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SUPPLEMENTARY INFORMATION

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Organizing principles for vegetation dynamics

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Supplementary Table 1. Examples of optimality-based plant models

Process/Trait	Optimality hypothesis	References	Test	Traditional approach in DGVMs
Leaf scale optimality				
Photosynthetic capacity	*Fitness proxy:* Leaf net carbon assimilation *Optimized variables:* leaf N allocation to the light and Rubisco limited photosynthetic capacities *Benefits:* Photosynthesis *Costs:* Respiration *Constraints and drivers:* Structural leaf N, light, Temperature (T), [CO_2]	Coordination hypothesis (Maire et al. 2012)	Gas exchange data	PFT-dependent photosynthetic capacity
	Fitness proxy: Leaf net carbon assimilation *Optimized variables:* leaf N allocation to the light and Rubisco limited photosynthetic capacities and storage *Benefits:* Photosynthesis *Costs:* Respiration *Constraints and drivers:* light, T, [CO_2]	(Xu et al. 2012, Ali et al. 2016, Quebbeman and Ramirez 2016)	Gas exchange data	
Leaf stomatal conductance and photosynthesis	*Fitness proxy:* Minimized C cost per C assimilation *Optimized variables:* Photosynthetic capacity and water conducting capacity per C assimilation *Benefits:* Photosynthesis *Costs:* Construction and maintenance C costs of capacities *Constraints and drivers:* VPD, T, altitude	Least cost hypothesis (Prentice et al. 2014), (Wang et al. 2017) (Stocker et al. 2019)	Leaf ^{13}C and flux tower measurement across a range of different environments	PFT-dependent photosynthetic capacity and generic light- and temperature responses
Stomatal conductance	*Fitness proxy:* Daily C gain *Optimized variable:* stomatal conductance (g_s) over time *Benefits:* Daily photosynthesis *Constraint and driver:* transpiration rate	(Cowan and Farquhar 1977, Manzoni et al. 2013)	Gas exchange data	Empirical model with 2 or 3 PFT specific parameters
	Fitness proxy: Net carbon gain *Optimized variable:* g_s *Benefits*: Photosynthesis *Costs:* C costs of hydraulic damages *Constraints and drivers:* T, humidity, light, wind speed, [CO_2], soil water potential	(Sperry et al. 2017) (Wolf et al. 2016, Anderegg et al. 2018)	Leaf trait data	
Leaf life span	*Fitness proxy:* C gain per unit time *Optimized variable:* Leaf lifespan *Benefits:* Photosynthesis (declines with leaf age) *Costs:* Respiration	(Kikuzawa 1991, Xu et al. 2017)	Plant trait data	PFT dependent Leaf longevity

Leaf thermo-regulation	*Fitness proxy:* Leaf C gain per leaf C invested *Optimized variable:* Leaf T *Benefits:* Photosynthesis *Costs:* Leaf C investment *Constraints and drivers:* LMA, T_{90}, g_s, LDMC, leaf temperature acclimation rate (τ)	(Michaletz et al. 2016)	Gas exchange data. Trait data: LMA, T90, g_s, LDMC, τ	Not considered
Leaf angle	*Fitness proxy:* Canopy photosynthesis *Optimized variables:* Leaf angle *Benefits:* Photosynthesis *Costs:* Respiration *Constraint and driver:* LAI	(Hikosaka and Hirose 1997)	Herbaceous plant canopy data	Not explicitly considered
Leaf size	*Fitness proxy:* Leaf water use efficiency of photosynthesis *Optimized variables:* Leaf size *Benefits:* Photosynthesis *Costs:* Water use *Constraints and drivers:* Light, T, humidity	(Parkhurst and Loucks 1972)	Observed leaf sizes in tropical trees, herbs, and lianas	Not considered
SLA, and leaf N per area	*Fitness proxy:* Canopy net C gain *Optimized variables:* LAI, N per leaf area *Benefits:* Photosynthesis *Costs:* Respiration *Constraints and drivers:* Canopy N and water use	(McMurtrie and Dewar 2011)	Plant trait data	PFT-dependent
Whole plant scale optimality				
Rooting depth	*Fitness proxy:* Net C gain *Optimized variable:* Rooting depth *Benefits:* C gain = WUE × water use *Costs:* Root respiration *Constraint:* Precipitation that predicts evapotranspiration (E)	(Guswa 2010, Yang et al. 2016)	Water balance-based observations of E	PFT-dependent
Root and shoot C allocation	*Fitness proxy:* Balanced growth (target plant C:N ratio) *Optimized variable:* Fraction of productivity allocated to roots or shoots *Benefits:* None explicit *Costs:* None explicit	(Reynolds and Chen 1996)	Theoretical model (not statistically tested against data)	Fixed fractions of NPP, PFT dependent
	Fitness proxy: Net growth *Optimized variable:* ESS for root biomass *Benefits:* C gain *Costs:* Leaf and root turnover, respiration *Constraints and drivers:* Soil water and N, light	(Farrior et al. 2013)	Field trials in grassland	
	Fitness proxy: Net C gain *Optimized variables:* Root:shoot ratio, leaf N concentration *Benefits:* C gain *Costs:* respiration	(Ågren and Franklin 2003)	Experiments with birch seedlings and tomato plants	

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Leaf phenology	*Fitness proxy:* Net C gain *Optimized variable:* LAI *Benefits:* C gain *Costs:* Respiration, leaf growth *Constraints and drivers:* Light, T, soil moisture *Not strictly optimization, but dynamic adjustment of LAI to increase productivity	(Caldararu et al. 2014)	Satellite-based LAI from the MODIS	Empirical function of climate variables, PFT-dependent
	Fitness proxy: Long-term mean net C gain *Optimized variable:* LAI during the dry season *Benefits:* C gain *Costs:* Respiration, leaf growth *Constraints and drivers:* Soil moisture under stochastic rainfall, N availability	(Vico et al. 2017)	Satellite-based fraction of drought-deciduous vegetation	
	Fitness proxy: Growth per leaf biomass *Optimized variable:* Leaf habit – evergreen or deciduous *Benefits:* Growth *Costs:* C costs of respiration and transpiration *Constraints and drivers:* Length of growing season, seasonality, soil fertility	(Givnish 2002)	Qualitative patterns of leaf habit and climate	
Leaf mass per area and leaf life span	*Fitness proxy:* Net C gain *Optimized variable:* ESS for leaf mass per area *Benefits:* C gain *Costs:* C for leaf construction and respiration *Constraints and drivers:* Soil N mineralization	(Weng et al. 2017)	Plant trait data	Fixed PFT dependent
C allocation in trees	*Fitness proxy:* Life-time reproductive production *Optimized variable:* ESS for leaf, stem and root biomass *Benefits:* Reproductive production *Costs:* biomass turnover, respiration, mortality *Constraints and drivers:* Light and water availability	(Farrior et al. 2015)	Theoretical model	Fixed fractions of NPP, PFT dependent
	Fitness proxy: Life-time reproductive production *Optimized variable:* ESS for leaf, stem and root biomass *Benefits:* Reproductive production *Costs:* biomass turnover, respiration, mortality *Constraints and drivers:* Light and nutrient availability	(Dybzinski et al. 2011)	Fluxnet data on NPP	

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C and N allocation in trees	*Fitness proxy:* Net C gain *Optimized variables:* Fine roots, canopy N, Vertical distribution of leaf N, LAI *Benefits:* C gain *Costs:* Turnover of leaves and roots, respiration *Constraints and drivers:* Soil N availability, [CO_2]	(Franklin et al. 2009)	FACE experiments	Fixed fractions of NPP, PFT dependent
Dynamic C allocation	*Fitness proxy:* Life-time reproductive production *Optimized variables:* Roots, Shoot, Storage, Reproduction over time *Constraints and drivers:* Soil moisture, light	(Iwasa 2000)	Theoretical model	Fixed fractions of NPP, PFT dependent
Foliage cover and photosynthetic capacity, canopy conductance, rooting depth and fine root distribution	*Fitness proxy:* Net C gain *Optimized variables:* projected cover, photosynthetic capacity, canopy conductance, fine root distribution (dynamic); rooting depth, tree cover (static) *Benefits:* Access to water and light for photosynthesis *Costs*: Respiration, leaf and root turnover *Constraints and drivers*: light, [CO_2] and water availability	(Schymanski et al. 2009, 2015)	Eddy covariance, FACE experiments	PFT-dependent, static or prescribed
LAI of crop plants	*Fitness proxy:* Net C gain *Optimized variable:* LAI (dynamic) *Benefits:* Photosynthesis per LAI increase including N resorption from senescing leaves *Costs*: Respiration, senescing leaves *Constraints and drivers*: Canopy N, Fraction N resorbed at leaf senescence	(Franklin and Ågren 2002)	Crop experiments	Empirical function of degree-days
Tree height	*Fitness proxy:* ESS for net C gain *Optimized variable:* height *Benefits:* C gain *Costs:* C for construction and respiration	(King 1990, Valentine and Mäkelä 2012)		Allometric function of stem diameter
Mycorrhizal C allocation	*Fitness proxies:* ESS for net growth of trees and ESS for N uptake strategy of mycorrhizal fungi *Optimized variable:* C export to mycorrhiza, leaves and stem, fungal allocation to N uptake *Benefits:* C gain *Costs:* C use for N uptake and tissue turnover *Constraints and drivers:* Soil N availability, [CO_2], connectivity among trees and fungi	(Franklin et al. 2014)	Experimental forest plots	Not considered

	Fitness proxies: Tree biomass *Optimized variable:* C export to mycorrhiza *Benefits:* C and N gain *Costs:* C allocation to mycorrhiza *Constraints and drivers:* Soil N availability and soil organic matter decomposability	(Baskaran et al. 2017)	Experimental forest plots	Not considered
Hydraulic traits and stomatal conductance	*Fitness proxies:* long-term mean transpiration rate (assumed proportional to GPP) *Optimized variable:* responses of xylem hydraulic conductivity and g_s to dry conditions *Benefits:* C gain (assumed proportional to GPP) *Costs:* reduced C gain due to inefficient water use *Constraints and drivers:* Soil moisture under stochastic rainfall	(Manzoni et al. 2014)	Global hydraulic trait datasets	Trait values are PFT dependent
	Fitness proxies: C gain over a year *Optimized variable:* Variable g_s over time *Benefits:* C gain over time *Costs:* Loss in C gain due to reduced plant water potential *Constraints and drivers:* Drought length and frequency, [CO_2]	(Bartlett et al. 2019)	Inter-trait relationships in tropical evergreen forest	
Defense	*Fitness proxies:* Net growth *Optimized variable:* C allocation to defense *Benefits:* Net growth *Costs:* C cost of defense *Constraints and drivers:* Grazing intensity	(Fagerstrom et al. 1987)	Theoretical model	Not considered
Xylem/phloem transport	*Fitness proxy:* energy export from loading phloem (proportional to square of net C gain) *Optimized variable:* canopy water potential *Benefits:* sucrose export to plant tissues *Costs:* maintenance of phloem flow *Constraints and drivers:* Limited transpiration rate	(Huang et al. 2018)	Theoretical model	Not considered

Abbreviations: , [CO_2] = atmospheric CO_2 concentration, E = evapotranspiration, ESS = evolutionary stable strategy, GPP = gross primary productivity, g_s =Stomatal conductance, LAI = leaf area index, , LDMC = leaf dry matter content, LMA = leaf mass per area, N = nitrogen, NPP = net primary productivity, PFT = plant functional type, T = temperature, T90 = temperature range with photosynthesis >90% of photosynthesis at optimal T, τ = leaf temperature acclimation rate, VPD = vapor pressure deficit, WUE = water use efficiency

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