A review of plant interaction mechanisms, or an updated version of Hunter and Aarssen (1988)

Supplementary material for

The Ecology of Plant Interactions: A Giant with Feet of Clay

by

Ciro Cabal, Fernando Valladares, and Ricardo Martínez-García

Introduction

To develop a mechanistic understanding of plant net interactions, we first need to know the several, somewhat independent, biophysical processes underneath it. In the context of plant interactions, we can classify biophysical processes as primary processes, intermediary processes, and interaction forces (see Glossary). The main primary processes underlying plant interactions are the effects of a plant canopy casting shade (Valladares et al. 2016), baffling wind (Leonard and Croft 2006), intercepting rainfall (Muzylo et al. 2009), and transpiring water (Flerchinger et al. 2015); the effects of both plant canopies and root systems producing litter (Xiong and Nilsson 1999); and the effects of root systems absorbing soil water (Lambers et al. 2008a), exuding plant water (Prieto et al. 2012), absorbing mineral nutrients (Lambers et al. 2008b), altering soil physical structure (Angers and Caron 1998), and exuding metabolites (Bertin et al. 2003). These primary processes ultimately affect, sometimes antagonistically, several interaction forces, as it is, for example, the case of shade in hot, semiarid habitats (**Figure SM1**).

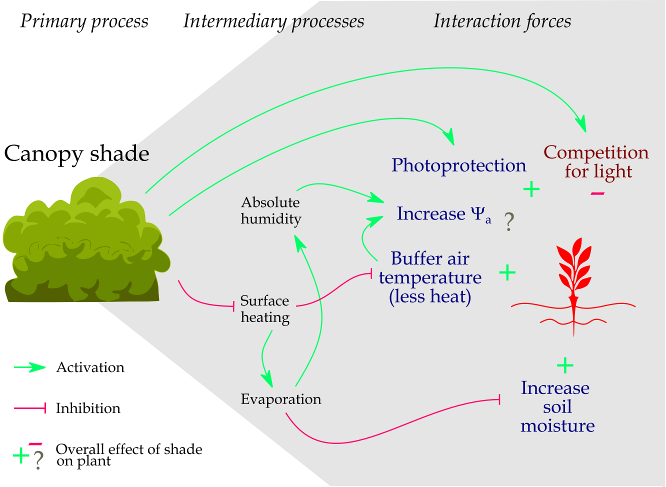

Figure SM1: *Schematic example of how a primary process, canopy shade, affects various interaction forces in hot semiarid and arid systems. (Focusing on a primary process is an alternative approach to focus on a single resource as in Fig 1c, main text).*

A comprehensive literature review on plant interactions allowed us to identify twenty-one types of interaction forces potentially relevant to understanding every single net interaction mechanistically (**Figure SM2**). In the following, we first define the terms used in this supplementary material and in our main text, and then provide a full summary of the literature review explaining each of these interaction forces, with references to studies addressing them.

Glossary

The study of plant-plant interactions can be approached at different levels, and it is important to have clearly defined terms to refer to each of these levels. The words used to refer to interaction forces, net directional interactions from an influencing to an influenced entity (species or individual), or bidirectional interactions, are often used in a confusing manner. A lexical unification that differentiates between these interaction levels would make plant community ecology more clear and comprehensible (Trinder et al. 2013). Some words are particularly misleading, like competition and facilitation, which lack of an consistent meaning in the literature. The concept of 'competition' is elusive because it is interchangeably used at all three biological scales. In community-level charts, 'competition' is used to name negative/negative (−/−) pairwise interaction, as opposed to 'mutualism' (+/+) (e.g., Godsoe et al. 2017). In some fields, such as plant positive interactions research, it is common to use 'competition' to refer to a negative net interaction instead of 'facilitation' (e.g., Filazzola and Lortie 2014). Finally, in an ecophysiology context, 'competition' is the fight among

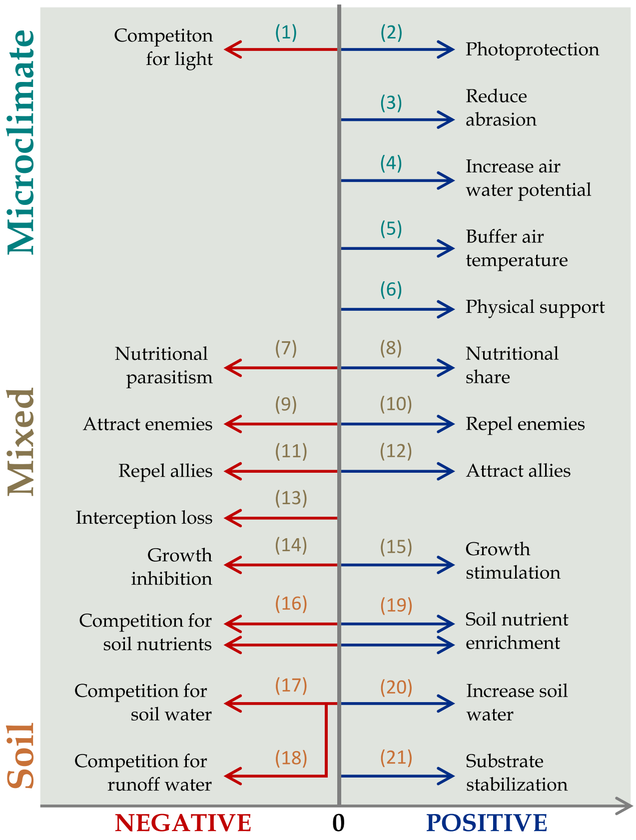

Figure SM2: *List of positive and negative existing interaction forces leading to a net interaction. Mathematical symbols on the left of the boxes indicate that the integration of all interaction forces determines the value of a single net interaction. Several arrows for soil nutrient interaction forces represent the fact that there are different nutrients involved (N, P, K, etc.). Numbers next to the arrows are a link to the to the interaction forces as discussed in the text.*

individuals for a specific trophic resource (Grime 1977). The word 'facilitation' also deserves attention because it is open to any possible feedback from the facilitated plant (negative, neutral, or positive) at the scale of pairwise interactions (Bronstein 2009).

Biophysical process: A local change in the matter or energy status of a plant's habitat.

Primary process: A biophysical process that is the direct effect of the presence or the activity of any plant on its immediate surroundings.

Intermediary process: Any biophysical process that mediates in a plant interaction but is not a primary process nor an interaction force.

Interaction force: A biophysical process by which a plant affects the environment of a neighboring plant in a way that has a direct effect on its fitness.

Competition: An interaction force that is of trophic nature; plants compete for each quantum of light, molecule of water, or nutrient ion (*sensu* Grime 1977).

Net interaction: The net outcome of all the interaction forces acting together, giving the net biological effect of a plant individual on the fitness of a neighbor.

Facilitation: A positive net interaction (*sensu* Callaway 1995).

Interference: A negative net interaction (*sensu* Harper 1961).

Pairwise interactions: General concept comprising the relationship of mutual influence between two plant individuals or species, including two effects going in opposite directions. Pairwise interactions can be 'antagonistic facilitation' (−/+), 'mutual interference' (−/−), 'mutual facilitation' (+/+), 'commensalism' (0/+), or 'amensalism' (0/−).

Microclimate interaction forces

(1) Competition for light

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).

Game theory, originally developed to study the interaction among rational decision-makers, became a powerful tool to investigate evolutionary questions towards the end of the twentieth century (Maynard Smith 1982). Following an evolutionarily stable strategy (ESS, the strategy that maximizes the net reward for an individual that selfishly interacts with other individuals of the population), selfish plant individuals allocate resources inefficiently (Rankin et al. 2007). While necessary to capture the relevant ecological responses of plants to interaction forces, it is only recently that it has become a very successful framework to study plant responses to biotic interactions, and it is still not widespread in the plant community ecology literature (Mcnickle and Dybzinski 2013).

To study competition for light from a game-theoretical perspective, we can think of a plant as a photosynthetic crown placed on top of a woody trunk. The crown area determines plants' potential to intercept light and, therefore, its yield. The individual optimal strategy for plants is to invest all their resources into maximizing a flat photosynthetic crown area at the ground level (**Fig SM3 a**). However, in interaction with neighbor plants, competition for light becomes asymmetric because taller individuals get most of it and shaded individuals almost none. Therefore, a plant may benefit from first growing the trunk to be taller than its neighbors and, after that, grow its crown. Nevertheless, suppose all individuals in the community follow this behavior. In that case, following the ESS, they escalate in the production of increasingly taller trunks and end up engaging in an ecological arms race that makes them invest most of their resources into conflict without getting any significant benefit from it (Falster and Westoby 2003, Dybzinski et al. 2011) (**Fig SM3 b**). Indeed, trees invest about 80% of their biomass in growing robust columns of wood on top of which they place their leaf canopy (Poorter et al. 2015). Finally, if plants pursue a collective optimal, they would have the same crown area exposed to sunlight but at the ground level (**Fig SM3 c**), thereby intercepting the same light at a much lower cost and investing that energy into reproduction.

(2) Photoprotection

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) Reduce abrasion

Abrasion can be defined as the destructive effect of small particles impacting a 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 2001), as well as in tundra climates, where ice crystals may cause wind-mediated mechanical abrasion (Smith et al. 2003).

(4) Increase air water potential

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 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 20°C 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 transpirating 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).

(5) Buffer air temperature

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).

(6) Physical support

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

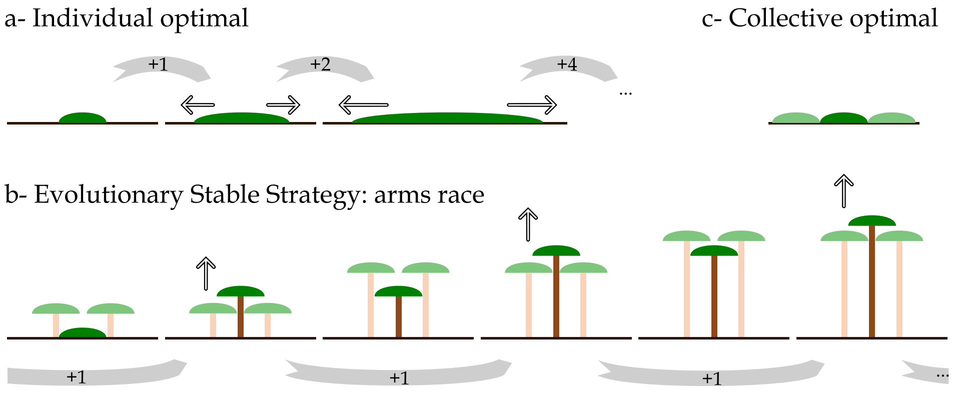

Figure SM3: *Graphical representation illustrating a-the individual optimal, b-the arms race, and c-the collective optimal in competition for light.*

Mixed interaction forces

(7-8) Nutritional parasitism and nutritional share

Parasitic plants are a diverse group of plants that develop a particular obligatory 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).

(9-12) Attracting or repelling enemies or allies

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 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 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).

(13) Interception loss

Plants can decrease soil moisture by a non-trophic process, 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).

(14-15) Growth stimulation or inhibition

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, or can also be exuded to the air as is the case of volatile organic compounds. Although competition forces are usually assumed as the dominant negative *interaction forces*, growth inhibition through 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). The effects that molecules exuded by a plant to the environment have on other plants' growth are not necessarily mediated by forced modification of the other plants metabolism, as is for instance the case of allelopathy (Zeng 2014). Indeed, it is well documented that plant can emit signals and communicate among each other, and the plant chemicals can actually act as a communication signal by which plants can cooperate or pass on information about incoming environmental stresses (Falik et al. 2011, Pierik et al. 2013, Novoplansky 2019, Bennett 2021, Bilas et al. 2021).

Soil interaction forces

(16-17) Competition for soil water and nutrients

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).

There are reasons to suspect that competition mechanisms are more complex 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). Nutrient acquisition by plant roots was 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 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.

As for the case of competition for light, plants may forage resources inefficiently in soil when competing with other plants as predicted by game theory models. Game-theoretical studies of competition for soil resources have predicted that plants may engage in a tragedy of the commons (Gersani et al. 2001, Zea-Cabrera et al. 2006, Cabal et al. 2020). The tragedy of the commons is a situation in a shared-resource system in which the collective action of a group of individuals

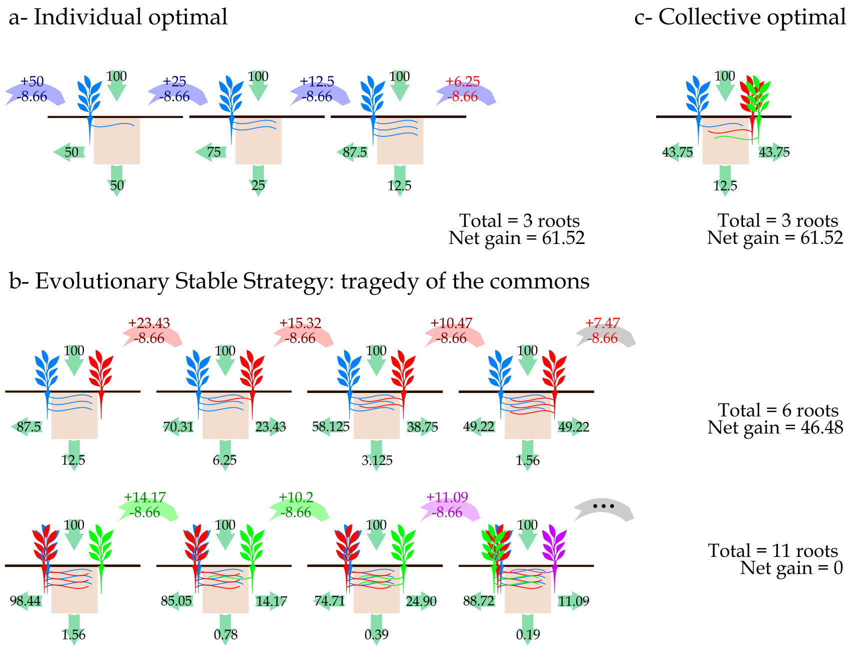

Figure SM4: *Graphical representation illustrating a-the individual optimal, b-the tragedy of the commons, and c-the collective optimal in competition for light.*

acting independently from each other and pursuing their own self-interest leads to the depletion of the shared resource (Hardin 1968). To illustrate how a tragedy of the commons emerges due to competition for soil resources, we can consider a scenario in which a plant can exploit a patch of soil that contains 100 units of a resource. In this patch, the plant grows roots with a cost of 8.66 units of resource per root, and each new root increases total foraging by half the amount of remaining resource in the patch. The first root would uptake 50 units of resource, the second root would increase the total uptake by 25 units, the third one by 12.5, and so on.

For a single plant, this increase in uptake is the marginal gain obtained from each consecutive root. Moreover, the form it grows implies that the allocation of new roots reduces the average resource uptake of pre-existing roots (hereafter, new roots "steal" resources from pre-existing roots). For example, if the plant allocates two roots, the uptake per root is (50+25)/2 = 37.5, and the second root has stolen from the first one 37.5-25=12.5 units of the resource. In the hypothetical situation described above, and for an individual optimal, the plant will not grow more than three roots because the marginal benefit of a fourth root is lower than its allocation cost (6.25<8.66) (**Fig SM4 a**). However, if a second plant accesses the same patch inhabited by the three-root plant, the new plant's marginal benefit upon allocating its first root—which coincides with the average uptake per root in the soil patch—is (50+25+12.5+6.25)/4=23.43. Notice that the second plant's marginal benefit allocating its first root is much larger than that of the first plant allocating a fourth root, 6.25. This difference arises because the new plant steals resources from its neighbor rather than from its own pre-existing roots. Iterating this calculation, one can see that for an ESS, the second plant still benefits from allocating a second and a third root in the same patch, and this whole process repeats if a third individual colonizes the patch, then a fourth, and so on (**Fig SM4 b**). The number of roots exploiting the soil patch increases with the number of plants that colonize it, which reduces the average resource uptake per root and ultimately leads to less efficient foraging. This exploitative process continues until the cost of allocating an additional root equals the average uptake per root, which is at 11 roots in our example. As plants increasingly deplete the resource in the patch, the net gain for the community, i.e., the sum of the net rewards of all coexisting plants, tends to zero. Empirical studies evidencing increased root allocation of plants in response to the presence of neighbors support this theoretical prediction (Maina et al. 2002; O'Brien et al. 2005; but see Semchenko et al. 2007). In our example, the collective optimal, which pursues the maximization of the net gain, is attained with three roots, regardless of how many plants these roots belong to (**Fig SM4 c**).

(18) Competition for runoff water

Competition for runoff water is a particular case of resource competition that often 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 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. 1997). Thereby, plants are competing for water in areas out of the reach of their root systems.

(19) Soil nutrient enrichment

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).

(20) Increase soil water

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).

(21) Substrate stabilization

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).

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.

Angers, D. A. and Caron, J. 1998. Plant-induced changes in soil structure: Processes and feedbacks. - Biogeochemistry 42: 55–72.

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.

Bennett, T. 2021. Plant-Plant interactions. - Plant, Cell Environ. Cell 44: 995–996.

Bertin, C. et al. 2003. The role of root exudates and allelochemicals in the rhizosphere. - Plant Soil 256: 67–83.

Bilas, R. D. et al. 2021. Friends, neighbours and enemies: an overview of the communal and social biology of plants. - Plant Cell Environ. 44: 997–1013.

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.

Bronstein, J. L. 2009. The evolution of facilitation and mutualism. - J. Ecol. 97: 1160–1170.

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

Cabal, C. et al. 2020. The Exploitative Segregation of Plant Roots. - Science 370: 1197–1199.

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

Callaway, R. M. 1995. Positive Interactions among Plants. - Bot. Rev. 61: 306–349.

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 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.

Dybzinski, R. et al. 2011. Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: An analytically tractable, individual-based model and quantitative comparisons to data.

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

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

Falik, O. et al. 2011. Rumor has it..: Relay communication of stress cues in plants. - PLoS One 6: 1–6.

Falster, D. S. and Westoby, M. 2003. Plant height and evolutionary games. - Trends Ecol. Evol. 18: 337–342.

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

Filazzola, A. and Lortie, C. J. 2014. A systematic review and conceptual framework for the mechanistic pathways of nurse plants. - Glob. Ecol. Biogeogr. 23: 1335–1345.

Flerchinger, G. N. et al. 2015. Modeling temperature and humidity profiles within forest canopies. - Agric. For. Meteorol. 213: 251–262.

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

Gersani, M. et al. 2001. Tragedy of the Commons as a Result of Root Competition. - J. Ecol. 89: 660–669.

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

Godsoe, W. et al. 2017. Interspecific interactions and range limits: contrasts among interaction types. - Theor. Ecol. 10: 167–179.

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

Grime, J. P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. - Am. Nat. 111: 1169–1194.

Hardin, G. 1968. The Tragedy of Commons. - Science 162: 1243–1248.

Harper, J. L. 1961. Approaches to the study of plant competition. - Symp. Soc. Exp. Biol. 15: 1–39.

Hunter, A. F. and Aarssen, L. W. 1988. Plants helping plants. - Bioscience 38: 34–40.

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

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.

Lambers, H. et al. 2008a. Plant water relations. - In: Lambers, H. et al. (eds), Plant Physiological Ecology. Second. Springer, pp. 163–223.

Lambers, H. et al. 2008b. Mineral nutrition. - In: Lambers, H. et al. (eds), Plant Physiological Ecology. Second. Springer, pp. 255–320.

Leonard, L. A. and Croft, A. L. 2006. The effect of standing biomass on flow velocity and turbulence in Spartina alterniflora canopies. - Estuar. Coast. Shelf Sci. 69: 325–336.

Levine, J. M. et al. 2017. Beyond pairwise mechanisms of species coexistence in 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.
Maina, G. G. et al. 2002. Intra-Plant versus Inter-Plant Root Competition in Beans : Avoidance , Resource Matching or Tragedy of the Commons. - Plant Ecol. 160: 235–247.
Maynard Smith, J. 1982. Evolution and the Theory of Games. - Cambridge University Press.
Mcnickle, G. G. and Dybzinski, R. 2013. Game theory and plant ecology. - Ecol. Lett. 16: 545–555.
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.
Muzylo, A. et al. 2009. A review of rainfall interception modelling. - J. Hydrol. 370: 191–206.
Niinemets, Ü. et al. 2017. Photosynthesis: ancient, essential, complex, diverse … and in need of improvement in a changing world. - New Phytol. 213: 43–47.
Novoplansky, A. 2019. What plant roots know? - Semin. Cell Dev. Biol. 92: 126–133.
O'Brien, E. E. et al. 2005. Root proliferation and seed yield in response to spatial heterogeneity of below-ground competition. - New Phytol. 168: 401–412.
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.
Pierik, R. et al. 2013. Molecular mechanisms of plant competition: Neighbour detection and response strategies. - Funct. Ecol. 27: 841–853.
Poorter, H. et al. 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. - New Phytol. 208: 736–749.
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.
Prieto, I. et al. 2012. Water release through plant roots: New insights into its consequences at the plant and ecosystem level. - New Phytol. 193: 830–841.
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.
Rankin, D. J. et al. 2007. The tragedy of the commons in evolutionary biology. - Trends Ecol. Evol. 22: 643–651.
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, H. J. 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.
Semchenko, M. et al. 2007. Challenging the tragedy of the commons in root competition: Confounding effects of neighbour presence and substrate volume. - J. Ecol. 95: 252–260.
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.
Trinder, C. J. et al. 2013. Plant ecology's guilty little secret: Understanding the dynamics of plant competition. - Funct. Ecol. 27: 918–929.
Valladares, F. et al. 2016. Shedding light on shade: ecological perspectives of understorey plant life. - Plant Ecol. Divers. 9: 237–251.
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.
Xiong, S. and Nilsson, C. 1999. The effects of plant litter on vegetation: A meta-analysis. - J. Ecol. 87: 984–994.
Yoshida, S. et al. 2016. The Haustorium, a Specialized Invasive Organ in Parasitic Plants. - Annu. Rev. Plant Biol. 67: 643–667.
Zea-Cabrera, E. et al. 2006. Tragedy of the commons in plant water use. - Water Resour. Res. 42: 1–12.
Zeng, R. Sen 2014. Allelopathy - The Solution is Indirect. - J. Chem. Ecol. 40: 515–516.