A review of plant interaction mechanisms

Supplementary material for:

The ecology of plant interactions: A giant with feet of clay

Ciro Cabal[1*], Ricardo Martinez-Garcia[2], Fernando Valladares[3, 4]

1- Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, US

2- ICTP-South American Institute for Fundamental Research - Instituto de Física Teórica da UNESP, Rua Dr. Bento Teobaldo Ferraz 271, 01140-070 Sao Paulo SP, Brazil.

3- LINC-Global, Department of Biogeography and Global Change, National Museum of Natural Sciences, MNCN, CSIC, 28006 Madrid, Spain

4- Department of Biology, Geology, Physics and Inorganic Chemistry, Rey Juan Carlos University, Móstoles, 28933 Madrid, Spain

* ccabal@princeton.edu

1 Competition

(1) Plants use solar photons and atmospheric carbon dioxide (CO_2) to create sugars for growth in a fundamental reaction: the photosynthesis (Niinemets et al. 2017). This reaction happens in photosynthetic plant tissues, normally the leaves. While atmospheric CO_2 pool is so well mixed and large that *competition* for carbon is usually neglected, leaves intensively compete to intercept solar light (Craine and Dybzinski 2013). By growing their crown horizontally, plants can increase their sunlight interception area. Plants sharing a canopy layer in closed vegetation systems are assumed to have territorial crowns (Purves et al. 2007). However, *competition* for light has a foremost vertical component, as photons come from above and light energy available for chlorophyll reactions is progressively reduced downwards thorough plant canopy due to shading effect. The amount of energy available for a leaf will depend on the area of leaves above it per surface area of ground (Jordan 1969), but not at all on the leaves beneath it. For that reason, *competition* for light is said asymmetric: Upper leaves in the vertical column get a disproportionate share of sun energy, a phenomenon known as resource preemption (DeMalach et al. 2016).

(2-3) Liquid water is fundamental for life as we know it, and represents 70 to 90% of plants fresh weight (Clarke 2014). Additionally, at least 14 mineral nutrients –besides of carbon– are essential for plants growth (White and Brown 2010). Plants act as hydraulic machines, they obtain most of their water and mineral nutrients from soils thorough fine roots, and pump it to other tissues with sap (Milburn 1979). Hence, plants compete belowground for water and nutrients through their fine roots(Cahill et al. 2010). Generally, plants have been observed to be territorial belowground (Schenk et al. 1999, Ward et al. 2013), and, in competitive setups, they adjust their fine roots density to resource availability (Gersani et al. 1998). However, because roots and soil processes are difficult to observe, there is much less we know mechanistically about belowground *competition* than about *competition* for light (Lux and Rost 2012). Additionally, there are reasons to suspect that competition mechanisms are more diverse in the soil than aboveground. For instance, just like sunlight, precipitation water dynamics has a dominant vertical component, as it enters the soil through the surface and progressively infiltrates to deeper soil layers, potentially giving an asymmetric advantage to superficial roots (Schenk 2005). Yet some plants are also known to obtain water from deep water reservoirs (Schenk 2006). Additionally, nutrient acquisition by plant roots was

50   conceptualized as a simple consumer-resource dynamics (Casper and Jackson 1997), yet it has been shown that resource preemption is plausible when mineral nutrients are patchy or episodically supplied (Schwinning and Weiner 1998). A further factor of complexity is given by the fact that fine roots, unlike leaves, compete for several resources at the same time, which potentially leads to complex plant responses. Plants in an experiment

55   grew larger root systems as a response to water addition in nitrogen limited soils, whereas when nitrogen was not limiting plants grew larger root systems when water was scarcer (Farrior et al. 2013), showing complex response to resources co-limitation and providing an excellent example of that complexity.

(4) Competition for runoff water is a particular case of resource competition that often

60   goes unnoticed. Before infiltration, surface water is subjected to runoff and can spread rapidly in the soil surface (Rietkerk et al. 2002). By modifying soil physical structure, plants increase infiltration rates and soil moisture –see soil amelioration **(10)**– in vegetated patches. Hence, they unbalance water infiltration patterns in space and necessarily decrease infiltration in non-vegetated bare soil (Montaña 1992, Bromley et al.

65   1997). Thereby, plants are competing for water in areas out of the reach of their root systems.

2 Climate amelioration

(5) Abrasion can be defined as the destructive effect of small particles impacting a

70   physical surface at high speeds. Leaf cuticle damage caused by abrasion may have profound impacts in plant hydraulic functioning and lead to uncontrolled losses of water (Milburn 1979). A plant canopy can reduce abrasion via baffling wind. Protection against wind-mediated abrasion has been reported as a positive *interaction force* in arid deserts and dunes, where sand particles can be projected by strong winds, (Okin and Gillette

75   2001), as well as in tundra climates, where ice crystals may cause wind-mediated mechanical abrasion (Smith et al. 2003).

(6) Water being fundamental for plants, hydric stress is a main threat to plant survival, and plant water losses lead to wilting and dead. Atmospheric water potential is a main driver of plant water status. Air water potential depends on absolute air humidity and

80   temperature; at higher temperature, relative humidity decreases and water is pulled strongly. Atmospheric desiccation can pull water from leaves at a tension as high as 936

bars at 20ºC when air humidity is 50% (Milburn 1979). Plants can increase atmospheric water potential, and hence reduce water stress, by shading in hot climates (mediated by reducing air temperature), baffling wind (mediated by reduced convective mixing with external drier air), and transpiring vapor (hence increasing absolute air humidity). Measured vertical humidity profiles have confirmed that atmospheric water potential significantly increases within vegetation canopies (Krédl et al. 2012), which results in an *interaction force* that drives positive interactions among plants (Soliveres et al. 2011).

(7) Extreme temperatures cause physiological tissue damage and can severely limit the growth and survival of plants, both in the cold (Pearce 2001) and the hot (Bita and Gerats 2013) ends. In snowy ecosystems, the baffling effect can buffer under-canopy extreme cold, as snow transported by wind is trapped by plant canopy and forms igloo-like structures that provide insulation (Sturm et al. 2001). In hot climates, extreme temperatures are buffered by canopy shade (mediated by reduced under-canopy solid surfaces heat emission), and by baffling (mediated by reduced convective mixing with external hotter air), representing an important *interaction force* in semiarid systems (Sánchez-Gómez et al. 2006).

(8) Even though plants usually compete for light, when other abiotic stress limits photosynthesis, excessive light may damage the photosynthetic apparatus and cause photoinhibition of photosynthesis (Powles 1984, Goh et al. 2012). By shading, canopies can provide photoprotection to leaves and plants underneath when these are experiencing stressful conditions. Photoprotection has been reported as a positive *interaction force* in cold climates where potential productivity is limited by low temperatures (Egerton et al. 2000), and in semi-arid systems under water stress (Cuesta et al. 2010).

3 Soil amelioration

(9) Even though all plants compete for soil mineral nutrients, they are also often able to enrich soils. By shedding litter plants redistribute mineral nutrients extracted from rocks located in deep soil layers and depositing them in soil surface through litter, thereby fertilizing the soil (Kellman 1979). The litter of some plants able to develop nodulation symbiosis with bacteria can also be enriched with nitrogen absorbed from the atmosphere (Bellingham et al. 2001). Plant canopies can also enrich soils by baffling wind, trapping atmospheric dust and increasing dry deposition (Belsky 1994). Some plants can produce

root exudates that chemically stimulate the release of soil nutrients that were not available to roots (Li et al. 2007). Additionally, substrate stabilization by plants hinders nutrient losses caused by erosion (Li et al. 2009). Overall, increased soil nutrients is an important *interaction force* mediating positive interactions among plants (Pugnaire et al. 2004)

(10) Plants have the potential to increase soil moisture, which also reduces plant water stress. This effect is mediated by changes in the physical structure of the soil caused by root growth, shedding litter (both *primary processes* increase soil porosity and hence surface water infiltration), exuding water (uptaken and transported by roots from areas with higher water potential, by the processes known as hydraulic lift, hydraulic descent, or lateral redistribution of water), buffering extreme temperatures (preventing water from freezing and from evaporating), and by baffling (intercepting and condensing water from fog, producing canopy precipitation). Plant-mediated increase of soil moisture is a not-well understood *interaction force* by which some plants can benefit neighbors at a cost to themselves (Ludwig et al. 2004).

(11) Plants need a substrate as physical support. Established plants in unstable substrates can stabilize soils by baffling (preventing wind erosion) and by intercepting rainfall (diminishing the splash of rainfall water effect detaching soil particles). Substrate stabilization is a widely acknowledged *interaction force* in primary succession in sand dunes, where established plants facilitate the recruitment and success of other individuals by preventing erosion (Eklöf et al. 2011).

4 Other cases

(12) We have mentioned how plants decrease soil moisture by root water absorption, and the various processes by which a plant may increase soil moisture. In addition to these processes, plants can cause a decrease in soil water by intercepting rainfall, due to the interception loss, i.e. the water that directly evaporates from canopy surface. Hence, plants can create rainfall depletion areas under their canopies, which leads to a significant *interaction force* in water limited ecosystems (David et al. 2006).

(13) Plants use light to photosynthesize and hence need to escape the shade created by canopies above it, usually by developing their own woody support (see **part 2**). However, epiphyte and hemi-epiphyte (lianas) plants profit from neighbors' woody parts to reach

145   the canopy. Physical support should therefore be considered as a positive *interaction force* in the case of lianas and epiphyte plants (Callaway et al. 2002).

(14-15) Plants can interact with their neighbors by metabolically hindering or stimulating their growth thorough phytochemical compounds. These metabolites are released to the soil either through shedding litter or exuded by roots. Although competition forces are

150   usually assumed as the dominant negative *interaction forces*, allelopathy may account for a substantial proportion of interference (Sinkkonen 2006). Growth stimulation of a plant by metabolites exuded by neighbors has also been reported as a positive *interaction force* (Rice 1986).

(16-17) Parasitic plants are a diverse group of plants that develop a particular obligatory

155   trophic relationship with their hosts thorough the haustorium, a specialized invasive organ connecting the xylem or phloem of the plant with its host (Yoshida et al. 2016). This relationship establishes two *interaction forces* with the same magnitude but opposing sign: The parasite benefits from sponging on water and nutrients in the same extent as its host is harmed by nutritional parasitism (Press and Phoenix 2005).

160   **(18-21)** Plants can interact indirectly, when a neighbor potentiates or hinders the interaction of the focal plant with a third party. The third party can either be another plant (Levine et al. 2017) or an individual of another trophic level (Lortie et al. 2016), and it can either have a positive (ally) or negative (enemy) *net interaction* with the focal plant. There are myriads or possible plant-plant indirect (or higher order) interactions, but here

165   we provide four examples, one for each possible outcome. A neighboring plant can attract an third-party ally to a plant, as it happens with magnet species with eye-catching reproductive organs that attract pollinators to the focal plant (Ghazoul 2006). A neighbor may repel an ally, as for instance do some invasive plants harming soil mycorrhizal communities beneficial to native plants (Mummey and Rillig 2006). A neighbor can also

170   attract an enemy, as does a nurse plant that facilitates the growth of the focal plant but similarly facilitates competitor plants, promoting interference among them (Al-Namazi et al. 2017). A neighbor can finally repel an enemy, as do many plants that protect their neighbors against pests and infectious diseases (Brooker et al. 2016).

175   # References

Al-Namazi, A. A. et al. 2017. Competition and facilitation structure plant communities under nurse tree canopies in extremely stressful environments. - Ecol. Evol. 7: 2747–2755.

Bellingham, P. J. et al. 2001. Differential facilitation by a nitrogen-fixing shrub during primary succession influences relative performance of canopy tree species. - J. Ecol. 89: 861–875.

Belsky, A. J. 1994. Influences of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition. - Ecology 75: 922–932.

Bita, C. E. and Gerats, T. 2013. Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. - Front. Plant Sci. 4: 1–18.

Bromley, J. et al. 1997. The role of surface water redistribution in an area of patterned vegetation in a semi-arid environment, south-west Niger. - J. Hydrol. 198: 1–29.

Brooker, R. W. et al. 2016. Facilitation and sustainable agriculture: A mechanistic approach to reconciling crop production and conservation. - Funct. Ecol. 30: 98–107.

Cahill, J. F. et al. 2010. Plants integrate information about nutrients and neighbors. - Science (80-.). 328: 1657.

Callaway, R. M. et al. 2002. Epiphyte host preferences and host traits: Mechanisms for species-specific interactions. - Oecologia 132: 221–230.

Casper, B. B. and Jackson, R. B. 1997. Plant Competition Underground. - Annu. Rev. Ecol. Syst. 28: 545–570.

Clarke, A. 2014. The thermal limits to life on Earth. - Int. J. Astrobiol. 13: 141–154.

Craine, J. M. and Dybzinski, R. 2013. Mechanisms of plant competition for nutrients, water and light. - Funct. Ecol. 27: 833–840.

Cuesta, B. et al. 2010. Facilitation of Quercus ilex in Mediterranean shrubland is explained by both direct and indirect interactions mediated by herbs. - J. Ecol. 98: 687–696.

David, T. S. et al. 2006. Rainfall interception by an isolated evergreen oak tree in a

205   Mediterranean savannah. - Hydrol. Process. in press.

DeMalach, N. et al. 2016. Size asymmetry of resource competition and the structure of
        plant communities. - J. Ecol. 104: 899–910.

Egerton, J. J. G. et al. 2000. Facilitation of Seedling Establishment : Reduction in
        Irradiance Enhances Winter Growth of Eucalyptus pauciflora. - Ecology 81: 1437–
210   1449.

Eklöf, J. S. et al. 2011. Habitat-mediated facilitation and counteracting ecosystem
        engineering interactively influence ecosystem responses to disturbance. - PLoS
        One 6: e23229.

Farrior, C. E. et al. 2013. Resource limitation in a competitive context determines
215   complex plant responses to experimental resource additions. - Ecology 94: 2505–
        2517.

Gersani, M. et al. 1998. Density-dependent habitat selection in plants. - Evol. Ecol. 12:
        223–234.

Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. - J. Ecol. 94: 295–
220   304.

Goh, C. H. et al. 2012. Photosynthesis and Environments: Photoinhibition and Repair
        Mechanisms in Plants. - J. Plant Biol. 55: 93–101.

Jordan, C. F. 1969. Derivation of Leaf-Area Index from Quality of Light on the Forest
        Floor. - Ecology 50: 663–666.

225   Kellman, M. 1979. Soil Enrichment by Neotropical Savanna Trees. - J. Ecol. 67: 565–
        577.

Krédl, Z. et al. 2012. Microclimate in the vertical profile of wheat, rape and maize
        canopies. - Acta Univ. Agric. Silvic. Mendelianae Brun. 60: 79–90.

Levine, J. M. et al. 2017. Beyond pairwise mechanisms of species coexistence in
230   complex communities. - Nature 546: 56–64.

Li, L. et al. 2007. Diversity enhances agricultural productivity via rhizosphere
        phosphorus facilitation on phosphorus-deficient soils. - Proc. Natl. Acad. Sci. 104:
        11192–11196.

Li, Y. et al. 2009. Effectiveness of sand-fixing measures on desert land restoration in Kerqin Sandy Land, northern China. - Ecol. Eng. 35: 118–127.

Lortie, C. J. et al. 2016. Functional assessment of animal interactions with shrub-facilitation complexes: A formal synthesis and conceptual framework. - Funct. Ecol. 30: 41–51.

Ludwig, F. et al. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. - Plant Ecol. 97: 199–205.

Lux, A. and Rost, T. L. 2012. Plant root research: the past, the present and the future. - Ann. Bot. 110: 201–204.

Milburn, J. A. 1979. Water flow in plants. - Longman Inc.

Montaña, C. 1992. The Colonization of Bare Areas in Two-Phase Mosaics of an Arid Ecosystem. - J. Ecol. 80: 315–327.

Mummey, D. L. and Rillig, M. C. 2006. The invasive plant species Centaurea maculosa alters arbuscular mycorrhizal fungal communities in the field. - Plant Soil 288: 81–90.

Niinemets, Ü. et al. 2017. Photosynthesis: ancient, essential, complex, diverse … and in need of improvement in a changing world. - New Phytol. 213: 43–47.

Okin, G. S. and Gillette, D. A. 2001. Distribution of vegetation in wind-dominated landscapes: Implications for wind erosion modeling and landscape processes. - J. Geophys. Res. Atmos. 106: 9673–9683.

Pearce, R. S. 2001. Plant freezing and damage. - Ann. Bot. 87: 417–424.

Powles, S. B. 1984. Photoinhibition of Photosynthesis Induced by Visible Light. - Annu. Rev. Plant Physiol. 35: 15–44.

Press, M. C. and Phoenix, G. K. 2005. Impacts of parasitic plants on natural communities. - New Phytol. 166: 737–751.

Pugnaire, F. I. et al. 2004. Soil as a mediator in plant-plant interactions in a semi-arid community. - J. Veg. Sci. 15: 85–92.

Purves, D. W. et al. 2007. Crown plasticity and competition for canopy space: A new spatially implicit model parameterized for 250 North American tree species. -

PLoS One: 2:e870.

Rice, E. L. 1986. Allelopathic growth stimulation. - In: Putnam, A. R. and Tang, C. S. (eds), The science of allelopathy. Wiley-Interscience, pp. 23–42.

Rietkerk et al. 2002. Self-Organization of Vegetation in Arid Ecosystems. - Am. Nat. 160: 524.

Sánchez-Gómez, D. et al. 2006. Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: Trade-offs and evidence for niche differentiation. - New Phytol. 170: 795–806.

Schenk, J. H. 2005. Vertical Vegetation Structure Below Ground: Scaling from Root to Globe. - Prog. Bot. 66: 341–373.

Schenk, H. J. 2006. Root competition: Beyond resource depletion. - J. Ecol. 94: 725–739.

Schenk, H. J. et al. 1999. Spatial Root Segregation: Are Plants Territorial? - Adv. Ecol. Res. 28: 145–180.

Schwinning, S. and Weiner, J. 1998. Mechanisms Determining the Degree of Size Asymmetry in Competition among Plants. - Oecologia 113: 447–455.

Sinkkonen, A. 2006. Ecological relationships and Allelopathy. - In: Reigosa, M. J. et al. (eds), Allelopathy: A Physiological Process with Ecological Implications. Springer, pp. 373–393.

Smith, W. K. et al. 2003. Another perspective on altitudinal limits of alpine timberlines. - Tree Physiol. 23: 1101–1112.

Soliveres, S. et al. 2011. Microhabitat amelioration and reduced competition among understorey plants as drivers of facilitation across environmental gradients: Towards a unifying framework. - Perspect. Plant Ecol. Evol. Syst. 13: 247–258.

Sturm, M. et al. 2001. Snow-shrub interactions in Arctic Tundra: A hypothesis with climatic implications. - J. Clim. 14: 336–344.

Ward, D. et al. 2013. Walter's two-layer hypothesis revisited: Back to the roots! - Oecologia 172: 617–630.

White, P. J. and Brown, P. H. 2010. Plant nutrition for sustainable development and

global health. - Ann. Bot. 105: 1073–1080.

Yoshida, S. et al. 2016. The Haustorium, a Specialized Invasive Organ in Parasitic Plants. - Annu. Rev. Plant Biol. 67: 643–667.

295