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## Incorporating clonality into the plant ecology research agenda

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# Trends in Plant Science

## Incorporating clonality into the plant ecology research agenda

--Manuscript Draft--

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| <b>Abstract:</b>             | A longstanding research divide exists in plant ecology: studies either examine specifically plant clonality or are focused on all plants generally but considering them being nonclonal. This gap cascades into a lack of knowledge about the similarities and differences between clonal and nonclonal plants. We aim to bridge this gap by identifying areas that would benefit from incorporating clonal strategies and dynamics into one integrated research platform. These fields are: i) response to habitat productivity, ii) interactions among neighbours, iii) response to disturbance, and iv) population structure and evolution. We are convinced that this would provide valuable insights into the eco-evolutionary dynamics of all plants. |
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**Opposed Reviewers:**

Dear Dr. Susanne Brink, Editor of *Trends in Plant Science*,

On behalf of all co-authors, I would like to submit our manuscript of an Opinion piece entitled "*Incorporating clonality into the plant ecology research agenda*" to *Trends in Plant Science*.

Please, accept my apology for delay with submission.

With best regards

Jitka Klimesova

1 **Highlights:**

2 Clonal plants can represent a substantial proportion of species in floras and plant  
3 communities. Because they share several functions that are not present in nonclonal plants,  
4 the differences in their proportions are likely to scale up as community and ecosystem  
5 differences.

6 Clonal reproduction is provided by specialised organs which directly or indirectly affect other  
7 plant traits. Clonal growth organs usually serve for the storage of carbohydrates and buildup  
8 of the bud bank, both necessary for resprouting in recurrently disturbed habitats. These  
9 storage organs (to an unknown but potentially important degree) affect global carbon cycling.

10 Clonal growth leads to increased plant size in the horizontal dimension and to a different  
11 degree of ramet aggregation that influences exploration of soil resources, pollination, and  
12 biotic interactions.

13 Clonal growth serves as a reproductive insurance mechanism that further affects plant  
14 demography and possible evolutionary rates.

15

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# 1 **Incorporating clonality into the plant ecology research agenda**

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17 **Keywords:** belowground organs; clonality, plant functions

18

19

20 **Abstract**

21 A longstanding research divide exists in plant ecology: studies either examine specifically plant  
22 clonality or are focused on all plants generally but considering them being nonclonal. This gap  
23 cascades into a lack of knowledge about the similarities and differences between clonal and  
24 nonclonal plants. We aim to bridge this gap by identifying areas that would benefit from  
25 incorporating clonal strategies and dynamics into one integrated research platform. These fields  
26 are: i) response to habitat productivity, ii) interactions among neighbours, iii) response to  
27 disturbance, and iv) population structure and evolution. We are convinced that this would provide  
28 valuable insights into the eco-evolutionary dynamics of all plants.

29

30

## 31 **Introduction**

32

33 An overwhelming portion of plant ecological research focuses solely on aboveground parts.  
34 As a result, our understanding of belowground plant functions is lagging behind the aboveground  
35 compartment [1, 2]. While the study of root acquisitive functions (and fine roots as **acquisitive**  
36 **organs**; see Glossary) has made recent large advances [3], **nonacquisitive organs** such as  
37 storage roots, rhizomes, and bulbs, have still been given little attention, despite their almost  
38 ubiquitous presence [4]. These organs provide functions that are common to all plants, such as  
39 the storage of carbohydrates and buds, but also enable functions limited to only some plants,  
40 namely clonal growth. The ability to multiply clonally separates plants into two groups:  
41 nonclonal plants that multiply only by seed, and clonal plants that can also multiply by vegetative  
42 growth. However, **clonality** does not only affect reproductive mode, it is also involved directly or  
43 indirectly in many aspects of plant life and function.

44           There has been a long tradition of research on plant clonality (see [5] for a recent  
45 overview), but it has largely remained restricted to a small group of researchers that are focused  
46 exclusively on clonals and only use a few model species, otherwise ignoring nonclonal plants.  
47 Consequently, we do not have enough comparative information about key differences and  
48 similarities between clonal and nonclonal species. Therefore, it is no surprise that functional  
49 syntheses incorporating all plants have largely ignored the clonal/nonclonal dichotomy or have  
50 pigeonholed clonality as a special, if not exotic feature, important only for a narrow range of  
51 ecological functions (but see [6]).

52           Here, we draw a roadmap aimed at bridging this research divide (i.e. clonal-and nonclonal-  
53 oriented), by showing that although it is not universal, clonality is a widespread feature of plants  
54 (Box 1, 2) and that modifies or determines many essential plant functions and processes, such as  
55 i) response to productivity, ii) interactions among neighbours, iii) response to disturbance, and iv)  
56 population structure and evolution (Table 1 – Key Table). We provide examples where taking  
57 clonality and its absence into account may substantially affect the way we look at plants, making  
58 our understanding of plant functional differentiation more complete and finally allowing deeper  
59 insights into plant eco-evolutionary dynamics.

60

## 61 **Clonality along the productivity gradients**

62

63           One key gradient that shapes plant form and function is associated with habitat productivity  
64 and the related plant economics spectrum [7, 8]. It was primarily defined for leaves, wherein thin,  
65 short-lived, acquisitive leaves with low protection against herbivory and high photosynthetic  
66 rates are found at the fast end of the spectrum, whereas leaves with contrasting features are



67 positioned at the slow end [9]. In addition to the leaf economics spectrum, this productivity  
68 gradient determines biomass allocation strategies (i.e. biomass investment to organs that acquire  
69 different resources), this is typically described as the root/shoot ratio [10, 11]. Plants in highly  
70 productive environments (i.e. those characterised by high competition for light) tend to invest  
71 preferentially into stems and leaves, while plants growing in nutrient-limited environments  
72 primarily increase allocation to fine roots that promote belowground resource acquisition [12].

73         These textbook relationships generally consider all belowground organs to be responsible  
74 for resource acquisition. However, the specialised belowground **clonal growth organs** of clonal  
75 plants add further functional dimensions. They do not participate in resource acquisition, but in  
76 addition to clonal reproduction, these organs store and share resources among the rooting units  
77 that they connect [2]. This leads to three major consequences for economics and allocation  
78 relationships.

79         First, **storage organs** divert a significant amount of resources which might otherwise be  
80 used for growth and competition for light [13]. Although the leaf economics spectrum has been  
81 expanded by incorporating other organs (e.g. roots; [7]) and functions into the plant economics  
82 spectrum, belowground storage organs have remained sidelined and their role in resource  
83 economy along the productivity gradient is essentially unknown [14]. Second, the occurrence of  
84 belowground storage organs confounds the use of the simple root/shoot ratio as a proxy of  
85 relative investment into nutrient- vs light-acquiring organs [10, 15]. Therefore, the available  
86 comparative data [16] cannot be interpreted as evidence for differential roles between light- and  
87 nutrient-acquiring investment. In particular, the lifespan of belowground storage organs and its  
88 link to the leaf economics spectrum is of key importance and may affect carbon sequestration and  
89 cycling globally [17, 18]. Third, in addition to resource storage (also present in many nonclonal

90 perennials), clonal organs are often involved in the horizontal transport of resources, including  
91 carbon and soil-borne nutrients [19, 20]. The extent of resource sharing in clonal plants depends  
92 on the lifespan of their clonal connections, which has been described in terms of the integrator  
93 and splitter strategies. Integrators (i.e. species with clonal connections maintained long after the  
94 new **ramet** has become established) are favoured in harsh and low-productivity environments  
95 whereas splitters (with short lifespan of connection) in benign conditions [20, 21, 22]. As plants  
96 transport limited resources (water, nutrients) or ameliorate stress (e.g. aeration of organs in  
97 waterlogged soil), such connections between different parts of a clone may equalise conditions  
98 over heterogeneous environments with potentially ecosystem-wide effects [17].

99       Currently, we know very little about the role of storage and clonal growth organs in the  
100 plant economics spectrum as well as how traits of these organs vary along productivity gradients.  
101 While theoretical models have shown how resource storage may (or may not) contribute to  
102 fitness [23], there are almost no comparative studies showing differences in relative size or  
103 lifespan of storage organs across a number of species along productivity gradients [24, 25]. While  
104 the **splitter-integrator continuum** has been extensively studied, such studies seldom incorporate  
105 relevant trends and traits for nonclonal plants [22]. Therefore, we cannot identify general rules  
106 about the contribution of clonality (and its types) to fitness via translocation across different  
107 micro-environmental patches. Including clonal growth organs, their resource-sharing, and their  
108 storage capacities into a broader research on economics spectrum will fill gaps in understanding  
109 plant strategies in response to habitat productivity.

110

111 **Interactions among neighbours**

112

113 Plants compete for many resources, especially light, water, and nutrients. Under productive  
114 and undisturbed conditions, competition for light along the vertical dimension takes precedence  
115 [26]. It is inevitably asymmetric and often leads to competitive exclusion. However, competitive  
116 exclusion by overtopping may be delayed or blocked by reducing vertical size differences [27].  
117 After disturbance or in harsh environments, the vertical dimension may lose its importance and  
118 the success of individual species is then determined by the amount of space they can occupy in  
119 the horizontal dimension [28].

120 This space occupation can be attained by generative reproduction or by clonal growth. Both  
121 these processes determine aggregation and mobility patterns in communities, but strongly differ  
122 in their outcomes. While seed dispersal is not directly controlled by the mother plant and  
123 typically follows an exponential or hyperbolic decay curve [29], clonal reproduction is more  
124 active and associated with species-specific fixed distances [30]. Distinct morphologies of  
125 individual species then determine their aggregation patterns, ranging from loose patches to  
126 densely packed aggregations of individuals (often termed the **guerrilla-phalanx growth forms**,  
127 another strategy scheme not suited to encompass nonclonal plants; [31]). Aggregation can be a  
128 way for plants to respond to environmental harshness ranging from intraspecific (namely clonal)  
129 to interspecific (facilitative) aggregations [32, 33].

130 Another important attribute of clonal reproduction can be parental support of offspring,  
131 which may last long into their maturity, and can contribute far greater access to resources than  
132 afforded by an increase in seed size by nonclonal plants. Resources stored in the seed are  
133 necessarily fixed and also lack the feedback mechanism, and thus versatility, present in clonal  
134 connections. Clonal growth is also often associated with density regulation of neighbouring

135 ramets from the same genetic individual (i.e. **genet**) [34] which reduces competition among them  
136 (Box 3).

137 Finally, an essentially technical yet key detail in plant competition concerns dominance.  
138 Dominant species (i.e. those accounting for the highest number of individuals or biomass in a  
139 community) are assumed to affect community-level processes more than subordinate species  
140 [35]. This assumption is used to scale up plant traits, typically collected at the individual plant  
141 level, to ecosystem functions, which is typically based on the proportions of individual species  
142 aboveground [36]. However, plant species strongly vary in their investment of biomass into  
143 belowground organs, and the clonal-nonclonal divide plays an important role. This implies that  
144 scaling up plant traits by aboveground plant dominance is improper, especially when plant  
145 belowground functions are the focus of the study and in open, seasonal, or disturbance-prone  
146 ecosystems that are characterised by species with large allocation into belowground  
147 nonacquisitive organs [4, 37]. This discrepancy may be ameliorated by investing larger effort to  
148 collecting information on belowground organs and traits.

149

## 150 **Clonality and disturbance**

151

152 Disturbance is another essential driver of plant strategies worldwide [38, 39]. It has been  
153 hypothesized that clonal plants are particularly common at intermediate disturbance levels [38],  
154 but this strongly depends on the disturbance regime in terms of both frequency and severity. The  
155 existing literature often distinguishes between **seeders and resprouters**: seeders (regenerating  
156 from seeds), and resprouters (i.e. plants that resprout after disturbance from specialised bud-  
157 bearing organs) [38]. Clonal plants are typically resprouters, but currently available data do not

158 establish a clear relationship between resprouting and the degree of clonality a plant possesses,  
159 hence limiting possible generalisation. While experiments with temperate species have shown  
160 that clonal plants accumulate higher belowground biomass (in storage and/or bud-bearing organs)  
161 than nonclonals [40, 41], there are no comparative data on storage and **bud banks** in clonal and  
162 nonclonal plants available for the majority of disturbance-prone ecosystems.

163 Further, simple quantification of plant investment into bud-bearing organs is not sufficient  
164 for assessing the cost of their formation. Loss of a bud is a loss of the outcome of a complex  
165 morphogenetic event and cannot be immediately replaced even if the necessary resources are still  
166 available. Consequently, such loss must be assessed with respect to the architectural constraints  
167 of a given plant. For example, stem-derived clonality provides the plant with a limited number of  
168 axillary buds and thus confers only a limited ability to survive disturbance, and therefore it is  
169 found mainly in grazed or mown systems. In contrast, root-derived clonality, with a potentially  
170 unlimited number of adventive buds, can be very successful under severe disturbance regimes  
171 like ploughing or landslides [42].

172 Compared to the other topics, the disturbance-clonality relationship has been addressed  
173 more in-depth, making clear that clonality needs to be taken into account when building a  
174 comprehensive scheme of response to disturbance. Additional research on the morphological  
175 means of clonal and nonclonal bud-bearing organs and their relationship to specific disturbance  
176 regimes would be beneficial.

177

## 178 **Population structure and evolution**

179

180 Plant species have remarkable diversity in their life histories, which partly corresponds to  
181 the changes of their bodies in response to productivity and disturbance gradients. This is reflected  
182 by the different relative roles of survival, reproduction, and growth in plant life cycles. Again,  
183 this simple scheme essentially excludes clonal growth, which can play a decisive role in both the  
184 growth and reproduction components of plant life cycles, with consequences on population  
185 structure, reproductive strategy, and diversification rates.

186 First, clonal reproduction has a number of short-term ecological effects. It may serve to  
187 boost population growth rates under favourable conditions [43] and provide reproductive  
188 assurance to genetic individuals. Clonal plants thus have consistently lower investment into  
189 reproduction via seed than nonclonal plants [44, 45]. While species differ strongly both in the  
190 presence and magnitude of clonal reproduction, we only have limited data for the extent of this  
191 differentiation (see also Box 2). In particular, there is almost no demographic information on  
192 species with extensive clonal growth because these cannot be studied using simple marking-  
193 based demographic techniques [46].

194 Second, the population structure of species that are capable of clonal growth is very  
195 different from that of nonclonal species because of the uncoupling of genetic and ecological  
196 individuals [43]. Although the overall genetic diversity of clonal species does not necessarily  
197 differ from that of nonclonal species, some clonal species may have many genetically identical  
198 ramets within a population – a situation that is otherwise found only in apomictic or highly  
199 autogamous species [47]. This phenomenon, amplified by the spatial aggregation of genetically  
200 identical ramets, may result in restricted pollen dispersal among genets [44, 47, 48] and have  
201 important consequences for autogamy, selection of floral traits, and display for pollinators (Fig. 1  
202 in [47]). These relationships have never been systematically explored, either by comparing clonal

203 and nonclonal species, or across different types of spatial organisations of clonal plants.  
204 Unfortunately, we also do not possess good estimates of genet lifespan in more than a few model  
205 plants [49]. Interestingly, both clonal growth and incompatibility are related to whole-genome  
206 duplication, and polyploid plants are more likely to be both self-compatible and clonal [50, 51],  
207 although links between these two patterns have not been addressed.

208 Finally, clonal reproduction strongly extends generation time and thus may change rates of  
209 molecular evolution and speciation, similarly to plant size [52]. While it has rarely been  
210 systematically explored, clonality may contribute to explaining latitudinal or environmental  
211 gradients in plant diversity as clonal plants tend to prevail in cold and wet environments [25].  
212 This may be one of the reasons for the slow evolution of aquatic angiosperms that have extensive  
213 clonal growth, although the comparison between resprouters and seeders in fire-prone areas does  
214 not support the same conclusion [53].

215 Unfortunately, we do not possess good estimates of genet lifespan in more than a few  
216 model plants therefore we are in need of new methodological approaches in studying  
217 demographic parameters in clonal plants [44, 49, 54].

218

## 219 **Conclusions**

220

221 Existing evidence has shown that clonal species differ systematically from nonclonals in a  
222 number of features and as their proportion in different communities and biomes varies (Box 2),  
223 these functional differences likely scale up to affect community- and ecosystem-level dynamics.  
224 It has also become clear that despite its previous treatment in the literature, clonality is not a  
225 binary trait (i.e. presence or absence) and there is a large functionally relevant spectrum spanning

226 across different clonal strategies and species. Incorporating clonality into the mainstream plant  
227 ecology research platform requires a closer look at the functions that vary across clonal strategies,  
228 and identifying comparable functions in nonclonal plants so that all species can be placed into a  
229 general strategy scheme.

230 Finally, we point out that one of the key reasons why clonality has been under-developed in  
231 plant ecology research at large, lies in the fact that it is inevitably tied to a whole-plant  
232 perspective, which is not easily incorporated into current approaches to plant functional  
233 differentiation (e.g. [8, 55]). Such approaches (be it trait-based comparative ecology, population  
234 ecology, or ecosystem ecology) have their strengths in reducing plant bodies and organs to simple  
235 functional traits applicable to any species. This means that dimensions of the plant life that are  
236 difficult to reduce to such a scheme are necessarily neglected. We believe that the inclusion of  
237 plant clonality into mainstream ecological research would capture better the essential feature of  
238 plant life (i.e. the hierarchical and modular structure of any individual; Box 3, [56]) and would  
239 add a whole-plant perspective that many of our studies have been lacking.

240



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246

247

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393

394 **Glossary:**

395 **Acquisitive organs:** organs acquiring resources, namely leaves as photosynthesising organs that  
396 capture light and produce organic compounds using water, light, and CO<sub>2</sub>; and fine roots that  
397 capture water and mineral nutrients. They are characterised by high surface to volume ratios.

398 **Bud bank:** a pool of dormant buds borne by belowground storage organs from which the plant  
399 regrows after seasonal rest or after the damage of aboveground parts.

400 **Clonality:** the ability of one genetic individual (genet) to produce more than one physically  
401 independent rooting unit (ramet) during its lifespan. The degree of clonal multiplication differs  
402 among species so that some of them can grow clonally but rarely do so (Potential clonality) while  
403 others multiply regularly and clonality is a regular part of their life cycle (Functional clonality).

404 **Clonal growth organs:** organs through which vegetative multiplication takes place. They are  
405 usually placed belowground and have different morphologies depending on the participation of  
406 stems (e.g. rhizomes), leaves (e.g. bulbs), and roots (e.g. root-sprouting).

407 **Genet:** the term denotes all ramets descending from one zygote irrespectively of their physical  
408 connections.

409 **Nonacquisitive organs:** organs providing resource storage, clonal multiplication, lateral spread,  
410 and bud bank that often connect aboveground stems and roots, but do not participate directly in  
411 acquiring resources. They are characterised by low surface to volume ratios.

412 **Phalanx-guerrilla growth forms:** horizontal distances between ramets of one clone vary  
413 strongly, ranging from tightly packed ramets (phalanx) to loose stands intermingled with other  
414 species (guerrilla). While intraspecific (and intragenotypic) interactions prevail in the phalanx  
415 strategy, interspecific interactions prevail in the guerrilla. The runner vs. clumper continuum  
416 denotes the same thing.

417 **Ramet:** the term identifies the smallest potentially independent unit in clonal plants with its own  
418 shoot and root system. Ramets may (but do need not to) be linked by clonal growth organs  
419 (rhizomes, roots, or stolons); a set of linked ramets is usually called clone or clonal fragment.

420 **Storage organs:** coarse organs of different morphological origin specialised for storing  
421 carbohydrates and building bud bank, generally located belowground.

422 **Splitter-integrator continuum:** clonal connections between ramets of one clone strongly vary in  
423 their duration, ranging from long-lived (integrators) to short-lived (splitters) connections among  
424 ramets. While integrators can share resources over many years (up to tens), the ability to share  
425 resources in splitters is lost after a few weeks or months when the offspring ramet becomes  
426 mature.



427 **Seeders and resprouters:** strategies described in ecosystems with recurrent severe disturbance,  
428 usually fire. Seeders do not survive disturbance as adult plants and thus regenerate after  
429 disturbance only from seeds; in contrast, resprouters survive and resprout from bud bearing  
430 organs, often located belowground.

431  
432 **Box 1.** Phylogenetics of clonality in angiosperms.  
433 Clonality is widespread in all major clades of angiosperms. It shows marked phylogenetic  
434 clustering, although transitions between clonal and non-clonal forms have been fairly common  
435 (Figure I). Specifically, all monocots are at least potentially clonal [57] (although not all of them  
436 are clonal functionally, i.e. having clonality as a part of their life cycle). From the morphogenetic  
437 point of view, clonal growth is attained by two distinct processes, either by the formation of  
438 adventitious roots on stems (stem-derived clonality, i.e. stolons or rhizomes) or by forming  
439 adventitious buds on roots (root-derived clonality). Phylogenetic transition rates among stem-  
440 derived clonality, root-derived clonality, and nonclonal forms show that both morphological  
441 types represent evolutionarily independent pathways for attaining clonal growth (Figure II).

442  
443 Figure I - Phylogenetic patterns of **functional clonality** in angiosperms showing large clusters of  
444 predominantly clonal species (e.g. monocots, rosids, Asterales) and also clusters where nonclonal  
445 forms prevail (fabids, Apiales). Red colour indicates the reconstructed probability of possessing  
446 clonal growth at a given node of the phylogenetic tree, covering 2909 angiosperm species of  
447 Central European flora. Estimate of Pagel's lambda for clonality here is 0.815 (95.0% confidence  
448 interval: 0.774-0.849; lambda = 1 indicates full phylogenetic signal corresponding to the  
449 Brownian motion evolution, lambda = 0 indicates complete phylogenetic randomness). Clonality

450 evolution was estimated using stochastic character mapping of 50 simulated character histories  
451 based on a continuous-time reversible Markov model of clonality-nonclonality transitions. These  
452 histories were used to estimate the expected number of evolutionary transitions over the tree and  
453 to reconstruct probabilities of the trait occurrence on individual tree nodes. For the data and  
454 further details see [58].

455  
456 Figure II - Root-derived clonality and stem-derived clonality represent two evolutionarily  
457 independent pathways to attain clonal growth. Transitions between stem-derived clonality and  
458 nonclonal forms have been common, as well as between nonclonal plants and root-derived  
459 clonality. Root-derived clonality appeared almost exclusively in nonclonal species as an  
460 alternative pathway to attain clonal growth [58]. The low frequency of transitions between stem-  
461 and root-derived clonality indicates that both types are alternative solutions to the same selective  
462 force acting on non-clonal species. Transitions were estimated using simulated stochastic  
463 character histories based on the continuous Markov chain rate matrix estimated from 2909  
464 angiosperm species of Central European flora. The frequency of transitions is expressed relative  
465 to the total number of transitions in the tree. Line width is proportional to the transition  
466 probability; transitions with zero relative frequency are indicated by the dotted line. For the data  
467 and further details see [58].

468  
469 **Box. 2.** Participation of clonal species in floras and communities.  
470 Clonal species are more common in wetter, colder and more disturbed environments. This can be  
471 shown both by large regional (Figure I) and local (Figure II) differences in the proportion of  
472 clonal plants, which reflect structure of species pools as well as of ecological filters.

473  
474 Figure I - Proportion of clonal species in different floras of the world, showing a consistent  
475 increasing trend in participation of clonal species towards higher latitudes and altitudes. Numbers  
476 indicate the total number of species analysed; stars indicate the number of species in a larger  
477 region when the number of species analysed was not available. It is to be noted that individual  
478 surveys [59-65] do not necessarily work with the identical definition of clonality, potentially  
479 adding some noise to the data. To exemplify this, we are showing Central European data using  
480 two definitions of clonality: "potential" clonality, i.e. including all species that have the potential  
481 to grow clonally, and "functional" clonality, i.e. including only species that regularly have clonal  
482 growth as a part of their life cycle.

483  
484 Figure II - Participation of clonal species in different vegetation types in one region (Czech  
485 Republic), showing a steep increase of clonal species proportion towards community types with  
486 higher water availability or moderate disturbance. It is based on a stratified set of 20486  
487 vegetation records from the Czech National Phytosociological Database [66], classified into  
488 vegetation types using EUNIS habitat classification. Participation is expressed as the proportion  
489 of clonal species out of all species in records of the given vegetation types; error bars indicate  
490 95% confidence intervals. Numbers indicate the total number of each vegetation type records.  
491 Modified from [67].

492  
493 **Box 3.** Plant architecture of clonal and nonclonal plants.  
494 Analysing architecture (Figure I) helps to elucidate plant response to the environment [68]. For  
495 example, plants respond to light limitation by adjusting their architecture and occupation strategy

496 in both clonal and nonclonal plants [69, 70]. As shown for the clonal shrub *Z. americanum*  
497 (Figure II), shoots are produced at regular intervals (Fig. 2) on long horizontal roots and they die  
498 if growing in the dense shade (Fig. 2 C) or develop into ramets with a complex structure (Fig. 2  
499 B). When the clone is developing in the understory, horizontal roots linking ramets senesce and  
500 trigger new taproots (Fig. 2 D) emitting radially horizontal roots and resetting soil exploration in  
501 all directions. Soil exploration in the horizontal dimension stops when it comes to contact with  
502 another clone from the same species (but not from other plant species) suggesting a chemical  
503 signaling responsible for this ‘root shyness’ between clones. This example illustrates important  
504 parts of clonal strategies: radial colonisation, exploration of suitable patches, and limitation of  
505 intraspecific competition.

506  
507 Figure I – Plant structure is based on the repetition of different levels of structural units, from  
508 phytomeres to growth and architectural units, to branch complexes. The complexity of the  
509 structure is shown by highlighting module (yellow), foliage of largest structural unit (purple), and  
510 rooting unit (beige) in nonclonal (1, 2, 4) and clonal plants (3, 5, 6, 7). In the simplest case, the  
511 genet is also a module and the rooting unit (e.g. annual herb: 2) but the clone can also be  
512 composed of several modules (e.g. rhizomatous forb: 6). In more complex structures, the module  
513 can be integrated into a larger structural unit that can correspond to a distinct rooting unit,  
514 therefore a genet (e.g. tree and shrub: 1, 4) or can be part of an even larger clone (e.g. multi-  
515 stemmed shrub: 5, root sprouting shrub: 7). In some plants, modules can include several rooting  
516 units, ramets (e.g. creeping herb: 3).

517

518 Figure II – Clone structure of *Zanthoxylum americanum* in open (left) and shaded environments  
519 (right). Ramets (B; green arrows or fully drawn) and small shoots (C) are regularly spaced along  
520 horizontal roots (light brown) emitted from a single taproot (A; dark brown). When the clone  
521 grows in the understory, horizontal roots frequently senesce, triggering development of secondary  
522 taproots (D) (4).

523

524

525

1 **Outstanding questions:**

2 What is the role of storage organs in the plant economics spectrum? Are conservative and  
3 acquisitive trait strategies related to clonal growth, and to the abundance and mass of bud-  
4 bearing and storage organs?

5 How do the main costs and benefits associated with clonality change with key environmental  
6 gradients, such as productivity and disturbance?

7 In there a general pattern of how clonal and nonclonal strategies differ in species interactions  
8 such as competition or facilitation in plant communities? Do such differences affect species  
9 coexistence and persistence in communities?

10 How does clonality affect population dynamics, seed reproduction, and population genetics?

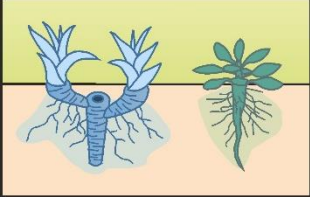
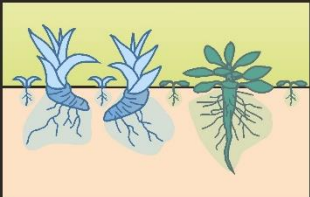
11 Do clonal plants have different evolutionary rates than nonclonal plants?

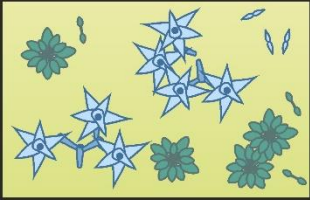
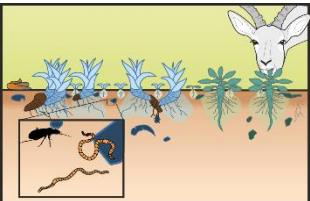
12 What is the role of clonal growth, bud-bearing and storage organs in ecosystem functioning  
13 (e.g. soil carbon cycling and storage, protection against erosion)?

14 How can we devise a general plant strategy scheme for all plants and incorporate key  
15 functions provided by clonality? How do we account for the different morphological means  
16 (such as stem- and root-derived) and strategies (such as phalanx and guerrilla or splitter and  
17 integrator) of clonality?

18

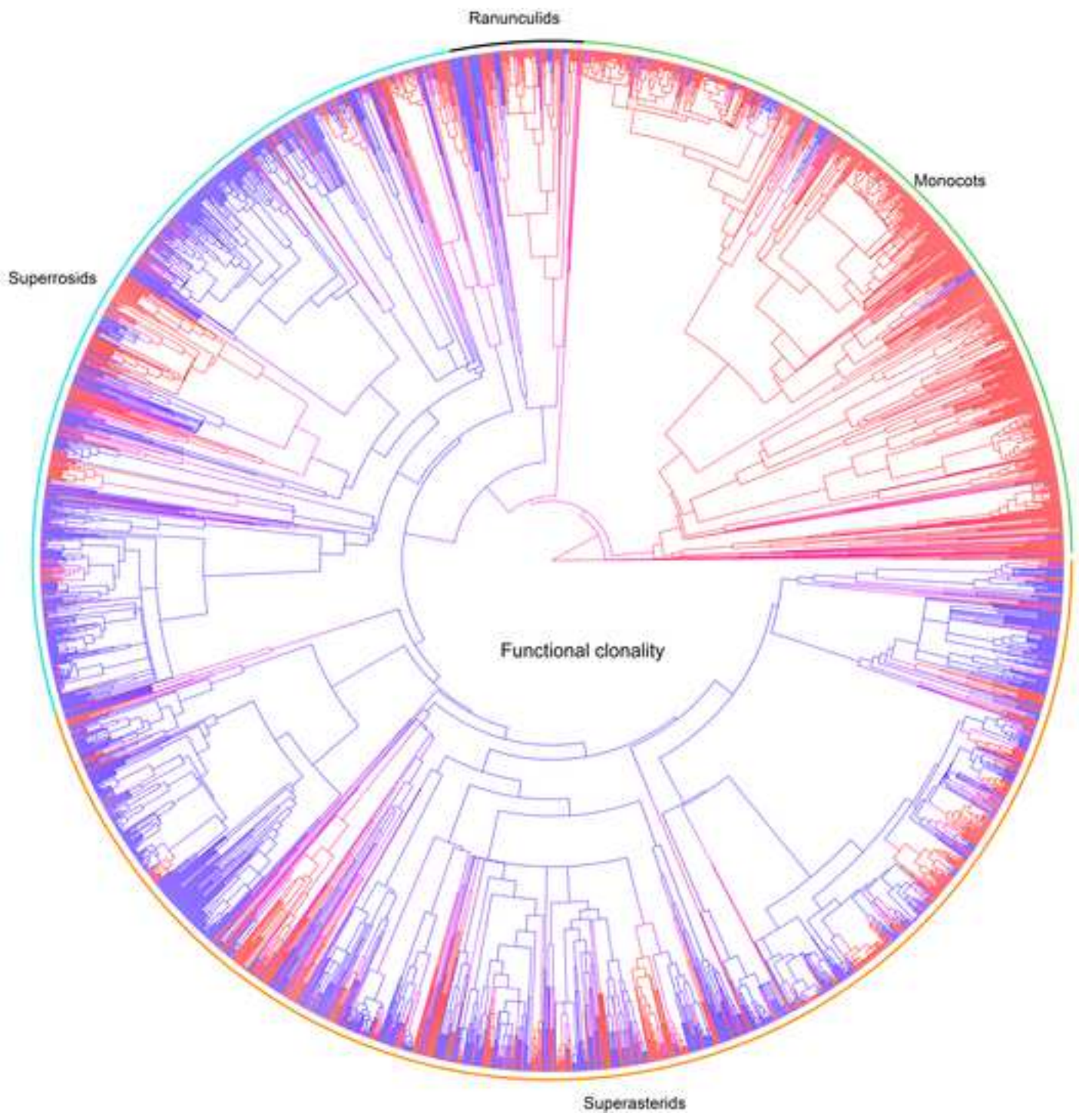
1 **Table 1.** Contrasting features of clonal and nonclonal plants.

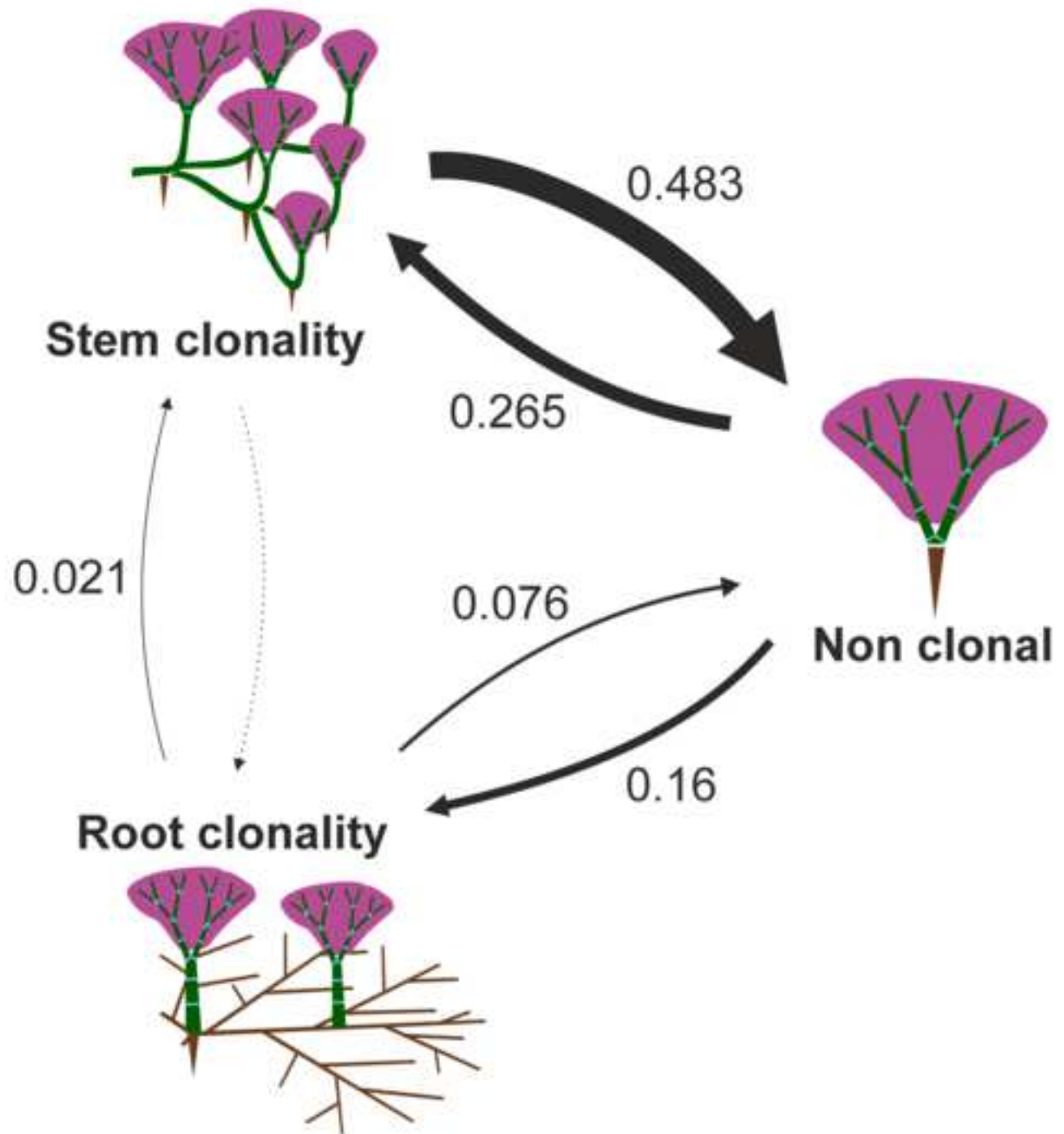
| Organisational level  | Functions & processes          | Clonal plants  | Nonclonal plants   | Available data                |
|---|--------------------------------|--|--|-------------------------------|
| Individual<br>   | Resource allocation            | Large biomass investment in storage and/or clonal growth organs  | Low biomass investment into storage organs (except resprouting nonclonals)   | Rare                          |
|   | Resource acquisition           | Rooting over a large area but with little resource foraging  | Deep rooting and with marked resource foraging   | Rare                          |
|   | Resource sharing               | Translocation of resources among rooting units forming a clone, specialisation of rooting units for obtaining abundant resources | No possibility of resource sharing (among rooting units) apart from mycorrhizas, no specialisation of rooting units for obtaining limiting resources | Rich (for clonal plants only) |
| Population<br> | Reproduction                   | Vegetative and generative  | Only generative  | Rich                          |
|   | Natural selection              | Decoupling of genetic and physiological and functional individuals   | Genetic corresponds to a physiological individual  | Rare                          |
|   | Regeneration after disturbance | Vegetative and generative  | Mostly generative  | Rich                          |
|   | Regeneration niche             | Can establish in dense vegetation, large parental provisioning   | Dependent on canopy gaps, small parental provisioning  | Moderate                      |
|   | Competition                    | In vertical and horizontal directions  | Mainly vertical direction  | Rare                          |

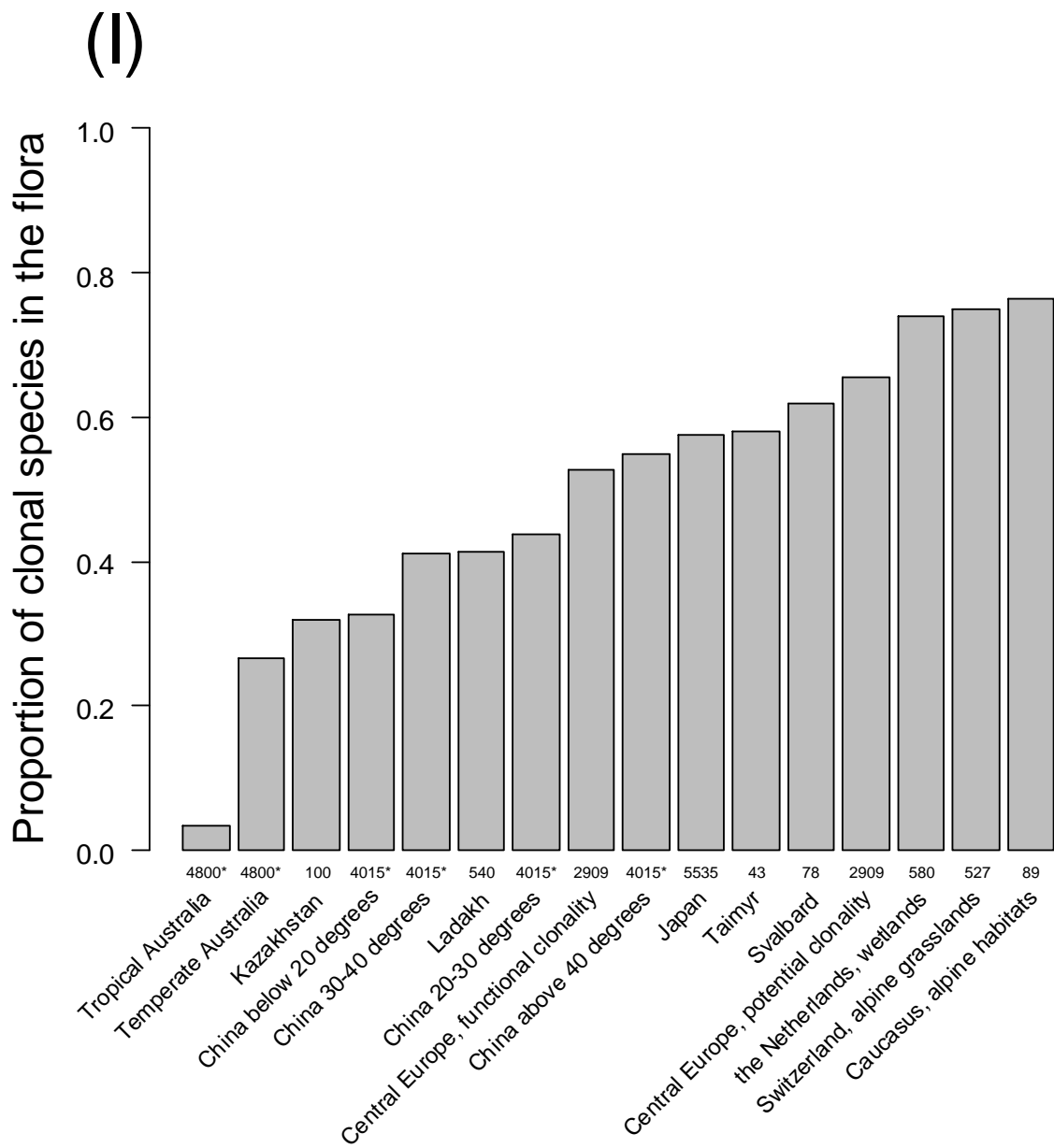
|  |                               |  |   |  |
|--|-------------------------------|--|---|--|
| <p>Community</p>    | Coexistence                   | Alleviation of competition by mobility (guerrilla strategy) or aggregation and clonal integration (phalanx strategy) | Negative density dependence   | Rare   |
|  | Facilitation                  | Aggregated rooting units (phalanx) may serve as nurse plants   | Only cushion plants   | Rare   |
|  | Evolvability                  | Slow   | Fast  | Unknown  |
|  | Dominance                     | Aboveground abundance is not a good proxy for belowground abundance  | Aboveground abundance is a good proxy for abundance belowground (except resprouting nonclonals) | Rare   |
|  | Carbon cycling                | Continuous litter input belowground thanks to exudation, senescing rhizomes and roots                                | Continuous carbon input belowground through exudation and senescing roots                       | Moderate (only for exudates and senescing roots) |
| <p>Ecosystem</p>  | Environment homogenisation    | Translocation of resources in the horizontal direction through ramets forming a clone                                | Water and nutrients uplift from deep soil layers thanks to deep rooting                         | Moderate (only for non-clonal)                   |
|  | Aeration of waterlogged soils | Aeration through rhizomes and roots  | Aeration through roots  | Unknown  |

2  
3  
4

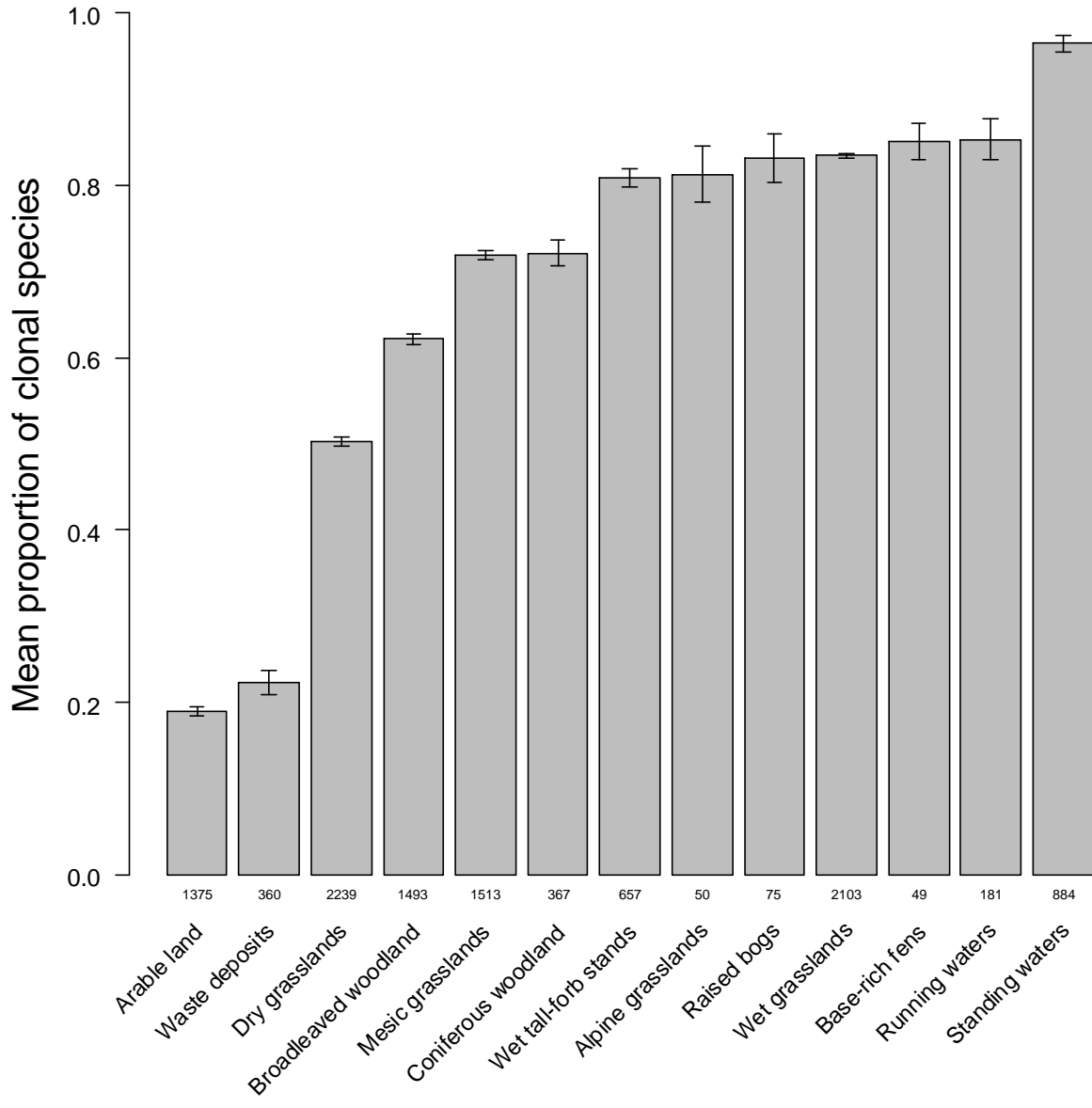








(II)



### A Whole plant architecture

### B module

