**Model concept**

* 1. **Topic, research questions and hypothesis**
* **Topic**: Modelling net assimilation, and leaf miner population dynamics under different scenarios of learning behavior in an apple tree stand
* **Research question 1**: How does infestation and population dynamics of the leaf miner *Phyllonorycter sp.* influence the stand productivity of an apple stand (*Malus domestica*)?
* **Research question 2:** How does the change in photosynthetic activity of apple trees influence the population size of the leaf miner Phyllonorycter sp.?
* **Research question 3:** How does decreased water availability affect stand productivity and leaf miner population dynamics?
* **Research question 4:** Does learning behavior in *Phyllonorycter sp.* contribute to higher damage and increased leaf miner populations?
* **Hypothesis 1**: Leaf miner infestation initially decreases carbon assimilation and plant growth but increases water use efficiency
* **Hypothesis 2**: Potential negative effects of leaf miner infestation are mitigated by defense reactions of plants and change host preferrence of leaf miners
* **Hypothesis 3**: Learning behaviour accounts for higher population sizes in leaf miners

**2. Entities and state variables**

* **Trees:** age, biomass, height, leaf number/biomass, energy/water/oviposition status, plant vigour, leaf miner density
* **Leaves** as individual entities with properties leaf area/water content/stomatal conductance/carbon assimilation/levels of defense chemicals/present and past state of infestation
* **Leaf miners:** age, sex?, developmental stage, egg-carrying state, behaviour state, learning state, energy status
* **Environment:** soil water content, temperature, growing season/dormant season, precipitation, plant vigour of external environment

**3.1 Flow/causal diagram, important factors and processes**

* **Patches:**

🡪 **Soil water availability:** desiccation over time, water content from seasonal variation in central Germany

🡪 **Seasonality**: linear seasonal increase in temperature and incoming photosynthetically radiation, infestation stop in dormant phase: death of larvae in cold winters, stop feeding/mine generation

* **Trees**
* individual leaf generation: a number of leaves per tree is generated with properties leaf area, position, net assimilation, stomatal conductance, level of defense chemicals, nutritional value, height(?), wood/leaf biomass(?), phenotypic variation, number of mines 🡪 values are part of the agentset trees 🡪 vary with position in tree within certain limits
* branch generation: a number of branches with span of lengths is generated
* if host selection occurs only within one individual tree: separate tree in different parts according to height 🡪 leaf number per segment, status of leaves/branches in relation to nutritional value/defense chemicals/plant vigor/leaf temperature/leaf water potential/net assimilation/stomatal conductance per segment, increase leaf number per height segment depending on total net assimilation of segment 🡪 amount of increase results in different plant vigor values, alternatively distribute branches and leaves around a segment 🡪 randomly set a number of distances dependent on height segment and total height, set leaf status peripher/internal dependent on distance, gas exchange is recorded by height segement dependent on oviposition events
* alternative to host selection within individual tree: crown approximated as sphere 🡪 separate sphere in different sectors with leaf superindividuals as agents, main axis as stem and branches 🡪 walking medium for insects, main stem as vertical line, main branches as lines at certain angles from main stem, leaves distributed along main axis
* leaf water potential: function of soil water potential and leaf temperature
* maximum carboxylation rate: Parameter determined by biochemical properties of enzyme Rubisco
* net assimilation: maximum possible assimilation is determined by maximum carboxylation rate, actual assimilation is limited by photosynthetically active radiation/leaf water potential
* stomatal conductance is linearly dependent of net assimilation
* infestation: each oviposition event is recorded per individual leaf/tree, in case of oviposition a specified leaf is chosen to generate mines on, reduction of net assimilation based on reduction of photosynthesis in mined/intact leaf areas, assimilation is reduced per mine dependent on leaf area 🡪 leaf area divided by typical area of a mine
* level of defense chemicals: increase in individual/all? leaves during /after infestation, decrease of substances over time? 🡪 preferred approach defense chemicals increase asymptotically until certain threshold of total infestation events, defense chemicals increase as a result of growth increment
* growth increment: generating a number of new leaves/branches each week of certain area/length span depending on carbon assimilation, this asymptotically decreases towards end of trees lifespan
* water use efficiency: calculated from net assimilation and stomatal conductance (or better use transpiration?)
* plant vigor: increases with growth increment 🡪 could be also quantified as nutritional value from Inbar et al.
* **Leaf miners**
  + - * + Main part of adults emerge from larvae of fallen leaves from previous season (?), smaller fraction of adults newly emerge from plot edges every new season
        + carrying eggs: portion of insects carries egg?
        + Flying: random flight, becomes oriented flight towards closest tree if close to trees
        + Searching (adults): insect flies from tree to tree testing their suitability 🡪 the more trees they have tested the higher their experience 🡪 different options for learning behavior, if no suitable plant is found in certain time insects move out of plot 🡪 if plant vigor of outside environment is equally low 🡪 chance of returning to current plot
        + Alternative to flying: leaf miners move along one tree and only fly to the next one if host quality very bad, insect has a height status which increases with each timestep 🡪 equivalent to insect moving up in a tree, if different statuses of height segment fulfill conditions oviposition occurs
        + host selection: leaf miner density above threshold makes adult insect leave for another plant 🡪 function of number of infestation on individual leaves
        + oviposition decision dependant on threshold of defense chemicals/nutritional value, leaf area? 🡪 probably not was not found to be important in different experiments (https://www.jstor.org/stable/1940549, https://www.publish.csiro.au/BT/BT11268) 🡪 on other hand there were more mines per leaf only due to increased leaf area, maybe shoot length? 🡪 was found to be significant in Preszler and Price, carrying eggs?
        + hatching success: number of successfully hatched eggs decreases with amount of defense chemicals, results in larval population
        + larval mortality: a fraction of larvae dies depending on nutritional value as estimate of feeding quality, chance of dying in relation to defense chemicals, larvae are not actual agents 🡪 oviposition directly results in damage, damage is inflicted by a likelihood which represents larval mortality
        + Alternatively larval mortality is unaltered by defense chemicals/nutritional value/plant vigor but instar duration is increased 🡪 which option to chose depends on leaf miner population in relation to plant vigor 🡪 same trend as in Inbar et al.?
        + each larvae generates leaf mine areas 🡪 constant
        + pupation and adult hatching after certain time 🡪 temperature dependent
        + moving away/death in winter 🡪 temperature threshold
        + initial population size of this year dependent on final population size of last year?, could also make it dependent on final amount of pupa from last season 🡪 overwintering on fallen leaves
        + learning behavior option 1: insects become more picky about their host selection 🡪 only plants of high vigor are chosen, tolerance threshold is lowered
        + learning behaviour option 2: insects adapt their host selection preference according to availability of plants with high vigor 🡪 after certain number of plants of low vigour the preference threshold is increased
        + combined approach of learning behavior: if larvae was reared on optimal host plant (thresholds in vigor/defense chemicals/nutritional value) adult insect is picky about host selection, if larvae was reared on suboptimal plant insect is more tolerant about host selection
* **Link to flow diagram:** https://docs.google.com/drawings/d/124zBLjeEQ6edV9Ln5801cWKTQ-YuAEhOHfl4fFoeEzs/edit

Diagram

Description automatically generated

* **Link to causal diagram**: https://docs.google.com/drawings/d/1x2WqNzr3NP\_SqhUNAYFwroSXJEgpVCA2c\_1yF9k\_t6o/edit

Diagram

Description automatically generated

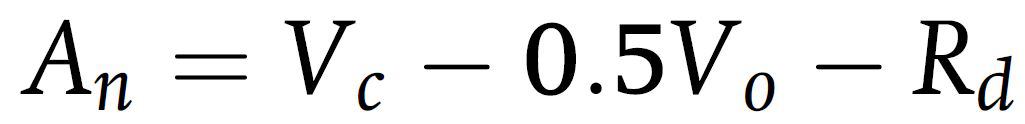
**3.2 Model procedures update: important equations**

* **Plant physiology**
  + Environment: photosynthetically active radiation as linear seasonal changes**,** soil moisture as seasonal changes from literature 🡪 use data from Helmholtz centre and values of field capacity https://www.google.com/search?q=annual+soil+moisture+germany&rlz=1C1CHBF\_deDE975DE975&sxsrf=APq-WBsC\_TZYhcaxyaVcfe8b-COuI1WB3A:1645716461111&source=lnms&tbm=isch&sa=X&ved=2ahUKEwizrsLI05j2AhUfQvEDHd\_YAb4Q\_AUoAXoECAIQAw&biw=1366&bih=568&dpr=1#imgrc=guNKqBIQZZK-yM

https://en.wikipedia.org/wiki/Soil\_moisture

* + Leaf water potential: linear relationship to soil water content?, damped oscillations? 🡪 linear relationship of leaf water potential and soil water potential, derive soil water potential from soil water content as relationship of respective soil type (module soil hydrology), figure out equation of assumed soil type

(https://www.researchgate.net/publication/5471942\_Water\_relations\_and\_drought-induced\_embolism\_in\_two\_olive\_Olea\_europaea\_L\_varieties\_%27Meski%27\_and\_%27Chemlali%27\_under\_severe\_drought\_conditions/figures?lo=1)

* + Maximum possible carboxylation rate as estimation from kinetic properties:  (Bonan, 2019 🡪 equations 11.1/11.2/11.3)
    - Maximum carboxylation rate: https://www.researchgate.net/publication/304397937\_Surveying\_Rubisco\_Diversity\_and\_Temperature\_Response\_to\_Improve\_Crop\_Photosynthetic\_Efficiency
    - Maximum oxygenation rate: calculate over specificity factor 🡪 https://onlinelibrary.wiley.com/doi/full/10.1111/j.1365-3040.2005.01300.x#:~:text=The%20specificity%20factor%20of%20Rubisco,photosynthetic%20carbon%20assimilation%20and%20photorespiration.
  + Decrease of net assimilation according to formulas of photosynthetically active radiation/leaf water potential/CO2 concentration(Bonan, 2019) 🡪 those graphs refer to Pinus banksiana 🡪 upscale net assimilation for apple in reference to Pincebourde dataset, alternatively use higher photosynthetic rates from Massonet et al.
  + Net assimilation proportional to open photosynthetically active leaf area/stomatal conductance 🡪 alternatively use data from Massonet et al.
  + Water use efficiency: ratio of net assimilation to stomatal conductance (water loss through stomata)
  + Formula to translate net assimilation into growth increment (linear?)
    - Le Goff et al. assume a linear relationship of three trees but shouldn’t the relationship be log-linear?
    - https://rseco.org/content/612-plant-biomass.html
    - seems that C accumulation follows exponential development over tree age and reaches saturation close to tree death 🡪 but I could image this holds only for old trees (https://www.researchgate.net/publication/280309071\_Carbon\_accumulation\_along\_a\_stand\_development\_sequence\_of\_Nothofagus\_antarctica\_forests\_across\_a\_gradient\_in\_site\_quality\_in\_Southern\_Patagonia/figures?lo=1)
    - biomass in apple: first half of growing season shoot elongation, second half of year fruit development (Reyes et al.) 🡪 until further notice photosynthesis could be translated linearly into leaf/shoot growth in first half of the year and fruit production in second half of year, ratio of generated leaf biomass to generated branch biomass 🡪 around 0,3:0,7 (https://www.researchgate.net/publication/227712559\_Carbon\_Sequestration\_by\_Fruit\_Trees\_-\_Chinese\_Apple\_Orchards\_as\_an\_Example/figures?lo=1)
  + Formula influence of leaf temperature on leaf water potential
    - linear decrease in wheat and barley (https://nph.onlinelibrary.wiley.com/doi/full/10.1111/nph.16214#:~:text=Leaf%2Dto%2Dair%20vapor%20pressure,a%20status%20of%20water%20deficit.)
    - also linear decrease in grapewine: https://www.ajevonline.org/content/58/2/173.figures-only
    - leaf temperature itself can be calculated via damped oscillations of ambient temperature (course ecosystem atmosphere processes, plant herbivore interactions lecture 2 slide 5, https://www.frontiersin.org/articles/10.3389/fpls.2020.00019/full#:~:text=On%20average%2C%20leaf%20temperatures%20are,within%20a%20photosynthetically%20functional%20range.)

**Further research**

* + Formula to calculate stand productivity, investigate other possible factors
  + Customize functions that they fit *Malus domestica* (apple)
  + How to extrapolate calculations from one leaf to whole crown
* **Plant leaf miner interactions**
  + Leaf mining on stomatal conductance/net assimilation: decrease by formulas of non-linear models by Pincebourde et al. 🡪 also use the dependence of this relationship from irradiance
  + Leaf mining on intact leaf area: find out relationship of individual leaf miner number and mine area 🡪 calculate intact leaf area, each mine covers approximately 4% of leaf area, 10-12 mm long and 4-5 mm wide (http://www.omafra.gov.on.ca/english/crops/facts/sptent.htm)
  + Net assimilation of intact leaf area: multiply intact leaf area as fraction of total leaf area with net assimilation
  + Leaf mining on defense chemicals: **find out rate of conversion**, otherwise use rates from Inbar et al. 🡪 effect of growing conditions on plant defensive compounds?, could also use results from Zamljen et al. (apple stink bugs defense chemicals)
  + Defense chemicals on oviposition/development/larval population: regression analysis from Inbar et al. 🡪 only influence of defensive chemicals on insect population and performance available
  + Plant vigor on host selection: regression from Inbar et al. 🡪 only influence of plant growth on insect performance available, could also use article of apple vegetative growth and aphids (https://www.researchgate.net/publication/321360711\_Rosy\_apple\_abundance\_is\_shaped\_by\_vegetative\_growth\_and\_water\_status)
  + Influence of leaf miner infestation on defense chemicals: binary solution 🡪 defense chemicals either there or not, otherwise use Zamljen et al.
  + Influence of nutritional value on leaf miner mortality 🡪 linear increase with slope m=1?, Conqueret et al. report similar mining activity at low nitrogen levels but slower developmental rates, Han et al. report higher mortality at lower nitrogen and water levels

**Further research**

* Effect of defense chemicals/plant vigor on different developmental stages of leaf miners, maybe use combined effect of defense chemicals and plant vigor like in Inbar et al.
  + Influence of defense chemicals on larval mortality: take results from vaccination experiment (Black et al.)
* **Leaf miner population size**
  + Ambient air temperature on oviposition/development/larval population: use linear models from Rojas and Wyatt, von Arx et al., Martin et al. 🡪 Conversion from hatching rates to larval population, as well as larval population to adult population through pupation 🡪 make it a function of ambient temperature and literature values of generation time from temperature development models, assume survival rates
  + Interesting aspect from Geng and Jung: survival rate of adult leaf miners depending on age

**Further research**

* + Influence of population density on host selection 🡪 select a threshold of number of eggs/mines per leaf
    - 2/4 mines per leaf? (http://www.omafra.gov.on.ca/english/crops/facts/sptent.htm)
    - use as reference for density dependence (<https://www.nrs.fs.fed.us/pubs/gtr/gtr_ne153/gtr_ne153_219.pdf>)
    - alternatively use Bawin et al. 🡪 oviposition choice experiment at different infestation levels
    - interesting study on mortality and number of mines related to number of eggs per leaf: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.0021-8790.2004.00867.x
  + Influence of experience/flying behavior on host selection 🡪 becoming better at choosing the right host, becoming more accurate at choosing the best host in available plants 🡪 it has been documented that insects are able to identify improved food quality and best food quality available at a site
  + Include spring emergence from Geng and Jung 🡪 only if variation in seasonality is included

**4. Scales**

* **Time step:** half week
* **Temporal extent**: 20 years
* **Spatial grain:** 10 cm x 10 cm
* **Spatial extent**: 3 m x 3 m

**5. Input (parameters)**

* **Trees**
  + - * + translation soil water content to leaf water content
        + parameters to model stomatal conductance/carbon assimilation from leaf water content/incoming solar radiation/temperature
        + assimilation rate dependent on stomatal conductance per surface area
        + temperature range of active photosynthesis
        + water content threshold permanent wilking point
* **Leaf miners**
  + - * + flying speed
        + searching time threshold before moving out of plot
        + vigour threshold for host selection
        + defense substance threshold for oviposition decision
        + clutch size (or variable?)
        + feeding time
        + pupation time/rate
        + mine area per larvae
        + life expectancy of insects
* **Environment**
  + - * + daylength/temperature threshold growing/dormant season
        + survival threshold larvae cold winters

**6. Output (variables)**

* **Trees**
  + - * + water use efficiency
        + total stomatal conductance
        + total photosynthetically active area
        + total carbon assimilation
        + stand productivity
* **Leaf miners**
  + - * + adult/larval population size
        + searching time
        + characteristics of selected hosts --> plant vigour/leaf chemistry
        + generation time
* **Environment**
  + - * + soil water content?

**7. Parameter list**

**7.1 Tree physiology**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Parameter** | **Association** | **Range** | **Usage** | **Source** |
| **Kc** (Michaelis Menten constant for CO2) | Biochemical parameter | 5-45 µM | Calculate carboxylation rate | Orr et al. (2016) |
| **SC/O (**Specificity factor) | Biochemical parameter | 90-110 | Calculate carboxylation rate | Orr et al. (2016) |
| **Rd** (respiration) | Biochemical parameter | 0,0015 \* Vc (max) | Calculate carboxylation rate | Bonan (2019) |
| a/b/c/d Ricker curve **phot. active radiation** | Biochemical parameter | 5,257445737 0,004497597 1,228546302 -0,725667455 | Delimitation photosynthesis | Bonan (2019)  R script parameter estimation |
| **Alternative 1**  a/b/c/d Ricker curve **phot. active radiation** | Biochemical parameter | 10,923923437  0,002786338 0,708200928 -1,751814937 | Delimitation photosynthesis | R script Pincebourde non linear models |
| a/b/c/ polynomial **leaf water potential** | Biochemical parameter | -1,1090866  0,9083979  4,1937435 | Delimitation photosynthesis | Bonan (2019)  R script parameter estimation |
| a/b/c/ polynomial **CO2 concentration** | Biochemical parameter | -1,017093e-05  1,953602e-02  -1,081342e+00 | Delimitation photosynthesis | Bonan (2019)  R script parameter estimation |
| a/b linear equation relationship **net assimilation to stomatal conductance** | Gas exchange parameter | 0,1857238  -2,3694871 | Relationship net assimilation to stomatal conductance | Bonan (2019)  R script parameter estimation |
| a/b linear equation relationship **growth rate** to **net assimilation** | Growth rate parameter | 0,0135838  -0.0014767 | Relationship growth rate to net assimilation | Lit et al. |
| **Leaf growth** increment in comparison to **branch growth** increment | Growth rate parameter | 0,3/0,7? | Growth increment of leaves/branches | Wu et al. |
| **Leaf/branch growth** increment in comparison to **fruit growth** increment | Growth rate parameter | Differing ratios of fruit growth increment to branch growth increment | Distribution of total growth rate to branches and fruits | Reyes et al.  R script parameter estimation |
| a/b linear relationship of **leaf water potential** in dependence of **ambient temperature** | Leaf physiology parameter | -0,018  -0,217 | Initial leaf water potential | Williams and Baeza |
| Influence of **branch growth rate** on **plant vigor** | Branch physiology and attractiveness | Maximum/minimum possible growth rate associated to Maximum/minimum plant vigor | Attractiveness of host for leaf miners | Guesstimate |
| **Leaf temperature** of **unexposed leaves** | Leaf physiology parameter | Fluctuating randomly at 2-13 °C lower than ambient temperature | Leaf temperature unexposed leaves | Deva et al. |
| **Leaf temperature** of **exposed leaves** | Leaf physiology parameter | Fluctuating randomly at 2-13 °C higher than ambient temperature | Leaf temperature exposed leaves | Personal communication Sylvain Pincebourde |
| a/b/c polynomial **water retention curve** | Environmental parameter | 11058383  -6535395  966029 | Soil water potential | Example water retention curves soil hydrology  R script parameter estimation |
| a/b/c/d polynomial **soil water content** | Environmental parameter | 0,0010000613  -0,0122641332  0,0008892295  0,4150609283 | Seasonal soil water content | Data Helholtz centre Leipzig  R script parameter estimation |
| a/b linear relationship **leaf water potential** to **soil water potential** | Leaf physiology parameter | 2,62394  -0,16299 | Leaf water potential | Ennajeh et al.  R script parameter estimation |
| a/b polynomial number of leaves per tree in dependence of tree age | Tree anatomy parameter | -15,68353  1136,47399 | Infestation dynamics | Guesstimate from 20000 leaves per mature tree |

**7.2 Plant insect interaction**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Parameter** | **Association** | **Range** | **Usage** | **Source** |
| **Reduction of net assimilation** due to leaf mining 🡪 corrected for green island | Leaf physiology parameter |  | Quantify leaf mining damage | R script Pincebourde non linear models |
| Area per mine | Plant leaf miner interaction | Circular, 10-12 mm long and 4-5 mm wide | Quantify leaf mining damage | Pincebourde et al., Ontario website leaf miner ecology |
| Linear influence of **plant vigor** on **host selection** | Leaf miner host selection | Maximum/minimum plant vigor associated to maximum/minimum host preference | Oviposition decision of leaf miners | Guesstimate based on results from Inbar et al. |
| Influence of **leaf mining** on **defense chemicals/nutritional value** | Plant defense | Binary 🡪 reduced/not reduced | Oviposition decision of leaf miners | Guesstimate based on results from Coqueret et al. |
| Influence of **nutritional value/defense chemicals** on **host preference** | Leaf miner host selection | If reduced host either selected/avoided | Oviposition decision of leaf miners | Guesstimate based on personal communication with Sylvain Pincebourde |
| Influence of **nutritional value/defense chemicals** on **larval mortality** | Leaf miner mortality | If nutritional value reduced 🡪 mortality 20% | Increase in leaf miner mortality due to plant defense reaction | Askew and Shaw (realistic?, further research) |
| Influence of **plant vigor** on **larval mortality** | Leaf miner mortality | Maximum/minimum plant vigor associated to maximum/minimum host preference 🡪 **0%-20%** | Increase in leaf miner mortality due to plant vigor | Guesstimate 🡪 (realistic?, further research) |
| Alternative influence of **plant vigor** on **larval mortality** | Leaf miner mortality | Maximum/minimum plant vigor associated to maximum/minimum host preference 🡪 **0%-40%** | Increase in leaf miner mortality due to plant vigor | Guesstimate 🡪 (realistic?, further research) |
| Influence of **plant vigor** on **instar duration** | Leaf miner development | Minimum plant vigor associated to increased instar duration by factor 1,5 | Increase in leaf miner development due to plant vigor | Guesstimate 🡪 (realistic?, further research) |
| Influence of **nutritional value** on **instar duration** | Leaf miner development | Minimum nutritional value associated to increased instar duration by factor 1,5 | Increase in leaf miner development due to plant plant defense | Guesstimate 🡪 (realistic?, further research) |
| Baseline leaf miner mortality | Leaf miner mortality | 40% | Leaf miner mortality under otherwise optimal conditions | Askew and Shaw |

**7.3 Leaf miner physiology/phenology**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Generation time of leaf miners | Leaf miner phenology | 8 weeks? | Annual leaf miner population dynamics | Ontario government |
| a/b/c polynomial influence of **leaf temperature** on **leaf miner development** | Leaf miner phenology | 0,0213  -0.0542  0,0009 | Annual leaf miner population dynamics | Geng and Jung temperature effect |
| Leaf miner initial population size | Leaf miner phenology | 10000 to 20000 individuals trapped in an orchard (per 10 trees) 🡪 upscale by factor 10 then divide by 10 trees then divide again by 10 for start of the year | Model starting conditions | Gagné and Barrett |
| a/b/c polynomial influence of **leaf temperature** on **egg number** | Leaf miner physiology | 71,3686  17,8132  6,1431 | Eggs per female | Ontario government |
| a/b/c polynomial influence of **age** on **oviposition rate** | Leaf miner physiology | 0,0545  0,5286  1,7591 | Eggs per female | Geng and Jung temperature effect |
| a/b linear relationship of **leaf temperature** on leaf miner **generation time** | Leaf miner phenology | 3.254e-03  -2.323e-02 | Generation time of leaf miners | Geng and Jung temperature effect |
|  |  |  |  |  |
|  |  |  |  |  |