Spatial and temporal shifts in photoperiod with climate change

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1. *Introduction*
   (a) Photoperiod is a critical cue used by organisms to synchronize their activities with seasonal climatic changes (add other citations- there are many possibilities! if you have favorites, please add along with 1-2 words of what the activity is)(e.g., Hsu et al., 2011; Singh et al., 2017).
   (b) As species undergo climate change-induced shifts in space and/or time, the daylength they experience will be altered.
   (c) Many experiments have altered photoperiod, often interacting with temperature changes; however, photoperiod treatments in these experiments are not typically designed to be applied to climate change forecasting.
   (d) Here, we ask:
      i. How will climate change alter the photoperiod experienced by organisms, given observed climate change-induced biological shifts, both spatially and temporally?
      ii. What are the implications of these altered photoperiods for forecasts of climate change impacts?
      iii. Can the large quantity of experiments altering photoperiod be applied to forecasting biological implications of climate change (i.e. do they occur at the appropriate scale)?
2. *How will climate change alter the photoperiod experienced by organisms?*
   (a) Spatial shifts in species ranges and temporal shifts in species phenology and activity will alter the photoperiods experienced by organisms under climate change.
   (b) To date, most work has focused on how spatial range shifts with climate change will affect photoperiod (Saikkonen et al., 2012), but temporal shifts are actually likely to yield bigger changes in experienced photoperiod than spatial shifts (Figure 1).
   (c) Shifts in photoperiod may vary with latitude and time of year, especially since phenology varies with latitude (Figure 2), and species responses to photoperiod vary with latitude (Figure 2).
   (d) Photoperiod sensitivity can also vary with latitude (Figures 3, 4), so it is unclear how these two things interact. Cat has added a text file to the latitude analysis folder that summarizes papers that have looked at latitudinal effects on photoperiod.
3. *What are the implications of these altered photoperiods for forecasts of climate change impacts?*
   (a) Phenology will be altered, given that daylength is known to affect vegetative growth, cell elongation, and budburst (Linkosalo and Lechowicz, 2006; Erwin, 1998; Sidaway-Lee et al., 2010; Hsu et al., 2011).
   (b) It has been proposed that photoperiod may eventually become a limiting factor, constraining the ability of trees to shift their phenology with warming (Koerner and Basler, 2010; Vitasse and Basler, 2013; Morin et al., 2010).

(c) Interactions between photoperiod and forcing and chilling could result in muted or exaggerated phenological shifts, compared to what would be expected based on temperature change alone. Say something about crossing thresholds of daylength and the "external coincidence model" for photoperiod control (Bastow and Dean, 2002; Kobayashi and Weigel, 2007; Andrés and Coupland, 2012; Singh et al., 2017)?

(d) Effects of photoperiod on forecasting of biological impacts of climate change needs additional investifation. In some forecasting methods (e.g. species distirbution modelling), the role of photoperiod is largely ignored (i think this is true? add some citations). In other cases, photoperiod is incorporated into foreacasts, along with other variables such as evaporative demand, and temperature (e.g. ED Jolly et al., 2005; Medvigy et al., 2013). These models need to be more widely tested, e.g. in different ecosystems/species, and need to incorporate recent findings about the role of photoperiod in phenology.

4. *Can existing experiments be applied to forecasting?*

   (a) In some cases, yes, experiments manipulate photoperiod at relevant scales (Figure 5, Table 1).

   (b) However, most experiments manipulate photoperiod much more dramatically than will occur with climate change (Figures 5, 6,7, but see (Basler and Körner, 2012)), so it is difficult to extrapolate findings. (This may not be true for all latitudes- for example high latitudes experience more dramatic changes in photoperiod across the year.)

   (c) There is a great need to better understand exactly how photoperiod acts as a cue (linear response? threshold? how does it interact with temperature to break dormancy?)

5. *Conclusions*

   (a) Organisms may experience large changes to the photoperiod they experience, under climate change, even if they do not shift their ranges spatially.

   (b) More studies needed with fine-scale changes in photoperiod.

To do:

1. Make Table of studies testing if photoperiod varies by latitudinal origin- cat started on this.

Random notes that may be useful:

1. Bradshaw and Holzapfel (2001) showed that the pitcher plant mosquito, Wyeomyia smithii, has evolved a shorter critical photoperiod in association with a longer growing season. Northern populations of this mosquito now use a shorter day-length cue to enter winter diapause, doing so later in the fall than they did 24 years ago.

2. Decreasing day-length is the main environmental cue inducing growth cessation and bud set in many perennial plants, including poplar

   (a) Lagercrantz U: At the end of the day: a common molecular mechanism for photoperiod responses in plants?. J Exp Bot. 2009, 60: 2501-2515. 10.1093/jxb/erp139.

   (b) Howe GT, Gardner G, Hackett WP, Furnier GR: Phytochrome control of short-day-induced bud set in black cottonwood. Physiol Plant. 1996, 97: 95-103. 10.1111/j.1399-3054.1996.tb00484.x.

3. Response to photoperiod is under strong genetic control

(a) Bradshaw HD, Stettler RF: Molecular genetics of growth and development in Populus. IV. Mapping QTLs with large effects on growth, form, and phenology traits in a forest tree. Genetics. 1995, 139: 963-973.

(b) Keller SR, Soolanayakanahally RY, Guy RD, Silim SN, Olson MS, Tiffin P: Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, Populus balsamifera L. (Salicaceae). Am J Bot. 2011, 98: 99-108. 10.3732/ajb.1000317.

(c) Weih M: Intensive short rotation forestry in boreal climates: present and future perspectives. Can J Forest Res. 2004, 34: 1369-1378. 10.1139/x04-090.

References

Andrés, F., and G. Coupland. 2012. The genetic basis of flowering responses to seasonal cues. Nature reviews. Genetics 13:627.

Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. Agricultural and Forest Meteorology 165:73–81.

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Erwin, J. E. 1998. Temperature and light effects on stem elongation (plant growth regulation by physical and mechanical stimuli, for further development of horticulture in east asia). Journal of the Japanese Society for Horticultural Science 67:1113–1120.

Hsu, C.-Y., J. P. Adams, H. Kim, K. No, C. Ma, S. H. Strauss, J. Drnevich, L. Vandervelde, J. D. Ellis, B. M. Rice, et al. 2011. Flowering locus t duplication coordinates reproductive and vegetative growth in perennial poplar. Proceedings of the National Academy of Sciences 108:10756–10761.

Jolly, W. M., R. Nemani, and S. W. Running. 2005. A generalized, bioclimatic index to predict foliar phenology in response to climate. Global Change Biology 11:619–632.

Kobayashi, Y., and D. Weigel. 2007. Move on up, it's time for change—mobile signals controlling photoperiod-dependent flowering. Genes & development 21:2371–2384.

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Linkosalo, T., and M. J. Lechowicz. 2006. Twilight far-red treatment advances leaf bud burst of silver birch (betula pendula). Tree physiology 26:1249–1256.

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Morin, X., J. Roy, L. Sonié, and I. Chuine. 2010. Changes in leaf phenology of three european oak species in response to experimental climate change. New Phytologist 186:900–910.

Saikkonen, K., K. Taulavuori, T. Hyvönen, P. E. Gundel, C. E. Hamilton, I. Vänninen, A. Nissinen, and M. Helander. 2012. Climate change-driven species' range shifts filtered by photoperiodism. Nature Climate Change 2:239.

Sidaway-Lee, K., E.-M. Josse, A. Brown, Y. Gan, K. J. Halliday, I. A. Graham, and S. Penfield. 2010. Spatula links daytime temperature and plant growth rate. Current biology 20:1493–1497.

Singh, R. K., T. Svystun, B. AlDahmash, A. M. Jönsson, and R. P. Bhalerao. 2017. Photoperiod-and temperature-mediated control of phenology in trees–a molecular perspective. New Phytologist 213:511–524.

Vitasse, Y., and D. Basler. 2013. What role for photoperiod in the bud burst phenology of european beech. European Journal of Forest Research 132:1–8.

Tables

Table 1: **Growth chamber experiments and their photoperiod treatments**, compared to the spatial and temporal shifts required for organisms to experiments photoperiod changes equivalent to those treatments. For shifts in space, 'ER' indicates that the photoperiod treatments exceeds the change of photoperiod from moving up to 40 degrees latitudinally on June 21. For shifts in time, 'ER' indicates that the range of photoperiod treatments exceeds the change in daylengths at that latitude during the entire year. 'max NA' indicates that the maximum daylength treatment does not exist at that latitude; 'min NA'indicates that the minimum daylength treatment does not exist at that latitude.

idstudy	continent	lat	long	day_range	delta	space	time
ashby62_exp1	north america	42.99	-89.41	8-16	4.00	18.2	min NA (9)
basler14_exp1	europe	46.31	8.27	9.2-16	1.00	6	-22
caffarra11b_exp2	europe	52.32	-6.93	10-16	2.00	7.5	-30
devries82_exp1	europe	51.98	5.66	8-24	16.00	ER	ER
falusi90_exp1	europe	46.03	10.75	9-13	4.00	16	-82
falusi96_exp3	europe	38.27	15.99	9-13	4.00	21.6	-111
ghelardini10_exp1	europe	43.72	11.37	8-16	8.00	21.9	ER
heide05_exp1	europe	56.18	-4.32	10-24	14.00	ER	ER
heide08_exp1	europe	48.40	11.72	10-24	14.00	ER	ER
heide11_exp1	europe	59.67	10.67	10-20	10.00	ER	max NA (18.7)
heide12_exp1	europe	56.50	-3.06	10-24	5.00	8.9	-64
heide15_exp2	europe	56.50	-3.06	10-15	1.00	3.2	-13
heide93_exp1	europe	59.50	10.77	8-24	16.00	ER	ER
heide93a_exp1	europe	59.67	10.83	8-24	16.00	ER	ER
heide93a_exp3	europe	47.50	7.60	13-16	1.00	5.7	-18
howe95_exp1	north america	40.55	-124.10	9-24	2.00	13.1	-64
laube14a_exp1	europe	48.40	11.71	8-16	4.00	14.3	-87
myking95_exp1	europe	56.10	9.15	8-24	16.00	ER	ER
myking97_exp1	europe	59.67	10.77	12-24	12.00	ER	max NA (18.7)
nienstaedt66_exp1	north america	44.17	-103.92	8-20	12.00	ER	ER
okie11_exp1	north america	32.12	-83.12	0-12	12.00	ER	ER
partanen01_exp1	europe	61.93	26.68	6-16	10.00	ER	-105
partanen05_exp1	europe	61.82	29.32	5-20	5.00	ER	-67
partanen98_exp1	europe	60.03	23.05	8.66-12	3.34	5.1	-37
pettersen71_exp1	europe	59.66	10.77	10-24	2.00	4	-23
Sanz-Perez09_exp1	europe	40.40	-3.48	10-16	6.00	23.6	ER
skuterud94_exp1	europe	61.50	24.33	8-24	16.00	ER	ER
viheraaarnio06_exp1	europe	60.45	24.93	16-17	1.00	2.1	-12
viheraaarnio06_exp1	europe	67.73	24.93	20-21	1.00	ER	-5
viheraaarnio06_exp2	europe	60.45	24.93	15-19	4.00	5.1	-62
viheraaarnio06_exp2	europe	67.73	24.93	22-23	1.00	ER	-3
worrall67_exp 3	north america	41.31	-72.93	8-16	8.00	24.3	ER
zohner16_Exp1	europe	48.16	11.50	8-16	8.00	ER	ER

Figures

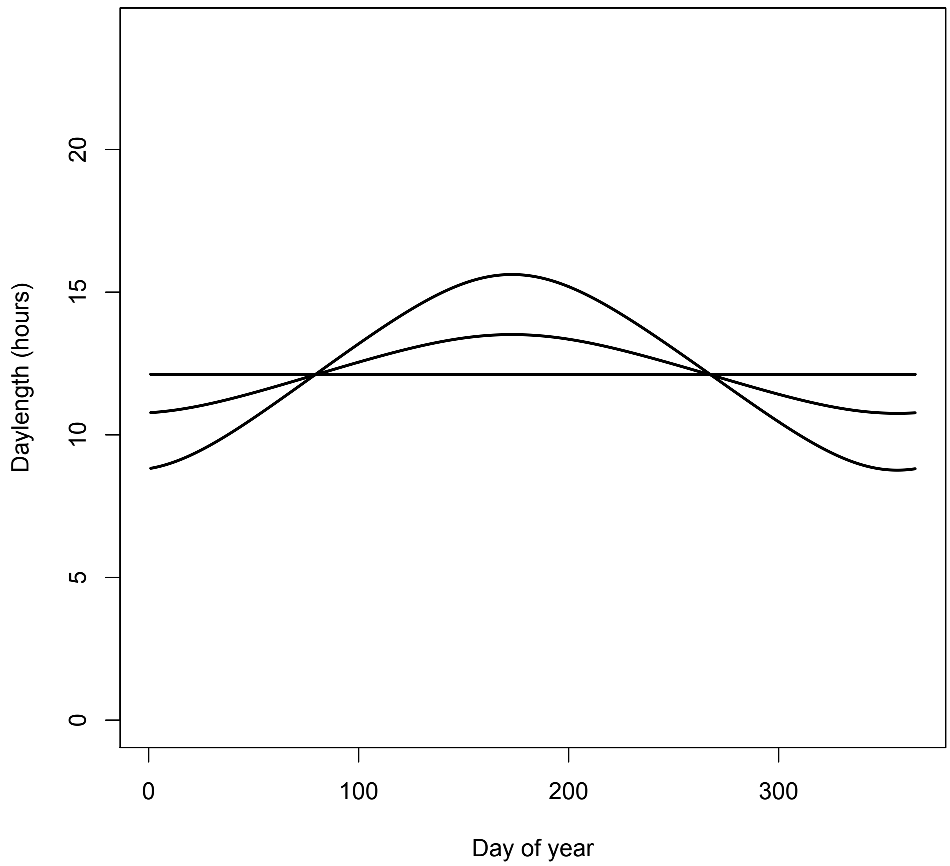

Figure 1: **Photoperiod varies with latitude and throughout the year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts.

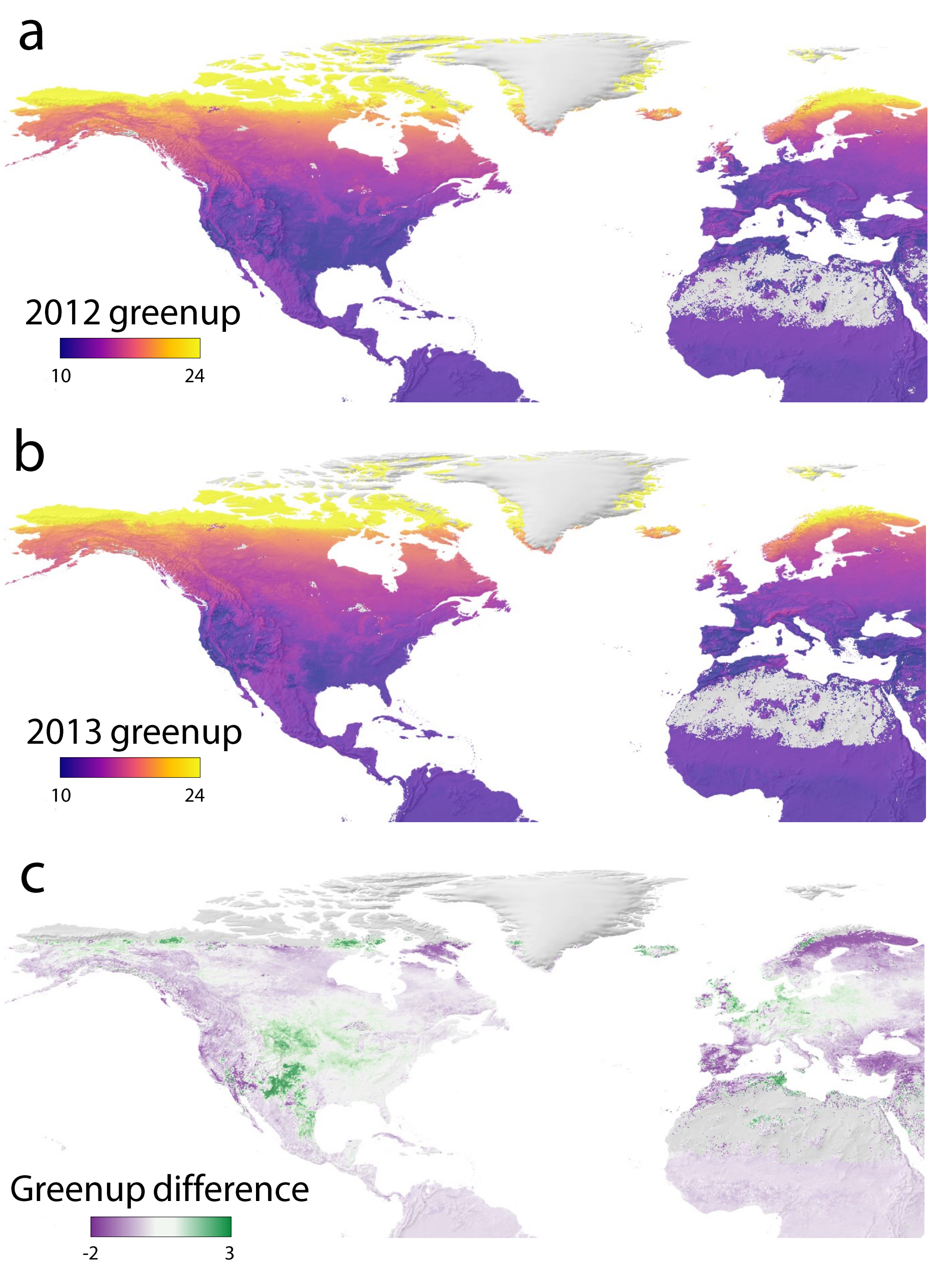

Figure 2: **Green-up date varies with latitude** and varies among years.

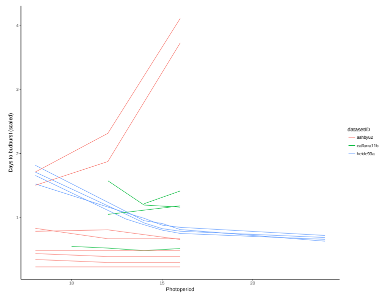

Figure 3: **Photoperiod affects budburst**, generally by interacting with chilling and forcing. Thus, responses to photoperiod vary greatly among studies, depending on methodologies and other manipulating factors (e.g., temperature).

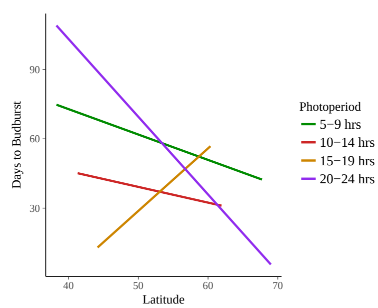

Figure 4: **Responses to photoperiod vary with latitude**.

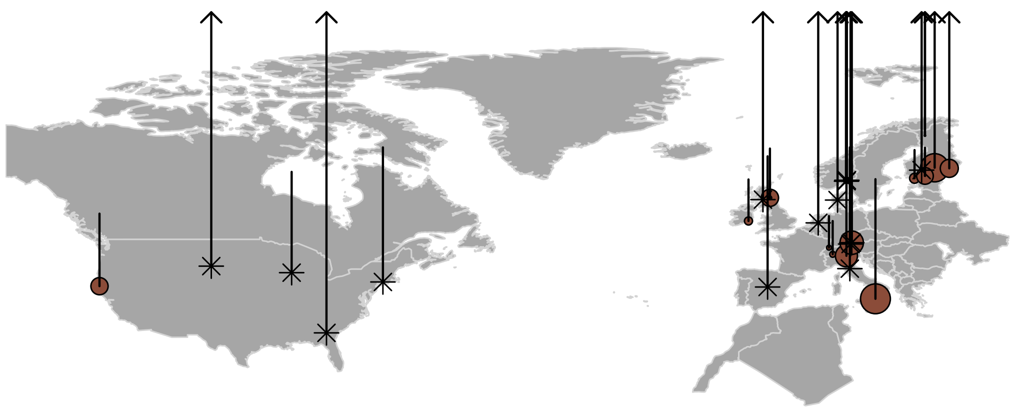

Figure 5: **OSPREE experiments that manipulate photoperiod**, and their equivalent spatial and temporal shifts).

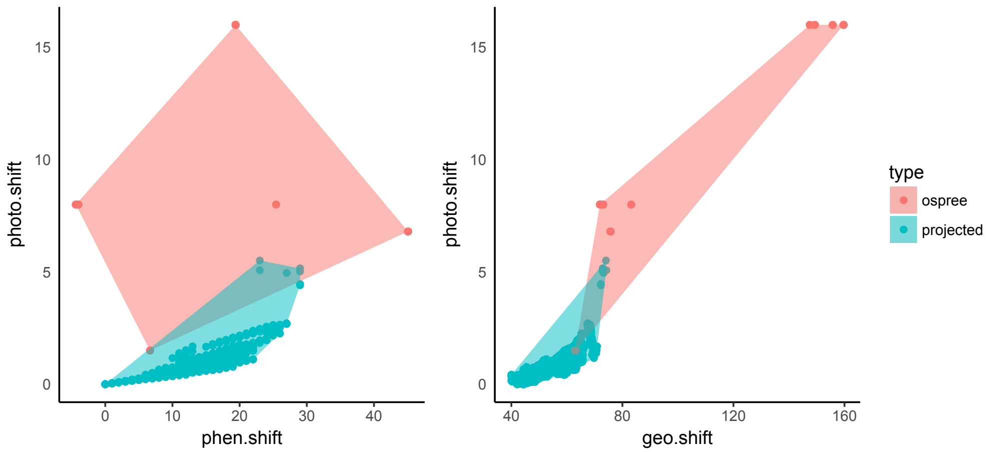

Figure 6: **Experimental treatments of photoperiod, compared to current and projected photoperiod experienced by Fagus sylvatica during budburst.**

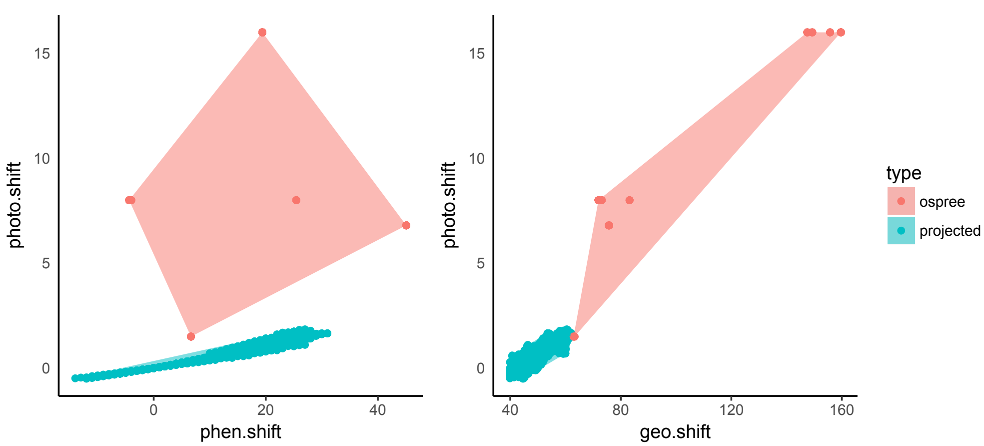

Figure 7: **Experimental treatments of photoperiod, compared to current and projected photoperiod experienced by Quercus robur during budburst.**

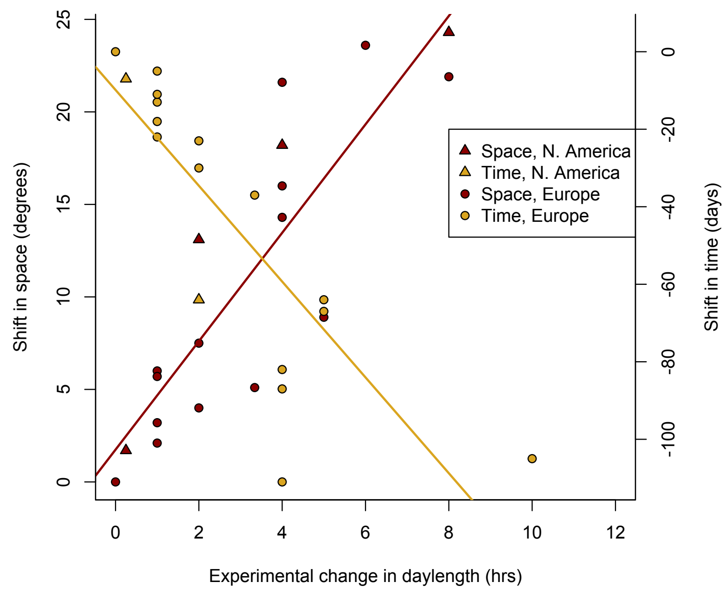

Figure 8: **Shifts in the daylength in OSPREE treatments, and their equivalent spatial and temporal shifts).**