**Competition for water and light among perennial plant species**

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**1. Competition for water only:**

*Cohort model (lines up with simulator)*

We begin with a model of competition for water in assemblages of perennial plants. We assume that species are so limited by water that the canopy never closes, and the plants therefore do not compete for light. In the model, water is supplied by storms of size (total volume expressed as the volumetric soil water equivalent) which occur at frequency (storms per year). Between storms, a species transpires the shared pool of water, growing at a fixed rate until the soil water content is driven below its critical water content, . At this point, species closes its stomates and respires at a rate until the soil water content, , is replenished above by subsequent storms. The total growth of an individual, , between rain events is thus a function of the amount of time it grows at rate vs. , given by the amount of time until the soil water dips below the critical water content:

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| --- | --- | --- |
|  |  | (1) |

Where is the amount of time that elapses after a rain event before drops below , and is equal to the time between rain events in years.

To understand the dynamics of growth over timescales longer than individual rain events we employ a separation of timescales, assuming that the growth rate of an individual between rain events is equal to its average growth rate over the course of that interval. Therefore, species grow monotonically between rainstorms instead of growing until time and then respiring until the next rain event. The average growth rate of an individual, , between rain events is given by the following expression:

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| --- | --- | --- |
|  |  | (2) |

The total biomass of an individual of species after rain events is equal to the following, assuming a constant :

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| --- | --- | --- |
|  |  | (3) |

where is an allometric constant relating growth in diameter and biomass, and is equal to , or the length of each inter-rain interval.

We next assume that individuals reproduce at a rate per unit biomass per unit time, and die at a rate . We also assume that seeds germinate only during rain events, meaning that age cohorts are defined by storm arrivals. The lifetime reproductive success of an individual of species *at equilibrium* is then calculated by summing reproduction across all ages/sizes:

|  |  |  |
| --- | --- | --- |
|  |  | (4) |

where is the length of time an individual of species grows after a rainstorm before reaching the critical water content while at population dynamic equilibrium. We can only derive an expression for at population dynamic equilibrium, because otherwise varies by age and the expression for reproduction becomes recursive.

We next use equation 4 to derive an expression for the break-even time, , which is the amount of time species must grow between each inter-rain interval to maintain population dynamic equilibrium. Setting we find:

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| --- | --- | --- |
|  |  | (5) |

where is the polylogarithm function, equal to . Note that when , .

The total leaf area of species at equilibrium is found by summing across all cohorts the product of the equilibrium seed production in each rain interval , and the expected leaf area of each cohort:

|  |  |  |
| --- | --- | --- |
|  |  | (6) |

Next, assuming plants consume water proportional to their leaf area at the start of each inter-rain interval (i.e. assuming new growth contributes negligibly to transpiration), the water consumption dynamics within each inter-rain interval at equilibrium are governed by:

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| --- | --- |
|  | (7) |

Using equations 6 and 7 to solve for , we find:

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|  | (8) |

where and once species are ordered according to such that species 1 has the highest and species has the lowest. The equilibrium population density of species is then given by:

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| --- | --- |
|  | (9) |

meaning species has a feasible equilibrium population density when the following conditions are met:

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| --- | --- |
|  | (10) |

The first condition stipulates that there is a tradeoff among coexisting species between their longevity and their competitive ability. The second ensures that species ’s growth rate is above the minimum feasible growth rate, which is the growth rate that allows a species to overcome population decline due to independent morality when never closing its stomates.

We derive this minimum growth rate by considering the lifetime reproductive success of an individual which never shuts down. The LRS of this individual is given by:

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| --- | --- |
|  | (11) |

To get the minimum feasible we set the above expression to 1, finding:

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| --- | --- |
|  | (12) |

*Continuous-time model*

Continuous time model, equations 1 and 2 are identical. The deviation occurs only once we begin to consider the between storm growth dynamics. The lifetime reproductive success of an individual at population dynamic equilibrium is given by:

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| --- | --- |
|  | (13) |

And when species is not in equilibrium the lifetime reproductive success on an individual in cohort is equal to:

|  |  |
| --- | --- |
|  | (14) |

The break-even time for species is given by:

|  |  |
| --- | --- |
|  | (15) |

And the equilibrium population density is:

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| --- | --- |
|  | (16) |

Though it initially appears from equation 16 that a species’ equilibrium population density does not depend on the frequency of storms, , it does in fact depend on storm frequency via the break-even time’s dependence on inter-rain interval length, . To see this, we re-express in terms of and then take the partial derivative of equilibrium population density with respect to , finding:

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| --- | --- |
|  | (17) |

For , where and , and

The first of these expressions is negative provided the feasibility condition is met, while the second is strictly negative, meaning species’ equilibrium population densities decline with increasing inter-rain intervals.

The minimum feasible growth rate in this new model formulation is: .

*Effect of changes in storm frequency*

The latest feasible species, species , for a given combination of and is the one with , provided species meet the strict tradeoff requirement for coexistence. This species will remain the latest feasible species regardless of storm frequency, as its existence is predicated on growing for exactly as long as the interrain interval length. Its equilibrium population density, however, will increase with decreasing . Thus, it cannot be excluded through modifications to or .

The next latest species also cannot be excluded due to modifications to provided it was able to persist originally. To illustrate, assume all species are evenly spaced in . When this is true, the condition for coexistence is that . Because break-even time is a linear function of , and because break-even time must be 0 when , then if the coexistence condition is satisfied for one value of , it must be satisfied for all values of . Therefore, species with earlier phenology than species , but which are not the earliest species (species 1), cannot be excluded due to changes in .

It is worth noting that while the tradeoff is maintained in terms of the sign of its first and second derivatives, the absolute shape of the tradeoff is modified by changes to . The second latest species, species , experiences changes in break-even time according to the inter-rain interval length. When is decreased, also decreases according to the partial derivative of break-even time with respect top

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| --- | --- |
|  | (18) |

We can approximate (18) if we assume , which it is when either mortality is small relative to inter-rain interval length, or fecundity is high. The approximation is:

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| --- | --- |
|  | (19) |

Which is constrained to be less than 1, and increases with decreasing open-stomate growth rate Also note that if species share fecundity and mortality rates, then (19) increases with decreasing , meaning that when the tradeoff between break-even time and critical water content is met, later species will experience larger changes in break-even time for equivalent changes in . Thus, when is decreased, the form of the tradeoff will be compressed.

The argument for the species with the highest critical water content is a bit more complex. The earliest feasible species for a given combination of , , and is the one with a growth rate and critical water content pairing such that a straight line drawn from these points to the point given by is exactly tangent to the tradeoff curve. This species is the best competitor for water over the course of its lifespan, meaning that at equilibrium it consumes water at the highest rate of any species. Other species may grow faster as individuals, and therefore consume water a greater rate per capita than the earliest feasible species. However, the total water consumption rate of these species’ populations is limited by time: they must grow long enough to at least replace their population and thus cannot consume water as fast (as a population) as slightly slower growing species.

Perhaps surprisingly, the identify of this best competitor does not change with modifications to . A mathematical explanation will follow, but the reason is that the relative competitive ability of a species is independent of inter-rain interval length. A species’ competitive ability is defined by the maximum rate at which a population can consume water and reach a total lifetime reproductive success of 1. This rate is determined by each species’ vital rates (critical water content, mortality, growth, respiration and reproduction) as well as the inter-rain interval length, . Two species’ relative competitive ability, however, is determined only by the difference in their vital rates. This makes some intuitive sense. The temporal component of competitive ability is determined by a species’ ability to accrue future reproduction. Changing the inter-rain interval length alters the total amount of time a species has to grow between storms, because it alters the length of time respiration occurs for, but it does not impact the ability of species to accrue reproduction during the time they are actively growing.

We can see this mathematically by deriving the relative competitive ability of two species. To do so, we first write down an expression for the maximum water consumption rate for species :

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| --- | --- |
|  | (20) |

Thus, the relative competitive ability of two species, and is given by the following expression.

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| --- | --- |
|  | (21) |

Here noting that break-even time is a function of inter-rain interval length by writing . Substituting the expression for break-even time into this expression, we begin to see how the relative competitive abilities are independent of :

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|  | (22) |

Where . It is plain that once is factored out from (22) it will cancel, making independent of .

*Effect of changes in storm size*

The effect of changes to the size of storms is straightforward. The species with the highest critical water content that can invade an empty system is the species with a critical water content infinitesimally smaller than the field capacity of the soil, . However, this species will need to achieve an infinitesimal population density in order to stretch the soil water availability to its break-even time. This may be unrealistic, and the earliest phenology species which can invade an empty system may be set by ecophysiological limits. Evaporation will also set an upper limit.

For a species invading a system with existing competitors, the storm size must exceed a certain value, set by the invading species’ critical water content and break-even time, for that species to be successful:

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|  | (22) |

As the storm size declines, this condition becomes more difficult to meet, early-phenology strategies become infeasible and diversity declines as a result.

*Simulator*