

Growth form and plasticity of the hybrid *Potentilla anglica* and its two parent species

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Abstract: Phylogenetically closely related plant species with different growth forms usually show conspicuous differences in their meristem utilization pattern and in their response to changes in environmental conditions. Despite such differences, viable hybrids between species with fundamentally different growth forms can be found in some genera. In a greenhouse experiment, the hybridogenous species *Potentilla anglica* was compared with its parent species, *Potentilla erecta* and *Potentilla reptans*. *P. erecta* has an erect growth form and *P. reptans* is strictly stoloniferous. The question was addressed to what extent the hybridogenous species resembled or differed from their parent species with respect to growth-form-related characteristics such as meristem utilization and changes in morphology and development as caused by changes in the light climate.

Potentilla reptans and *P. anglica* had a stoloniferous growth habit. However, the hybridogenous species produced less rooting points than the stoloniferous parent species which resulted in fewer potentially independent ramets. In the two parent species the differences in growth form were associated with different meristem utilization patterns and different responses to light treatments. Compared to the parent species *Potentilla anglica* responded in an intermediate way as far as meristem utilization and plasticity of spacer length are concerned. New character combinations were found in *P. anglica*, such as a marked plasticity of meristem allocation to branch and rosette production. In addition, *P. anglica* allocated significantly more biomass to sexual reproduction than either of the parent species.

The lower degrees of plasticity of vertical spacers and the lower percentage of nodes forming ramets may indicate that the performance of *P. anglica* is inferior in conditions of intense above-ground competition or disturbance as compared to the two parent species. This may explain why *P. anglica* is generally less common in the field than its parent species.

Introduction

Phylogenetically closely related species may differ considerably in growth form. Differences in the orientation of the main stem result in two distinct growth forms, usually referred to as erect and stoloniferous. Each of these growth forms results in specific developmental, biomechanical and architectural constraints (Givnish 1986, Gottlieb 1986). Stoloniferous plants spread by means of creeping stems which can root on their nodes and produce vegetative offspring (Hutchings & Mogie 1990). In stoloniferous species the main axis and their lateral branches can grow indefinitely. This means that individual plants can develop into large and complex clonal systems, consisting of many

interconnected ramets and covering considerable areas under field conditions (Oinonen 1967, Cook 1985). In erect plants the growth of the main stem and its branches is limited due to biomechanical constraints: the stems of erect plants have to carry the whole above-ground plant body and can hence not grow indefinitely.

Such differences in growth form are generally brought about by a few genetically determined (but to a limited extent phenotypically plastic) changes in the structure and development of basic morphological elements (Gottlieb 1986), called modules. In accordance with Hallé et al. (1978) a module is defined as a basic structural unit produced by one meristem. Each module usually consists of an internode with an apical meris-

tem, and leaves with a lateral meristem in each leaf axil (White 1979). All meristems can potentially produce new modules. The size, morphology and ontogenetic development of modules determine to a large extent the basic growth form and plastic changes in plant architecture (White 1979, Watkinson & White 1986, Gottlieb 1986, Hutchings & Mogie 1990). Such plastic changes can, for instance, be caused by differences in module size (e.g., internode length) or by differences in meristem activity.

Plants with different growth forms face different problems when subjected to light limitations, suggesting that growth-form-specific plastic responses to variation in the light climate may have evolved in phylogenetically related species. In dense herbaceous canopies with a steep vertical light gradient (Fliervoet 1984, Hirose & Werger 1995) it is mainly the elongation of vertically oriented organs which contributes most to an enhanced light interception of leaves (Ballaré 1994). As a consequence, stoloniferous plants with leaves originating from meristems situated at ground level can only compete for light by plastic elongation of petioles, but not by stem growth and internode elongation. Plasticity in petiole length has indeed been found to be more pronounced in prostrate plants, while internode length was more plastic in erect species (Huber 1996).

Hybridization between erect and stoloniferous plants leads to a combination of contrasting patterns of meristem utilization and responses to environmental conditions. Such combinations will not lead to viable species in most cases. Nevertheless, in some genera such as *Potentilla* and *Ranunculus* hybridization between erect and stoloniferous species has resulted in fertile hybridogenous species (Krahulec 1994). An analysis of the morphology and plasticity of fertile hybrid species originating from parent species with contrasting growth forms may give an indication as to what extent combinations of contrasting "growth rules" associated with a specific growth form are passed on to the hybrid species. However, stable hybridogenous species have their own evolutionary background and may have been subject to selection processes different from the parent species.

The allopolyploid hybridogenous species *P. anglica* is compared with its two parent species *P. erecta* and *P. reptans* which have erect and stoloniferous growth forms, respectively. The aim of the study is to investigate to what extent traits found in the hybridogenous species can be explained by traits present in the parent species. In addition, shade induced changes in morphology and development will be compared between the hybridogenous species and its two parent species.

These comparisons are based on a description of the basic morphological and developmental characteristics determining the growth form of the clonal and the erect parent species.

Material and Methods

Species Description

This study was carried out with three herbaceous species of the genus *Potentilla*, namely *Potentilla erecta* (L.) Räuschel, *Potentilla anglica* Laich. (= *Potentilla procumbens* Sibth.) and *Potentilla reptans* L. *Potentilla anglica* is a fertile, naturally occurring allopolyploid hybrid of *P. erecta* and *P. reptans* (Matfield et al. 1970, Matfield & Ellis 1972). The two parent species, *P. erecta* and *P. reptans* are tetraploid ($2n = 28$), while *P. anglica* is octoploid ($2n = 56$). Several hybrids exist between *P. anglica* and the two parent species (Wolf 1908, Matfield et al. 1970), as well as between *P. erecta* and *P. reptans*.

All three species are perennials occurring in the temperate zone. *Potentilla erecta* is wide-spread in open habitats and can also occur in open forests (Hegi 1981, Weeda et al. 1987). This wide distribution may be due to the differentiation of ecotypes with a high morphological variability (Watson 1969). *Potentilla reptans* occurs mainly in open nutrient-rich places and is very common on man-made sites, such as pastures and highly disturbed habitats. Sometimes it can also occur in forest edges (Hegi 1981, Weeda et al. 1987). The hybridogenous species, *P. anglica* is not very common. In contrast to its parent species it can also occur in somewhat shaded places (Weeda et al. 1987).

Potentilla erecta has a below-ground storage organ and produces a basal rosette from which vertically oriented stems arise. In very open habitats, i.e., in the absence of surrounding vegetation which could serve as a mechanical support for the stems, *P. erecta* may show a more prostrate growth form. *Potentilla erecta* never roots on its nodes. The stems of *P. anglica* and *P. reptans* are always oriented in a horizontal direction. In spite of obvious differences in growth form, the three species are very similar with respect to their modular construction. The stems are sympodial and the apical meristem develops into an embryonic flower after having produced a module. These flowers do not always complete their development, i.e. they can stay "dormant". According to Serebryakova (1981) and Troll (1935), two alternate leaves are produced on each module before the apical meristem turns into a flower (Fig. 1). As the distance between these two leaves is usually very short the two lateral meristems appear to be opposite and will be referred to as one node. The

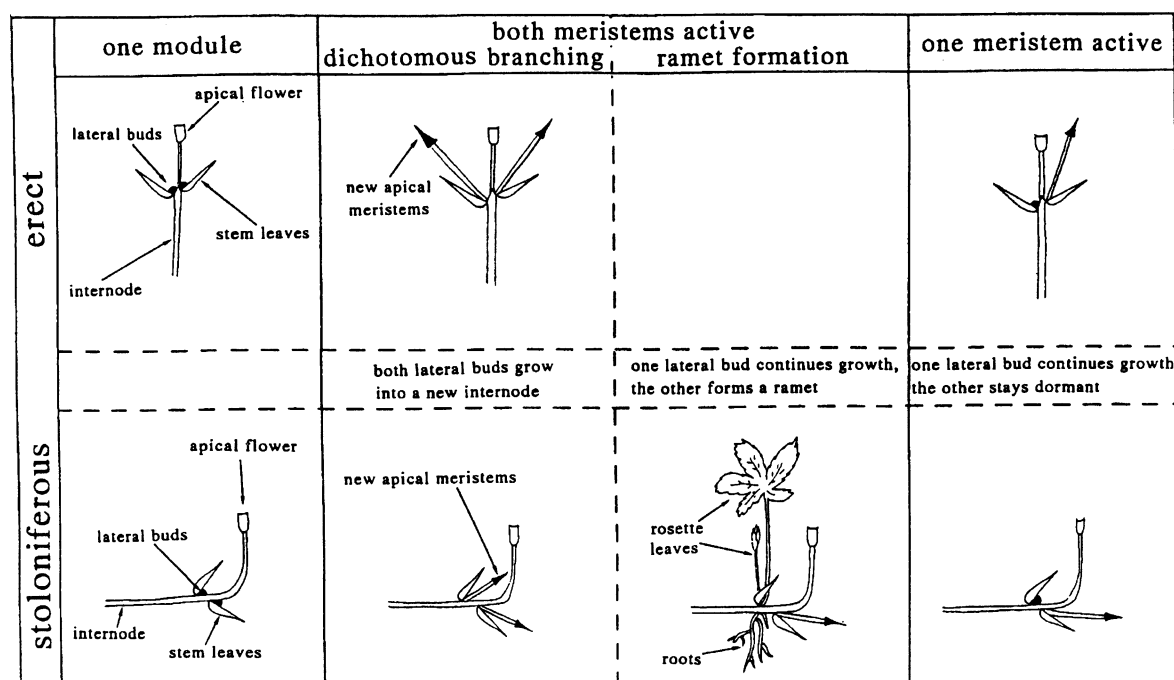


Figure 1. Schematic illustration of the structure of modules (after Serebryakova 1981) and modes of growth in sympodially growing erect and stoloniferous species of the genus *Potentilla*.

second lateral bud (the one close to the flower) normally forms a branch which continues the growth of the main axis. The other, developmentally younger, lateral bud can either remain dormant, produce another internode (subsequently referred to as *dichasial branching*; Barrenschenn 1991) or can grow into a rooted rosette (subsequently referred to as *ramet*; Fig. 1).

In erect *Potentilla* species dichasial branching at the top of growing internodes leads to the formation of two branches from the same node. In very rare cases dichasial branching can occur in stoloniferous species as well (Wolf 1908, Stuefer & Huber, pers. obs.). In stoloniferous *Potentilla* species secondary branches are produced by meristems situated in the axils of the rosette leaves (Huber & Stuefer, in prep.).

The experiment

All three species were grown from material obtained in the Netherlands. Ramets of *P. reptans* were collected in the vicinity of Utrecht. *Potentilla anglica* and *P. erecta* were collected in the vicinity of Eindhoven and in Oostvoorne, respectively. The three species were grown outside under uniform conditions in the Botanical Garden of the Utrecht University for at least one year prior to experimentation.

In April 1994 similar-sized individuals of each species were transferred to an open plastic greenhouse (light availability = 90% of full daylight). In order to standardize for plant size, all leaves except the three youngest ones were removed and the roots were cut to a length of 5 cm. The plants were planted individually into plastic pots (13 cm deep and 13 cm diameter) filled with river sand and 5 g of slow-release fertilizer (Osmocote Plus, Sierra International), which corresponded to a nitrogen release of about 10 kg ha⁻¹ week⁻¹. *Potentilla erecta* was grown on a soil mixture of sieved potting compost and sand (proportion 1:1) with an addition of 4 g Osmocote Plus. This substrate was used because this species, occurring naturally on soils with a high organic component, grows very poorly on pure sand (Huber, pers. obs.). The ramets along the oldest stolon of the two stoloniferous species were rooted in a plastic tray (15 cm deep, 15 cm wide and 100 cm long) filled with river sand. Young ramets along the stolon were supplied with the same amount of nutrients as the mother rosettes (≈ 10 kg N ha⁻¹ week⁻¹). Thirty similar-sized individuals of each species were allocated randomly to the experimental treatments at the beginning of May 1994.

Three treatments were applied with ten replicates each (Table 1). In two shading treatments whole plants were grown in shade cages. Neutral shading was achieved

by one layer of black shade cloth. Spectral shading was imposed by one layer of a plastic film (Lee Coltran International, # 122, 'fern green') which reduced the red:far-red ratio to 0.21 (measured with a LICOR Li-1800 spectroradiometer) and reduced light quantity to the same level as in the neutral shade treatment. Control plants received 100% PAR and the red:far-red ratio was 1.09 (Table 1). The control plants were grown in cages surrounded by a thin colourless plastic film in order to make microclimatic conditions comparable. Plants were watered daily with tap water throughout the experiment.

The length of all elongating internodes was measured every third day starting two weeks after the plants were allocated to the treatments. In addition, the length of the first petiole on each node was measured on the same days. These measurements were continued till the harvest of the plants. Because of differences in the developmental rate of the three species, plants were not harvested at the same time (duration of treatments: *P. erecta*: 4 weeks, *P. anglica*: 9 weeks, *P. reptans*: 7 weeks). Coleman et al. (1994) have shown that morphological parameters and biomass allocation can be influenced by development. Due to differences in the ontogeny of species, modules did not complete their development at the same time which resulted in different experimental periods for each species. This harvesting strategy does not allow comparison of absolute biomass values between species but is suitable for comparisons of developmental and morphological traits as well as for studying allocation patterns and growth form. For each node the fate of lateral buds was recorded (dormant, branch formation, ramet formation) and whether the apical meristem developed into a visible flower or not. At harvest, stem/stolon length were measured with an accuracy of ± 1 mm. The area of three similarly aged leaf-blades of each plant was determined with an accuracy of ± 1 mm² using a LICOR LI-3100 leaf area meter. In *P. erecta* the measurements were done on three leaves of the basal rosette as well as on three stem leaves. Moreover, the number of leaves on each ramet was counted on the primary stolon and the number of additionally formed

primary stolons on the mother rosette (for *P. anglica* & *P. reptans*) or stems on the basic rosette (for *P. erecta*). Dry weights of the different organs were determined after drying the plants to constant mass at 72°C.

Plant development and statistical analyses

The developmental stage of plants was measured by using the plastochron index (PI) which was first formulated by Askenasy (1878) and further developed by Erickson & Michelini (1957). Birch & Hutchings (1992 a, b) have shown that the PI is an effective measure to describe stolon development of clonal plants. Since in this experiment stolon/stem development could not be assumed to be constant over time a slightly modified version of the method of Hill & Lord (1990) to calculate PI's was applied (Huber & Stuefer, in prep.). For the two stoloniferous species 20 mm and for *P. erecta* 15 mm was used as a reference length for calculating PI values (see Birch & Hutchings, 1992 a, b). A new internode was considered as being formed when it had passed the reference length. Thus, a plastochron was defined as the time interval (expressed in number of days) between two successive internodes passing the reference length.

For all measured parameters, treatment effects were tested by a one-way ANOVA followed by Tukey tests (SAS 1988). The program package SAS (SAS 1988) was used for all statistical analyses.

Results

Meristem activity

In *P. erecta* nodes on the primary stem usually produced two branches (Fig. 2), leading to the typical dichasial growth form of this species. In *P. reptans*, only one branch continued stem growth on each node. In most plants the second meristem on each node remained dormant on the 1st, the 4th or the 5th node (data not shown). On almost all other nodes ramets were produced (Fig. 2). In *P. anglica* each node either produced two branches (as in *P. erecta*) or an internode and a ramet (as in *P. reptans*) (Fig. 2), resulting in a true hybrid growth form. This had also marked consequences for the rooting pattern, as in both stoloniferous species rooting only takes place on those nodes which produce a ramet, but never on nodes where the second meristem either remains dormant or produces a branch. This strict negative association between dichasial branching and rooting led to a strong decrease in the number of rooting points along the stolons of *P. anglica* (data not shown).

On the very first (proximal) nodes of the stem neither dichasial branching nor ramet formation occurred

Table 1. Light quantity (% PAR) and light quality (r/fr-ratio) in the three treatments (PAR levels are expressed as % of levels inside the greenhouse).

	% PAR	r/fr-ratio
control (C)	100	1.09
neutral shade (N)	24	1.09
spectral shade (S)	24	0.21

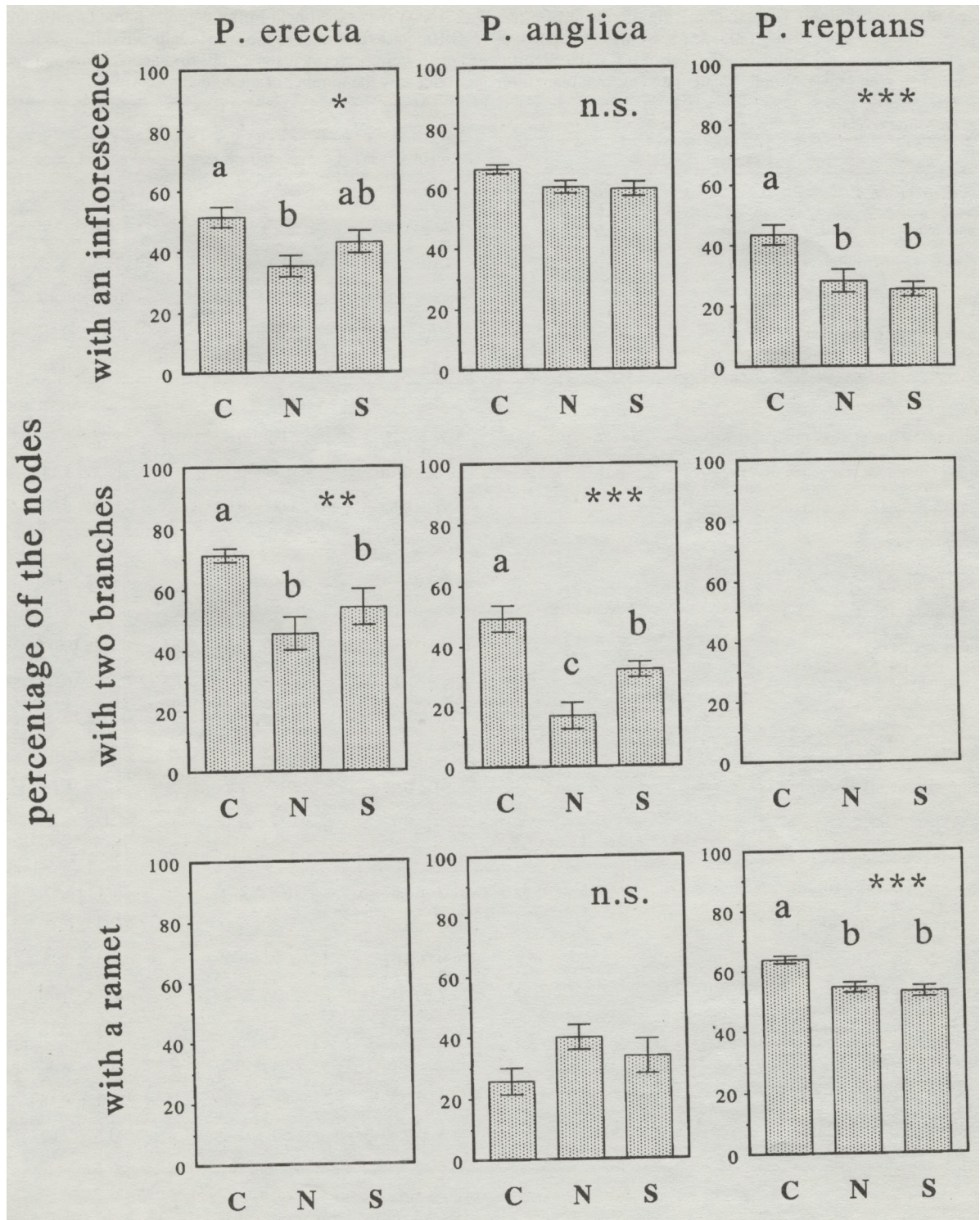


Figure 2. Patterns of meristem utilization (allocation to flowering , branching or ramet formation) in the three species. The results of a one-way ANOVA are given in the upper right corner of each box (significance levels as in Table 3). Different letters above the bars indicate differences between treatments at a significance level of 0.05. Treatment labels C: control treatment, N: neutral shade, S: spectral shade.

Table 2. Mean (\pm SE) values for various parameters concerning plant architecture, plant development, biomass production and plant morphology. For each variable the result of a one-way ANOVA is given next to the variable name (significance levels: n.s.: $p > 0.05$, *: $p \leq 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Different letters next to the values indicate differences between treatments at a significance level of $p \leq 0.05$. Significance tests were performed separately for each species and each variable. (Weight per module is calculated as total plant biomass divided by the number of modules.)

<i>a. Potentilla erecta</i>			
treatment	control treatment	spectral shade	neutral shade
<i>plant architecture</i>			
internode length [mm] *	23.4 \pm 2.14 ^a	26.8 \pm 3.31 ^{ab}	36.3 \pm 0.48 ^b
petiole length (rosette leaves) [mm] n.s.	27.3 \pm 2.28	33.7 \pm 3.05	36.5 \pm 4.33
petiole length (stem leaves) [mm] n.s.	0.98 \pm 0.33	1.59 \pm 0.44	0.80 \pm 0.40
first branching [nr. of nodes] n.s.	1.20 \pm 0.20	2.00 \pm 0.42	1.88 \pm 0.30
first flowering [nr. of nodes] n.s.	3.70 \pm 0.34	4.00 \pm 0.27	3.88 \pm 0.35
<i>development</i>			
duration of one plastochron [days] n.s.	4.09 \pm 0.29	5.06 \pm 0.32	5.03 \pm 0.29
dur. of internode elongation [days] n.s.	10.0 \pm 0.78	10.4 \pm 0.78	11.3 \pm 1.11
dur. of petiole elongation [days] n.s.	3.67 \pm 0.67	3.00 \pm 0.00	3.00 \pm 0.00
<i>morphology</i>			
total biomass [g] ***	2.06 \pm 0.23 ^a	0.77 \pm 0.16 ^b	0.86 \pm 0.10 ^b
root weight [g] ***	0.40 \pm 0.05 ^a	0.15 \pm 0.03 ^b	0.16 \pm 0.02 ^b
tuber weight [g] ***	0.31 \pm 0.04 ^a	0.11 \pm 0.02 ^b	0.10 \pm 0.01 ^b
internode weight [g] ***	0.48 \pm 0.06 ^a	0.17 \pm 0.02 ^b	0.22 \pm 0.04 ^b
leaf weight [g] ***	0.71 \pm 0.08 ^a	0.26 \pm 0.05 ^b	0.32 \pm 0.03 ^b
inflorescence weight [g] *	0.17 \pm 0.09 ^a	0.07 \pm 0.04 ^b	0.06 \pm 0.01 ^b
allocation to inflorescences [%] n.s.	8.50 \pm 0.95	7.75 \pm 1.83	6.22 \pm 1.13
root/shoot-ratio [g g ⁻¹] n.s.	2.36 \pm 0.72	2.28 \pm 0.39	2.42 \pm 0.28
weight per module [mg] *	20.1 \pm 2.08 ^a	13.2 \pm 1.48 ^b	15.2 \pm 1.34 ^b
number of rosette leaves n.s.	16.3 \pm 2.87	16.8 \pm 2.78	20.0 \pm 2.67
area of one rosette leaf [cm ²] n.s.	4.52 \pm 0.61	3.38 \pm 0.41	3.56 \pm 0.35
area of one stem leaf [cm ²] n.s.	0.54 \pm 0.04	0.54 \pm 0.06	0.46 \pm 0.06
SLA (rosette leaves) [cm ² g ⁻¹] ***	27.7 \pm 1.44 ^a	42.5 \pm 2.52 ^b	42.0 \pm 3.52 ^b
leaf-blade/petiole weight ratio [g g ⁻¹] n.s.	2.88 \pm 0.32	2.26 \pm 0.23	2.82 \pm 0.16
stem length [cm] n.s.	18.5 \pm 1.62	18.3 \pm 0.23	24.8 \pm 4.44
number of nodes on the primary stem n.s.	7.80 \pm 0.39	6.88 \pm 2.58	7.00 \pm 0.38
number of additional primary stems n.s.	13.5 \pm 2.47	8.50 \pm 1.48	8.17 \pm 1.62

(Table 2). This pattern was consistent for all species and treatments, except for *P. erecta* under high-light conditions where individuals produced on average two branches on the first node. In *P. erecta* and *P. anglica* dichasial branching and/or ramet formation was delayed by one node in shaded conditions (Table 2).

Due to high variability within treatments these responses were statistically not significant.

In *P. erecta* exposed to high-light conditions, 70% of all nodes had two active lateral meristems which grew into two branches. In *P. reptans*, about 60% of the nodes produced a ramet. Shading reduced both of these

Table 2. (continued)

b. <i>Potentilla anglica</i>			
treatment	control treatment	spectral shade	neutral shade
<i>plant architecture</i>			
internode length [mm] ***	48.7 ± 2.69 ^a	60.7 ± 3.45 ^b	75.9 ± 2.58 ^b
petiole length (mother plant) [mm] **	38.3 ± 9.01 ^a	57.3 ± 8.71 ^{ab}	76.8 ± 7.48 ^b
petiole length (stem leaf) [mm] ^{n.s.}	6.96 ± 0.35	6.66 ± 0.95	9.05 ± 0.82
first branching/ramet formation ^{n.s.}	2.44 ± 0.18	3.14 ± 0.26	3.30 ± 0.60
first flowering [nr. of nodes] *	4.33 ± 0.17 ^a	4.57 ± 0.20 ^{ab}	4.90 ± 0.10 ^b
<i>development</i>			
duration of one plastochron [days] **	4.62 ± 0.18 ^a	5.69 ± 0.15 ^b	5.18 ± 0.26 ^a
dur. of internode elongation [days] **	11.0 ± 1.00 ^a	16.0 ± 1.31 ^b	12.3 ± 0.67 ^a
dur. of petiole elongation [days] ^{n.s.}	16.0 ± 3.80	16.7 ± 0.84	15.9 ± 0.79
<i>morphology</i>			
total biomass [g] ***	10.1 ± 0.79 ^a	2.58 ± 0.24 ^c	6.04 ± 0.46 ^b
root weight [g] ***	2.16 ± 0.16 ^a	0.47 ± 0.05 ^c	0.77 ± 0.07 ^b
internode weight [g] ***	3.66 ± 0.37 ^a	0.73 ± 0.09 ^c	2.19 ± 0.22 ^b
leaf weight [g] ***	3.04 ± 0.26 ^a	1.10 ± 0.11 ^c	2.30 ± 0.18 ^b
inflorescence weight [g] ***	1.32 ± 0.12 ^a	0.28 ± 0.03 ^c	0.78 ± 0.04 ^b
allocation to inflorescences [%] ^{n.s.}	12.9 ± 0.61	11.0 ± 0.93	13.2 ± 0.51
root/shoot-ratio [g g ⁻¹] ***	0.28 ± 0.02 ^a	0.23 ± 0.02 ^a	0.15 ± 0.01 ^b
weight per module [mg] ^{n.s.}	63.1 ± 2.18	56.6 ± 4.94	62.3 ± 3.23
number of rosette leaves (mother plant) **	15.8 ± 1.29 ^a	9.57 ± 1.36 ^b	10.1 ± 1.34 ^b
number of leaves on primary stolon ^{n.s.}	13.8 ± 1.84	13.9 ± 1.22	13.1 ± 1.74
area of 1 rosette leaf (mother plant) **	7.41 ± 0.66 ^a	12.9 ± 1.92 ^b	13.2 ± 1.21 ^b
SLA (mother plant) [cm ² g ⁻¹] ***	26.3 ± 0.64 ^a	48.3 ± 2.17 ^c	37.4 ± 1.29 ^b
leaf-blade/petiole weight ratio [g g ⁻¹] ^{n.s.}	3.35 ± 0.18	3.33 ± 0.28	3.27 ± 0.21
stem length [cm] ***	66.5 ± 4.52 ^a	71.8 ± 3.86 ^a	101.1 ± 4.12 ^b
number of nodes on the primary stem ***	13.2 ± 0.28 ^a	11.9 ± 0.26 ^b	13.4 ± 0.22 ^a
number of secondary branches **	10.0 ± 0.93 ^a	4.71 ± 1.15 ^b	7.10 ± 0.85 ^{ab}
number of secondary nodes ***	57.4 ± 5.20 ^a	13.0 ± 3.54 ^c	38.4 ± 3.13 ^b
number of additional primary stems ***	10.8 ± 1.10 ^a	3.00 ± 0.54 ^b	4.40 ± 0.67 ^b

values (Fig. 2). In *P. anglica* exposed to full daylight, dichasial branching occurred more frequently than ramet formation; in 50% and 25% of the nodes, respectively. Shading partly reversed this pattern: dichasial branching was reduced significantly, while a higher percentage of nodes tended to form a ramet (Fig. 2). This response was stronger in neutral than in spectral shade.

The apical meristem of the first nodes along a stem did not flower in any of the three species. Flowering occurred only from the 4th node onwards (Table 2). In the two parent species flowering occurred on 40 - 50% of the nodes on the primary stem in high-light conditions (Fig. 2), and was significantly reduced by shading. In the hybridogenous species *P. anglica* flowering was more vigorous than in the two parent species (on 60

Table 2. (continued)

<i>c. Potentilla reptans</i>			
treatment	control treatment	spectral shade	neutral shade
<i>plant architecture</i>			
internode length [mm] ^{n.s.}	86.4 ± 2.58	94.3 ± 8.96	95.7 ± 0.28
petiole length (mother plant) [mm] ^{***}	73.8 ± 3.76 ^a	167.4 ± 13.5 ^b	215.2 ± 13.6 ^c
first ramet formation [nr. of nodes] ^{n.s.}	1.91 ± 0.09	2.12 ± 0.12	2.25 ± 0.13
first flowering [nr. of nodes] ^{n.s.}	3.82 ± 0.23	3.88 ± 0.30	3.92 ± 0.15
<i>development</i>			
duration of one plastochron [days] [*]	3.88 ± 0.29 ^a	4.79 ± 0.25 ^b	4.07 ± 0.15 ^{ab}
dur. of internode elongation [days] ^{n.s.}	11.1 ± 0.46	12.7 ± 0.33	11.5 ± 0.53
dur. of petiole elongation [days] ^{***}	13.4 ± 0.69 ^a	16.7 ± 0.53 ^b	17.2 ± 0.58 ^b
<i>morphology</i>			
total biomass [g] ^{***}	11.3 ± 1.27 ^a	4.22 ± 0.52 ^b	4.93 ± 0.78 ^b
root weight [g] ^{***}	2.51 ± 0.27 ^a	0.79 ± 0.10 ^b	0.73 ± 0.04 ^b
internode weight [g] ^{***}	3.65 ± 0.49 ^a	0.87 ± 0.14 ^b	1.10 ± 0.09 ^b
leaf weight [g] ^{***}	4.58 ± 0.48 ^a	2.40 ± 0.78 ^b	2.90 ± 0.16 ^b
inflorescence weight [g] ^{***}	0.52 ± 0.07 ^a	0.17 ± 0.04 ^b	0.20 ± 0.03 ^b
allocation to inflorescences [%] ^{n.s.}	4.58 ± 0.34	3.77 ± 0.48	4.04 ± 0.54
root/shoot-ratio [g g ⁻¹] ^{***}	0.29 ± 0.01 ^a	0.24 ± 0.02 ^b	0.18 ± 0.01 ^c
weight per module [mg] ^{n.s.}	163.1 ± 11.7	106 ± 10.7	170.4 ± 9.60
nr. of rosette leaves (mother plant) ^{***}	12.8 ± 1.52 ^a	7.30 ± 0.36 ^b	7.75 ± 0.48 ^b
number of leaves on primary stolon ^{***}	33.1 ± 1.27 ^a	20.9 ± 0.99 ^b	22.0 ± 0.67 ^b
area of one rosette leaf (mother plant) ^{**}	26.6 ± 2.05 ^a	46.7 ± 5.23 ^b	47.9 ± 4.50 ^b
SLA (mother plant) [cm ² g ⁻¹] ^{***}	22.1 ± 0.99 ^a	39.7 ± 1.47 ^b	39.8 ± 1.11 ^b
leaf-blade/petiole weight ratio [g g ⁻¹] ^{***}	3.78 ± 0.24 ^a	2.46 ± 0.12 ^b	2.04 ± 0.14 ^b
stem length [cm] ^{n.s.}	113.5 ± 4.80	103.5 ± 11.2	115.3 ± 3.45
number of nodes on the primary stem ^{***}	13.1 ± 0.25 ^a	11.5 ± 0.19 ^b	12.1 ± 0.19 ^b
number of secondary branches ^{***}	8.64 ± 1.01 ^a	3.44 ± 0.44 ^b	3.75 ± 0.39 ^b
number of secondary nodes ^{***}	17.5 ± 1.79 ^a	4.11 ± 0.72 ^b	5.33 ± 0.64 ^b
number of additional primary stems ^{***}	6.91 ± 0.68 ^a	2.90 ± 0.38 ^b	2.58 ± 0.31 ^b

-70% of all nodes). Flowering was not influenced by treatments in this species (Fig. 2).

Plant architecture

The erect species *P. erecta* produced rather short internodes and almost no petioles on stem leaves (Table 2a). Similarly to *P. reptans*, *P. anglica* produced long horizontal stolons with long internodes and leaves with long petioles on the ramets. However, petioles and internodes were somewhat shorter than in *P. rep-*

tans (Table 2b, c). Internodes and petioles also differed in their degree of plasticity (Table 2). In *P. erecta* only the internodes but not the petioles responded in a plastic way to the light treatments (i.e., elongated under shaded conditions), whereas in *P. reptans* only petioles but not internodes showed plastic elongation responses to shade. In the hybridogenous species both internodes and petioles were longer under shaded conditions as compared to high-light conditions. The response of the

petioles was less pronounced than in *P. reptans* (Table 2b, c).

At the distal end of each internode, stem leaves are produced in all three species. In *P. erecta* they were the only leaves situated along the stem and were much bigger than the stem leaves of *P. reptans*. The latter species, whose stem leaves were reduced to scale leaves, produced rosettes with large petiolated leaves which are the main photosynthetically active organs of this species. In *P. anglica* two types of leaves could be distinguished. On ramets, petiolated rosette-leaves were produced that were similar to those observed in *P. reptans*. The stem leaves on each node were very similar in shape and petiole length to the stem leaves of *P. erecta*. The two leaf types also differed in their degree of plasticity. The petioles of the smaller stem leaves did not respond in a plastic way to shade, while the petioles of the bigger rosette leaves growing in spectral shade were twice as long as under full daylight (Table 2).

Development

In all three species, every 4th to 6th day a new module was formed on the primary stem (Table 2). Shading tended to decrease the developmental speed of the main axis in all species. With respect to this parameter, the hybridogenous species resembled more the erect than the stoloniferous parent species. Single internodes elongated for 10 - 12 days in the two parent species (Table 2). Shading had no effect on the period of time within which internodes completed their development. Neutral shade retarded internode development in *P. anglica*.

The petioles of the two stoloniferous species started to elongate approximately seven days after the preceding internode was formed (Fig. 3). At this time internodes had not yet finished elongation. In *P. anglica*, shading led to a slight delay of the onset of leaf growth on ramets (Fig. 3). Independent of light conditions, the petioles of this species elongated for about 16 days (Fig. 3, Table 2b). In full daylight the petioles of *P. reptans* completed elongation within 13.5 days (Fig. 3, Table 2c). Shading resulted in a prolonged petiole elongation in this species. In *P. erecta* the petioles of leaves situated on the stem were very short (1-2 mm) and elongated for about 3-4 days only (Table 2a). The petioles of stem leaves of *P. anglica* elongated for 3 to 8 days.

Biomass production and allocation

Shading led to a significant reduction of biomass production in all species (Table 2). In *P. erecta* and *P. reptans* only light quantity had a significant effect on

biomass production, in *P. anglica* the biomass of plants growing under neutral shade was significantly lower than that of plants growing in spectral shade. In *P. erecta* the root/shoot ratio was not influenced by treatments, while it was reduced by shading in *P. reptans* (Table 2a, b). In the hybridogenous species *P. anglica*, the root/shoot ratio was significantly decreased in plants grown under spectral shade (Table 2c).

Biomass allocation to inflorescences (including flowering stalk, flowers and seeds) was different between species but was not affected by treatments (Table 2). In *P. erecta* 6 to 8% of the biomass was allocated to flowers, in contrast to only 3 - 4% in *P. reptans*. In the hybridogenous species biomass allocation to flowers was highest, reaching between 11 and 13% of total plant biomass.

In *P. erecta* the average weight of individual modules was significantly decreased under shaded conditions, i.e., total plant biomass was reduced more strongly by shading than the number of modules (Table 2a). In the two stoloniferous species, both biomass and number of modules were reduced to the same extent and the mean weight per module did not differ significantly between treatments (Table 2b, c).

In *P. erecta* the number of leaves produced at the basal rosette was not different between treatments (Table 2a). In the two stoloniferous species, however, the number of leaves produced on the mother rosette decreased significantly under shaded conditions. The total number of leaves produced on the primary stolon was reduced by shading in *P. reptans*, but not in *P. anglica* (Table 2b, c). In *P. erecta* the area of rosette leaves and stem leaves showed no response to light conditions (Table 2a). In the two stoloniferous species leaf areas were significantly enlarged by shading. The specific leaf area (SLA) showed an increase under shaded conditions in all three species, indicating thinner leaves being produced under shade (Table 2). Rosette leaves of *P. erecta* and of *P. anglica* had a constant leaf-blade/petiole weight ratio in all treatments, while in *P. reptans* shading led to a higher allocation to petioles relative to leaf blades (Table 2).

Discussion

Potentilla anglica is an allopolyploid hybridogenous species of *P. erecta* and *P. reptans*. Some traits which differ in the two parent species have most probably been inherited by *P. anglica*. This led to new character combinations in the hybridogenous species. *Potentilla anglica* exhibits a stoloniferous growth habit with regular rooting and ramet formation on nodes. Most of

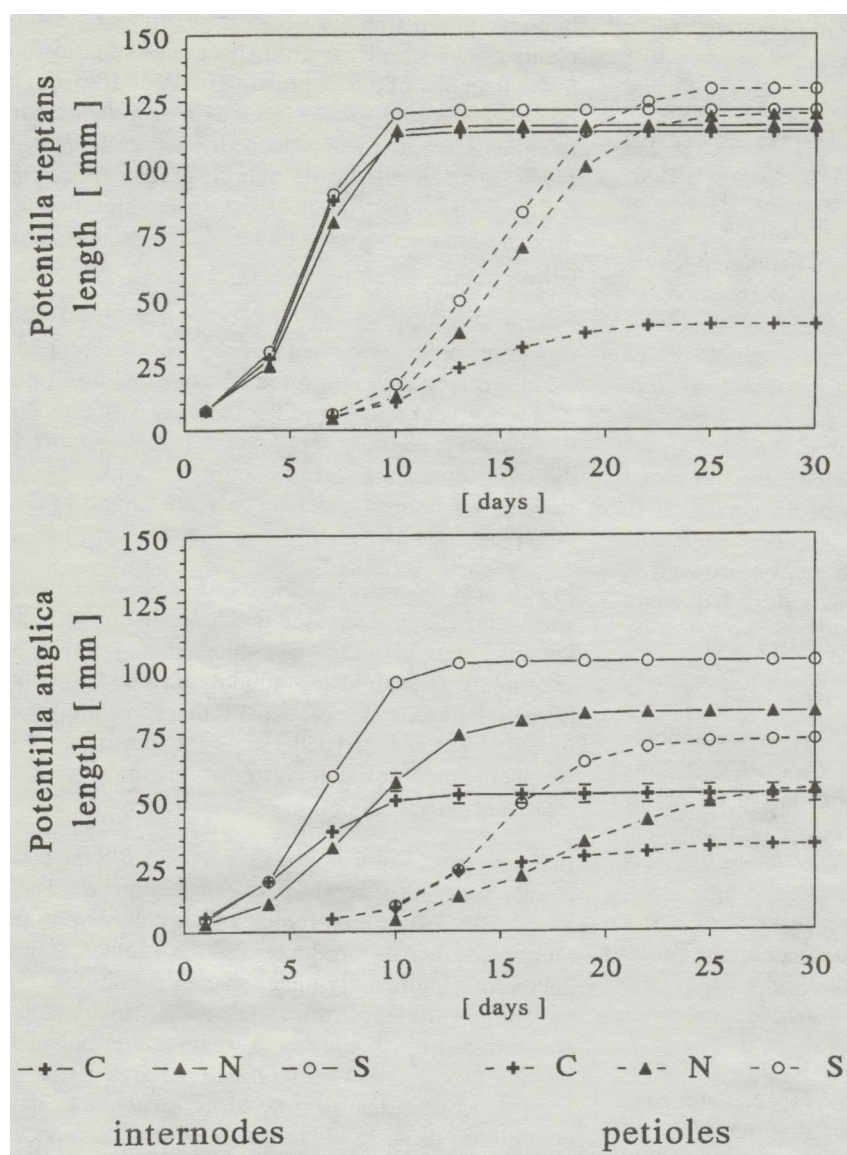


Figure 3. Development of the 6th internode and the petiole of the 1st leaf on the 6th node in the two stoloniferous species. Standard errors may be smaller than symbols and, hence, not be visible. Treatment labels are as in Fig. 2.

the other hybrids between *P. anglica* and the two parent species also have a prostrate growth form (Wolf 1908, Matfield et al. 1970, Matfield & Ellis 1972). This suggests that clonality is dominant over erect growth in this species complex.

Some structural traits of the parent species are clearly manifested in the architecture of the hybridogenous species. *Potentilla anglica* can either produce two branches on each node (similar to *P. erecta*) or one internode and a ramet (similar to *P. reptans*). Ramet formation and the production of a second branch exclude each other and can thus never occur on the same node. Since dichasial branching occurs frequently in *P. anglica*, this species produced a relatively low number of daughter ramets as compared to its clonal parent species. As adventitious root formation only occurs on

nodes forming a rosette, a high probability of dichasial branching, as observed in *P. anglica*, leads to a reduced number of rooting points along the stolon of this species. The low rooting frequency (ca. 30% of the nodes) results in bigger clone parts (in terms of number of modules) relying on water and nutrient uptake from the same rooting points, as compared to *P. reptans*. This feature may make *P. anglica* more susceptible to disturbance because a low number of rooting points increases the mortality risk for ramets in case of clone fragmentation.

Potentilla anglica has apparently inherited two different leaf types from its parent species (cf. Wolf 1908). It produces both, leaves which are very similar to the stem leaves of *P. erecta* with respect to size and shape, and rosette leaves with long petioles, which are

similar to the rosette leaves of *P. reptans*. The '*P. erecta*-type' stem leaves are produced on each node, while the '*P. reptans* type' rosette leaves are only produced on ramets. The two leaf types did not only differ in their appearance but also in their degree of plasticity. Only the rosette leaves of the '*P. reptans*-type' but not the stem leaves ('*P. erecta*-type') responded in a plastic way to shading. This is in agreement with the response of the respective leaf types in the parent species. A closer comparison between the rosette leaves of *P. anglica* and *P. reptans*, however, revealed that not all traits present in the rosette leaves of *P. reptans* were also present in the rosette leaves of *P. anglica*. Compared to *P. reptans*, the petioles of rosette leaves of *P. anglica* are less plastic in response to shade; additionally there was no plasticity in elongation time and in the leaf-blade/petiole weight ratio. In these latter traits the rosette leaves of *P. anglica* resembled the leaves of *P. erecta*. This may indicate, that not all leaf traits present in *P. reptans* have been passed on to *P. anglica*. The lower plasticity of petioles of *P. anglica* as compared to *P. reptans* may represent an important constraint for *P. anglica* as the plants can not compete as efficiently for light in dense herbaceous canopies as *P. reptans*, and are thus likely to be outcompeted in such habitats.

Potentilla anglica is a stable hybridogenous species which may already exist as an independent species for a long time (Wolf 1908, Matfield & Ellis 1972). The characteristics of hybridogenous species are to a great extent constrained by the traits evolved in the parent species and then passed on through hybridization. However, a fertile hybridogenous species will undergo natural selection like any other species which means that traits which have not been present or were expressed to a minor extent in the parent species may be selected for, eventually leading to a set of traits which is specific for the hybridogenous species only. Allocation to the different modes of reproduction may be one example for such processes in *P. anglica*. The three species differed markedly in their allocation patterns to sexual and vegetative reproduction. *Potentilla erecta* lacks clonality and is hence a species relying exclusively on sexual reproduction. *Potentilla reptans* has a very effective vegetative reproduction and can produce a new daughter ramet every three to five days on each growing stolon. Additionally, new secondary stolons are continuously formed from each rosette adding new ramet formation points to the system and allowing exponential spread of the plants under optimal conditions (Huber & Stuefer, in prep.). In this species only a very small percentage of the biomass is allocated to flowering, i.e., to sexual reproduction. *Potentilla anglica* produces much fewer ramets than *P.*

reptans, i.e., vegetative reproduction is reduced as compared to the clonal parent species. It seems that this has been compensated for by a high investment into sexual reproduction. The hybridogenous species does not only flower more frequently, it also allocates more biomass to flowers than either of the parent species. Unlike *P. erecta* and *P. reptans*, *P. anglica* does not respond to shading by reduced allocation to sexual structures. High investments into sexual structures is a new character for the hybridogenous species. This trait could also be a means to compensate for the low fertility of *P. anglica* seeds which was observed by Matfield & Ellis (1972).

The pattern of meristem allocation to branching or rosette formation seems to be a rather stable trait in the two parent species, as one species (*P. erecta*) always produces two branches, whereas the other (*P. reptans*) forms a branch and a rosette on each node. Exceptions to this rule are very rare (Wolf 1908, Huber & Stuefer, in prep.). In the hybridogenous species, however, both traits are combined. *Potentilla anglica* can produce both structures, rosettes or dichasial branches on each node which is an important determinant of the characteristic growth form of the hybridogenous species. Moreover, the proportion between branching and ramet formation can vary depending on environmental conditions (Fig. 2). This suggests that the decision what structure is being formed is taken locally, i.e., on each node and is influenced by resource availability. In full day-light under which *P. anglica* performed best (in terms of total biomass production) many branches and few rosettes were formed. Under such near-optimal conditions *P. anglica* had a similar branching pattern as *P. erecta*. Under poor growing conditions (e.g., neutral shade) plants seemed to switch from branch to rosette formation, adopting a branch structure more similar to *P. reptans*. This release of the strict meristem allocation pattern, as present in the parent species, resulted in a flexible growth pattern of the hybridogenous species as far as branching and clonal offspring production is concerned.

The meristem allocation pattern to branching vs. ramet production represents a structural trade-off and can be compared to the meristem-limited trade-off between flowers and vegetative growth as found in some erect (Geber 1990) and clonal species (Watson 1984, Bishop & Davy 1985, Geber et al. 1992). In these cases each meristem can either be allocated to reproduction or growth which imposes constraints on further growth of plants (Abrahamson 1980, Watkinson & White 1986). In *P. anglica* this meristem utilization pattern can lead to a trade-off between rapid vegetative spread and uptake of above- and belowground resources.

Plasticity in the meristem utilization pattern may have ecologically significant consequences for the horizontal spread of plants. Lateral expansion is enhanced if two branches rather than one are formed on each node, enabling plants to occupy open areas in shorter periods of time. On the other hand, a high degree of dichasial branching leads to less rosettes being formed, which in turn results in a low number of rooting points (see above) and also of petiolated leaves which may negatively affect the carbon economy of plants. High degrees of ramet formation enhance leaf-area production and clonal propagation but hamper rapid spread of the stolons. This suggests that plasticity in the allocation to branches vs. rosettes gives the hybridogenous species additional possibilities to respond to changes in environmental conditions which are not present in the two parent species. Thus, in the case of *P. anglica*, hybridization has led to the formation of a new growth form with new plasticity.

In this study the hybridogenous species *P. anglica* has been compared with its two parent species. Although it can be assumed that hybrids from plants with different growth forms have a low viability, *P. anglica* can survive and spread at places where the two parent species do not occur. To study the exact inheritance pattern of traits associated with the erect and stoloniferous growth form it would be necessary to produce artificial hybrids between the two parent species. This may be very difficult in the case of *P. anglica* (Matfield et al. 1970, Matfield & Ellis 1972) but it seems feasible in similar systems of other genera, such as in *Ranunculus*. Exact inheritance patterns could be studied by comparing artificial hybrids with both, the parent species and also with naturally occurring hybridogenous species. In this way, traits present in the parent species could be separated from traits inherited by the hybrid and newly acquired traits of the hybridogenous species.

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