in TMCF plots as they do not experience seasonal moisture stress.

Allocation of *NPP*

We found that the allocation of NPP_{AG} to its various components was remarkably constant along the transect, despite strong variation in total NPP and environmental conditions, confirming hypothesis (2). This suggests that there are underlying and emergent optimal ratios for NPP_{AG} partitioning despite strong gradients in environmental conditions and complete turnover in species composition.

Girardin *et al.* (2010) found evidence of significantly lower NPP_{canopy} (< 4 Mg C ha^{-1} y^{-1}, P > 0.0001) and NPP_{ACW} (≤ 4 Mg C ha^{-1} y^{-1}, P > 0.0001) in the cloud immersion zone than below the cloud base (NPP_{canopy} > 4 Mg C ha^{-1} y^{-1}, NPP_{ACW} ≥ 4 Mg C ha^{-1} y^{-1}). They suggested that the low TMCF NPP_{AG} is driven by a change in regime affecting photosynthesis within the cloud immersion zone. For six TMCF sites along the Kosñipata gradient, Girardin *et al.* (2010) estimated that approximately 32% of total NPP was allocated to the canopy across the transect. Although *NPP* decreased with

altitude, the proportional allocation of *NPP* to above- and below-ground components showed no altitudinal trend. For 10 forest sites across lowland Amazonia, Aragão *et al.* (2009) found a total mean *NPP* figure of 12.8 ± 2.73 Mg C ha^{-1} y^{-1}, with 36% ± 12% of *NPP* allocated to the canopy. For 71 tropical forest plots, Malhi *et al.* (2011) reported an allocation to canopy components of approximately 34% ± 6%. Together, these studies established NPP_{canopy} as a particularly good indicator of total above-ground *NPP*.

Here we find that this consistency in carbon allocation to each plant component is sustained within the canopy. We report a remarkable consistency in proportional allocation to each NPP_{canopy} component along the altitudinal gradient (Figure 3). In all plots, the bulk of NPP_{canopy} was allocated to photosynthetic material (leaves). Hence, the seasonal trends of NPP_{canopy} essentially capture the seasonal trends of leaf productivity.

Reproductive phenology

The flowering patterns of most of the lowland forest sites suggest that the peak in flowering took place in the mid-late dry season, coinciding with a peak in solar irradiance. The fruiting and flowering phenology of the

montane forest sites also appear to be correlated with light incidence. As flowers and fruit have a short canopy lifetime, we assume that flower and fruit litterfall are a metric of their productivity rate, with a lag time of 1–3 mo for the fruiting. Hence, the values presented here are reported as NPP_{fruit} and NPP_{flower} (Malhi *et al.* 2014), with the important caveats that (1) frugivory may lead to a substantial underestimate of total fruit production and (2) fruit litterfall has a highly variable species-specific lag time of up to several months.

An increase in flowering during the season of maximal solar irradiance in forests where moisture is not a limiting factor is a recurring theme in the literature on tropical reproductive phenology (Borchert *et al.* 2004, van Schaik *et al.* 1993, Wright & van Schaik 1994). Seasonal variation in solar irradiance may be caused by changes in cloud cover regime, day length and solar angles. Increasing day length (Rivera *et al.* 2002) and increasing light incidence (Calle *et al.* 2010) have been proposed as direct environmental cues of flowering.

However, Wright (1996) stresses the importance of establishing a clear distinction between proximate (i.e. direct environmental) cues of plant phenology and the ultimate selective factors that have shaped phenology over evolutionary times, such as plant-insect coevolution (Frankie 1975). Relationships with other phenophases such as leaf flush or shedding (Borchert 1983) and timing of plant-animal interactions such as seed dispersal, pollination and herbivory (Borchert *et al.* 2005, Leigh 1999, Wright & Calderon 1995) have been proposed as evolutionary forces that drive reproductive phenological schedules.

In the lowland sites, dry-season conditions may be particularly favourable for pollinator populations (less rainy conditions impeding foraging, less fungal pathogens) and flowering may be cued to synchronize with the abundance of pollinators.

Within the TMCF, in contrast, there was a broad dip in flower and fruit litterfall during the dry-season austral winter (Figure 5). This is a period of low rainfall, low cloud base, high relative humidity, frequent cloud immersion and low solar irradiance (Halladay *et al.* 2012, Marthews *et al.* 2012). Such conditions may again inhibit insect pollinator populations through difficult foraging conditions and the prevalence of pathogens.

Throughout the altitudinal gradient, the peaks in fruit litterfall occurred during the wettest season. This has been documented in several lowland forests, possibly to allow enough moisture for germination (Zimmerman *et al.* 2007), or to optimize fruit-animal interactions (Leigh 1999). We venture that the reduced fruit fall incidence during the periods of high cloud immersion frequency in TMCF plots may be a measure to avoid germination in periods of high pathogen and herbivory pressure.

The fruiting and flowering phenology of the 3045-m plot (Wayqecha) is shifted forward by 2 mo. This suggests that the reproductive seasonality of Wayqecha may be driven by phenological rhythms of dominant families, rather than being directly driven by solar irradiance.

Incidentally, the seasonality of twig litterfall is likely related to mechanical damage. The heavy rains, increased wind forces, weight of growing fruit and of frugivores may cause more broken twigs, explaining an increase in litterfall at times of high rainfall and tree reproductive activity.

Conclusions

This is the first study to examine seasonal rhythms of fractions of NPP along a tropical altitudinal gradient. As such, it provides important insights on the seasonality of tropical forests. We found evidence of synchrony between NPP_{canopy} and solar irradiance at all sites along the altitudinal gradient, even in plots that experienced seasonal water stress. We used litterfall, LAI and SLA data to estimate NPP_{canopy} and found that seasonality of canopy litterfall closely tracks seasonality of NPP_{canopy} at most sites, with a stronger correlation in lowland sites. In lowland forests, we recorded a shift in allocation from leaf to wood production that appeared to be correlated with the onset of wet-season rains. However, the environmental cue for a shift in allocation from leaves to wood appears to be different in TMCF. In terms of allocation, we found that the allocation of NPP_{AG} to its various components was remarkably constant along the transect, despite strong variation in total *NPP* and environmental conditions. Finally, we present community-level information on phenology, but our findings point to the importance of ecological interactions that drive the evolution of species-specific seasonal schedules. Hence, we suggest that documenting species-specific seasonality is a prerequisite for understanding the consequences of shifts in species composition in these forests.

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Appendix 1. Characteristics of study sites along the altitudinal gradient in the Peruvian Andes. Data from Zimmermann *et al.* (2009), Girardin *et al.* (2010, 2014), Salinas *et al.* (2011), Huaraca Huasco *et al.* (2014), Malhi *et al.* (2014), del Aguila-Pasquel *et al.* (2014), G. Asner and C.A. Quesada (pers. comm.). Soil carbon stock was estimated from the top 0–30 cm layer. Abbreviations: nutrients: phosphorus (P), nitrogen (N), carbon (C), organic layer (OL), mineral layer (ML); soil type: Alisol (Al), Gleysol (Gl), Arenosol (Ar), Cambisol (Ca), Umbrisol (Um); dominant Families: Moraceae (Mo), Fabaceae (Fa), Linaceae (Li), Clusiaceae (Cl), Bixaceae (Bi), Urticaceae (Ur), Myristicaceae (My), Urticaceae (Ur), Euphorbiaceae (Eu), Anacardiaceae (An), Sapotaceae (Sa), Cunoniceae (Cu), Lauraceae (La), Sabiaceae (Sa), Rosaceae (Ro).

Site	Allpahuayo		Tambopata		Tono	San Pedro		Trocha Union			Esperanza	Trocha Union	Wayq-echa
Plot code	ALP-11	ALP-30	TAM-05	TAM-06	TON-01	SPD-02	SPD-01	TU-08	TU-07	TU-04	ESP-01	TU-03	WAY-01
First year	2009	2009	2006	2006	2006	2006	2009	2006	2006	2006	2009	2006	2006
Last year	2011	2011	2011	2011	2009	2011	2011	2009	2009	2009	2011	2009	2011
Latitude	−3.95	−3.95	−12.8	−12.8	−12.9	−13.04	−13.0	−13.1	−13.1	−13.1	−13.2	−13.1	−13.2
Longitude	−73.4	−73.4	−62.3	−69.3	−71.6	−71.5	−71.5	−71.6	−71.6	−71.6	−71.6	−71.6	−71.6
Altitude (m asl)	120	150	223	215	1000	1527	1776	1885	2020	2758	2863	3044	3045
Slope (°)	1.4	1.5	4.5	2.2	8	27.1	30.5	38.8	18	21.2	27.3	22.4	30
Aspect (°)	n/a	196	186	169	n/a	125	117	158	n/a	118	302	114	112
Solar irradiance (GJ m^{-2} y^{-1})	5.22	5.22	4.8	4.8	n/a	4.08	4.36	3.96	n/a	3.49	n/a	n/a	3.51
Mean annual air temperature (°C)	25.2	25.2	24.4	24.4	20.7	18.8	17.4	18	17.4	13.5	13.1	11.8	11.8
Annual precipitation (mm y^{-1})	2689	2689	1900	1900	3087	5302	5302	2472	1827	2318	1560	1776	1560
Soil moisture (%)	26.8	10.8	21.8	35.5	39.8	37.3	37.6	9.7	15.5	37.3	24.3	41.5	23.1
Soil type	Al / Gl	Ar	Ca	Al	Ca	Ca	Ca	Ca	Ca	Um	Um	Um	
Total P (mg kg^{-1})	126	37.6	256	529	751	1630	1071	496	562	747	981	787	1413
Total N (%)	0.1	0.08	0.16	0.17	0.42	0.9	1.2	0.81	1.23	1.99	1.48	1.55	0.88
Total C (%)	1.19	1.13	1.51	1.2	5.01	13.6	22.7	14.3	28.7	28.3	28.6	27.2	19.3
Soil C stock (Mg C ha^{-1})	92.9	16.4	43.7	37.4	78.6	93.5	75.6	97.1	83.7	289	134	82.4	231
Soil organic layer depth (cm)	12	10	13	37	35	30	32	30	80	20	50	36	36
Soil pH	–	–	–	3.9	3.7	4	–	3.4	2.9	3	–	2.7	4.1
Soil profile (cm, OL/ML)	–	–	2/30	2/30	5/42	10/45	–	26/26	35/10	43/09	–	42/11	32/10
Dominant Families	–	–	Mo, Fa, Li	Cl, Bi, Ur	Cl, Mo, My	Ur, Eu, An	Sa, Mo, Cl	–	–	Cl, Cu, La	Cl, Cu, Sa	–	Cu, Cl, Ro