Variation in autumnal growth of hermaphroditic clones of *Glechoma hederacea* originating from two geographical regions and two habitats

Variabilita podzimního růstu hermafroditických klonů *Glechoma hederacea* pocházejících ze dvou zeměpisných oblastí a dvou stanovišť

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Eight hermaphroditic genotypes of *Glechoma hederacea* originating from two habitats and two geographical regions were compared under greenhouse conditions to test for differences in growth at the end of the vegetation period. During the 90 days of the experiment the plants developed primary stolons and secondary stolons, the latter up to four (rarely six) per node. Stolon lengths, mean internode length, mean leaf blade width and mean petiole length on primary stolons as well as the number of nodes, mean internode length and stolon length of the first two secondary stolons initiated at a node were genotype-dependent. The number of nodes and rooting nodes, mean internode length, stolon length and number of growing tips on the second pair of secondary stolons were population-dependent. No indication of ecotypic differentiation in clonal growth was found. The hypothesis suggesting that genotypes with short internodes and a high intensity of branching should dominate populations growing under high light levels (i.e. in meadows) was not supported.

Keywords: Clonal growth, genotypes, meadow, forest, Czech Republic, Sweden

Introduction

In many clonal plants sexual reproduction is of little importance because they may survive by vegetative multiplication for decades (Harper et White 1974, Cook 1985, Eriksson 1989) or even much longer (Cottam 1954). Unless clonal plants multiplicate regularly, survival of their populations may be endangered (Eriksson et Jerling 1990). Therefore, variation and plasticity in clonal growth may be of the same importance as variation and plasticity in reproductive outputs of unitary plants.

Resource utilisation by clonal plants have been described within the framework of foraging, i.e. "a process whereby an organism searches or ramifies within its habitat in the activity of acquiring essential resources" (Slade et Hutchings 1987a, b). Differences in foraging behaviour have usually been identified with extremes in species plasticity, i.e. guerrilla and phalanx growth forms (e.g. Slade et Hutchings 1987a, b, Noble et al. 1979, Room 1983, Eriksson 1986). Hutchings et de Kroon (1994) and de Kroon et Hutchings (1995) showed that most stoloniferous plant species shorten their internodes and increase branching intensity under high light levels. If there is natural selection favouring different growth under two light regimes, it can be expected that genotypes with respective characteristics should be selected for and prevail at particular sites (Lovett Doust 1981, 1987). In that case the genotypes originating from meadows (high light intensity) should have shorter internodes and higher branching intensity than genotypes from forests (low light intensity with light patches).

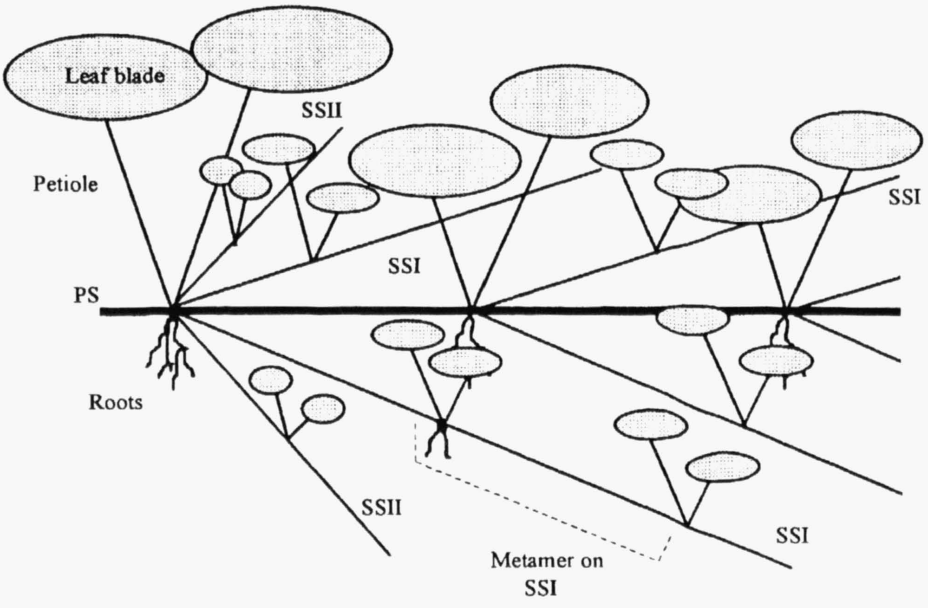

Fig. 1. – Schematic diagram of *Glechoma hederacea*. PS – primary stolons, SS – secondary stolons, a metamer consists of an internode, a node (including roots) and two attached leaves

I used electrophoretically identified hermaphroditic genotypes of *Glechoma hederacea* L. from two habitats in the Czech Republic and Sweden to evaluate variation in their clonal growth. The aim of this study was to find out whether autumnal growth of *G. hederacea* is genetically determined and whether there are any differences between plants collected in the two regions and in the two habitats.

Material and Methods

The plant species

Glechoma hederacea L. (*Lamiaceae*) is a perennial, clonal gynodioecious herb. Its stolons are annual, being fragmented early in spring. The stolons consist of several metamers (a node which may be rooted, and has two attached leaves and an internode). At the beginning of a vegetation season the plant is formed by a stolon fragment, one node, two attached leaves and two short orthotropic shoots with a few internodes and small leaves. The orthotropic shoots elongate in April ("spring growth") and flower in May and June. The erect branch continues its growth, bends down and becomes horizontal. Roots develop on most nodes which are attached to the soil surface. Horizontal growth ("summer growth") of a branch results in a stolon which may form numerous branches (Fig. 1). Usually either none or two secondary stolons are formed at each node. However, the number of secondary stolons originating from serial buds at petiole base may be up to four on each side of a node (pers. observ.). In autumn, numerous side branches are initiated and new internodes are shorter ("autumnal growth"). The short side branches overwinter. The

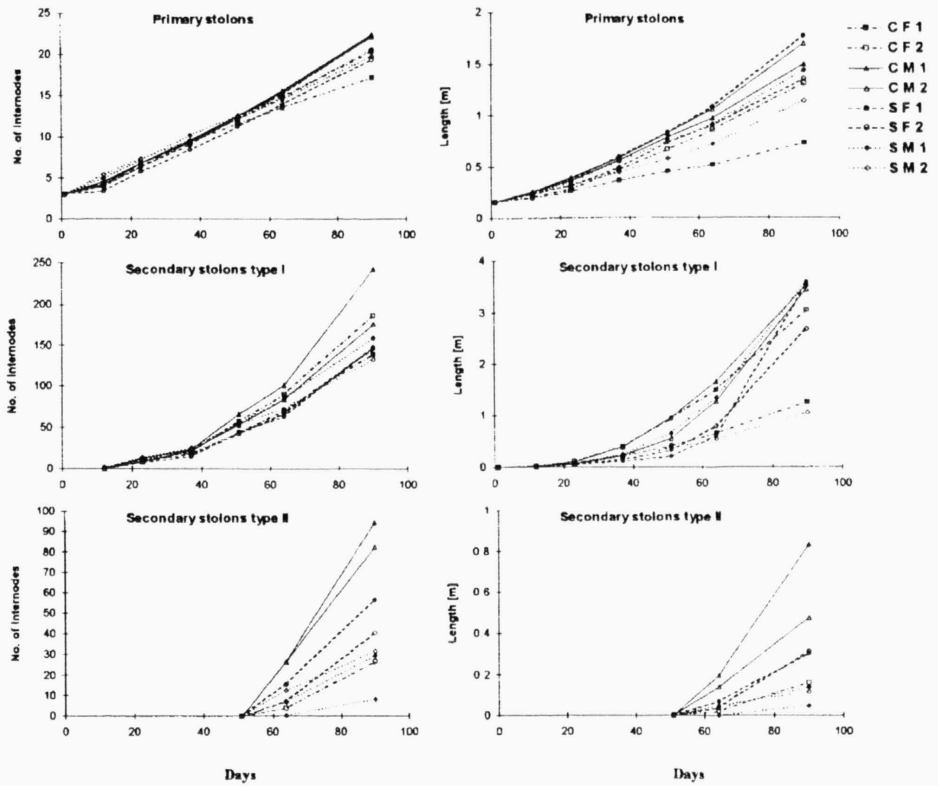

Fig. 2. – The number of internodes and total length of primary and secondary stolons in 8 genotypes of *Glechoma hederacea* observed during 90 days in a greenhouse. CF – genotypes from Czech forests, CM – genotypes from Czech meadows, SF – genotypes from Swedish forests, SM – genotypes from Swedish meadows. Two genotypes were sampled in each habitat.

autumnal behaviour is important for *G. hederacea* plants. As mortality is very low over winter (Slade et Hutchings 1989) the number of shoots is already determined in autumn.

Methods

Shoots of *G. hederacea* were sampled in two meadow and two forest localities in the Czech Republic (between the village of Halámky and the town of Třeboň: 49° N, 14° 50' E) and in two meadow and two forest localities in southernmost Sweden (between the villages of Dalby and Öved: 56° N, 13° E, for details see Widén et al. 1996). In the meadows *G. hederacea* was growing in full light conditions during the whole season, either due to a low stand height or low plant density. All forest *Glechoma* populations were sampled in mature tree stands where patches of light were relatively small and unpredictable both in time and space. In each locality shoots were sampled regularly in corners of a quadrate net with a 1m distance between neighbours. The plants were cultivated in a greenhouse and were assigned to individual genotypes using electrophoresis. Plant material from some localities was genetically uniform, in other cases numerous genotypes were identified

(Widén et al. 1996). Out of the 46 identified genotypes females were removed and one genotype of a hermaphroditic plant was randomly selected from each locality for this study.

The plants were cultivated in a greenhouse for two seasons to eliminate non-heritable components of plant growth. The experiment was set up in the beginning of October. Air temperature in the greenhouse was kept at 18/15 °C, light intensity was not manipulated. The plants were planted on three tables 1.5 × 6 m in size, with garden soil 30 cm in depth, parallel to the longer sides of the tables. The plants, consisting of two nodes, one internode and an apical growing tip, were initially directed perpendicularly to the longer table margin. The distance between neighbouring plants was 45 cm at the time of planting so that shading by neighbouring plants was small. The plants were watered as required for their optimum growth. No fertilisation was applied. Plant growth was followed for 90 days. For each genotype, five replications, originating from the mother plant by multiplication, were used. Length of internodes, leaf blades and petioles were repeatedly recorded. A nested one-factor analysis of variance was used to partition the total variance into components due to population origin (4) and genotype (8 in total, nested within population origin) (Zar 1984).

Primary stolons are thereafter labelled as PS. The secondary stolons (SS) of the first pair are abbreviated as SSI; the secondary stolons of the second pair are labelled as SSII.

Results

Plants of *G. hederacea* produced PS 0.7 to 1.8 m in length, on average, consisting of 17 to 22 internodes (Fig. 2); 65 to 97% of them were rooted. All plants produced SSI. Their mean total length ranged from 1 to 3.5 m. They consisted of 133 to 242 metamers; 15 to 32 % of them were rooted. SSII were produced by all genotypes but not by all plants. Their mean length was 0.04 to 0.83 m. The mean number of nodes ranged from 8 to 94; 0 to 20% of them were rooted.

Overall, the effect of genotypes on PS and the SSI was much stronger than that of populations (Table 1). The number of internodes on PS, the number of rooting nodes and the proportion of rooting nodes were affected neither by genotypes nor populations. Sum of internode lengths (= length of the PS), mean internode length, mean leaf blade width and mean petiole length on PS were genotype-dependent. The plants from Czech meadows and from Swedish forests grew better than the other genotypes (Table 2). The effect of population origin on all variables measured on the SSI was non-significant. However, the effect of genotype on the number of nodes, length of the SSI and their mean internode length was significant (Table 1). For the SSII the pattern was different. All variables except the proportion of rooting nodes were population-dependent but only the length of the SS and their mean internode length were genotype-dependent. The number of growing tips on the SSI was independent of the population and genotype factors, whereas both the number of growing tips on the SSII and total number of growing tips per clone were population-dependent.

At the end of the experiment (Day 90) some plants developed also SS III. They were, however, short. Tertiary stolons (= side branches developed on SS) were also initiated on some plants at the end of the experiment.

Between-genotype variation in the number of internodes on PS was relatively small compared with SS (Fig. 2). For stolon length, the variation was even much higher because

Table 1. One-way ANOVA with genotype nested within population.

Source of variation (DF)	Population (3)			Genotype (4)			Residual (32)	
	MS	VC	F	MS	VC	F	MS	VC
Primary stolons								
Number of nodes	21.0	12.2	1.79 NS	11.7	16.5	2.16 NS	5.4	71.3
Number of rooting nodes	29.8	11.3	0.86 NS	13.6	1.8	2.18 NS	12.4	86.9
Proportion of rooting nodes[1]	0.3	18.3	2.37 NS	0.1	12.8	0.06 NS	0.1	68.9
Sum of internode lengths	7401.9	22.8	1.85 NS	3997.3	47.6	9.02 ***	443.3	29.7
Mean internode length	9.0	23.5	1.83 NS	4.9	51.3	11.14 ***	0.4	25.3
Mean leaf blade width	484.0	27.5	2.33 NS	208.0	33.7	5.33 **	39.0	38.9
Mean petiole length	484.1	0.0	0.68 NS	708.9	61.7	9.05 ***	78.4	38.3
Secondary stolons type I								
Number of nodes	8793.1	16.1	1.92 NS	4570.3	22.7	2.85 *	1603.9	61.2
Number of rooting nodes	396.8	0.0	0.64 NS	616.7	14.9	1.88 NS	328.3	85.1
Proportion of rooting nodes[1]	0.020	1.58	1.09 NS	0.019	19.5	2.23 NS	0.008	78.9
Mean internode length	0.9	0.0	0.45 NS	2.0	38.1	4.08 **	0.5	61.9
Sum of internode length	40749.5	0.0	0.63 NS	65142.2	31.6	3.31 *	19702.6	68.4
Number of growing tips	107.9	7.7	2.10 NS	51.3	0.0	0.76 NS	67.4	92.2
Secondary stolons type II								
Number of nodes	9549.2	70.7	20.22 ***	472.2	1.9	1.34 NS	351.2	27.4
Number of rooting nodes	12.4	14.4	2.91 *	4.3	0.0	0.88 NS	4.9	85.7
Proportion of rooting nodes[1]	0.018	8.98	1.8 NS	0.010	6.36	1.43 NS	0.007	84.7
Mean internode length	0.2	16.2	14.90 ***	0.1	25.5	3.15 *	0.0	58.3
Sum of internode length	6458.4	60.3	7.22 ***	894.0	14.3	3.80 *	235.0	25.5
Number of growing tips	498.8	47.0	5.79 **	86.1	11.3	2.35 NS	36.7	41.7
Total no. of growing tips	1056.8	33.1	4.57 **	231.3	6.5	1.53 NS	150.9	60.5

MS: Mean square, VC – Variance component [%]
* – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$, NS – not significant ($P > 0.05$)
[1] – arcsin transformed before testing

some genotypes partly produced stolons with short internodes of the 'autumnal' or 'intermediate' type whereas others produced only typical plagiotropic 'summer' stolons.

Discussion

G. hederacea has been frequently studied in illuminated greenhouses, where the natural annual cycle is broken down due to the artificially induced long day and high temperatures (e.g., Slade et Hutchings 1987a, b, Birch et Hutchings 1992a,b, 1994, Price et Hutchings 1992, Price et al. 1992). Behaviour of *G. hederacea* in the field is, however, different (Slade et Hutchings 1989, Widén et Widén 1990, Widén 1992). In this study, carried out in autumn, day length was not manipulated and several features typical of autumnal growth of *G. hederacea* were developed.

The autumnal growth of *G. hederacea* is characterized by a rich production of SS and short internodes. The poor rooting at nodes and erect growth observed in some plants at the end of the experiment indicates that "spring growth" already started in these plants. On a few SS flower buds were developed at the end of the experiment. The erect growth with unrooted nodes was frequently observed on the SSII, with a lower frequency on the

Table 2. Means (standard errors) for performance of clones sampled in two regions and two habitats.

	Czech Republic		Sweden	
	Forest	Meadow	Forest	Meadow
Primary stolons				
Number of nodes	18.8 (1.21)	22.3 (0.82)	20.8 (0.85)	20.2 (0.47)
Number of rooting nodes	17.4 (1.08)	19.4 (0.73)	15.2 (2.03)	17.7 (0.67)
Rooting nodes [%]	92.9 (1.95)	87.3 (2.56)	71.4 (8.39)	87.7 (3.1)
Sum of internode lengths [m]	1.02 (0.13)	1.60 (0.08)	1.57 (0.10)	1.29 (0.093)
Mean internode length [mm]	50.33 (4.31)	68.77 (2.71)	71.34 (2.76)	60.53 (3.62)
Mean leaf blade width [mm]	42.4 (3.42)	53.7 (1.19)	49.1 (2.47)	38 (3.11)
Mean petiole length [mm]	48.7 (5.50)	61.2 (2.79)	56 (3.49)	45.9 (4.90)
Secondary stolons type I				
Number nodes	163 (17.54)	209 (20.16)	147 (12.89)	146 (9.31)
Number of rooting nodes	42.7 (6.01)	39.7 (5.79)	28.1 (8.06)	36.4 (6.76)
Rooting nodes [%]	26.2 (1.99)	18.8 (2.55)	16.9 (4.27)	24.5 (4.06)
Mean internode length [mm]	12.4 (1.5)	17.1 (2.8)	19.4 (3.4)	15.0 (3.2)
Sum of internode length [m]	4.27 (0.60)	3.97 (0.58)	2.81 (0.81)	3.64 (0.68)
Number of growing tips	33.1 (3.58)	41.1 (2.13)	36.5 (3.24)	36.5 (2.23)
Secondary stolons type II				
Number of nodes	17.6 (4.67)	88.6 (7.04)	48.6 (8.59)	30.6 (6.10)
Number of rooting nodes	1.7 (1.12)	2.8 (0.97)	1.3 (0.44)	0.1 (0.11)
Rooting nodes [%]	9.82 (5.89)	3.14 (0.97)	2.5 (1.02)	0.16 (0.17)
Mean internode length [mm]	4.4 (0.78)	7.2 (0.76)	6.2 (1.06)	3.9 (0.38)
Sum of internode length [m]	1.7 (1.12)	2.8 (0.97)	1.3 (0.44)	0.1 (0.11)
Number of growing tips	6.2 (2.01)	23.2 (2.16)	17.0 (2.55)	14.0 (2.42)
Total no. of growing tips	40.3 (4.82)	65.3 (3.44)	54.5 (5.59)	51.5 (3.69)

SSI and never on PS. It seems that the process of transformation of plagiotropic stolons with rooted nodes and long internodes to (partly) orthotropic stems without roots and with short internodes was induced by a shortened day-length, as temperature did not change during the experiment.

The genotypes used in this study differed in the extent of their "summer" and "autumnal" growth. The growth of PS was of the "summer type" in all plants. The number of internodes increased gradually with time in all genotypes, as described by Birch et Hutchings (1992a, b), see Fig. 2. There was no effect of genotype or population origin on the number of nodes produced after 90 days. However, length of PS as well as mean length of internodes differed between genotypes. There was a high variation in spreading of individual genotypes. However, this variation was not related to population origin of the plants.

In summer the PS of *G. hederacea* growths straight with angles of two subsequent internodes close to 180° (Cain 1994). Its role is mainly to spread the clone to new environments. Exploitation of the local environment is ensured by intensive branching. The first SSI started to grow after about 10 days, when about 5 internodes were developed. Their total length increased exponentially with time as their growth was linear and their number increased with time. At the end of the experiment the total length of the SSI was about two times that of the PS. The mean number of growing tips on the SS ranged from 33 to 41 and the differences between both populations and genotypes were non-significant.

The SSII appeared after about 60 days. Within 90 days they developed to some extent on all but one plant in the experiment. They were much shorter than the PS. However, in some genotypes, they developed vigorously (Fig. 2). The number of growing tips on these stolons differed markedly between plants from different populations. Similar results were obtained for the total number of growing tips.

The function of the SS is three-fold. First, they determine the storage level available for spring regrowth, second, they efficiently utilise patches of resources because their nodes are short, and third, they determine both spring growth of a clone and the number of shoots produced in spring because metamers established in autumn overwinter with a low mortality (Slade et Hutchings 1989).

The growth habit of *G. hederacea* results in a fast spreading of stolons by means of plagiotropic growth and in intense branching in resource-rich places. I demonstrated that individual genotypes differed in the speed of their spreading, with the fastest clones from Czech meadows and the slowest ones from Czech forests (Table 2). The total number of growing tips followed the same line. There is no indication that the plants studies from either one specific habitat (meadows vs. forests) or one given region (Czech Republic vs. Sweden) behave in a similar way. Therefore, using only parameters of clonal growth the plants studied cannot be grouped to ecotypes. The clones originating from Czech forests had both the shortest internodes and the smallest number of growing tips (probability of branching). The highest values of these variables were found in clones originating from Czech meadows. This pattern contrasts with the expectations based on the behaviour of *G. hederacea* in environments differing in light intensity (Slade et Hutchings 1987b). Much of the observed variation was genotype-dependent which means that variation in all populations was poorly affected by habitat-dependent selection.

The growth of the SSII was population-dependent. Most nodes on these stolons did not bear roots. They grew up and if the experiment had not been finished some of them would probably have flowered. These stolons are, however, rarely produced in the field unless growing tips on the PS and the SSI are damaged. Nevertheless, the results indicate that there could be a significant difference between populations in the extent of sexual reproduction on SS of higher orders.

Concluding, variation in clonal growth of *G. hederacea* is genotype-dependent. There is no indication of ecotypes in any habitat or geographical region. The idea suggesting that genotypes originating from forest, a shaded habitat heterogeneous in light supply, have longer internodes and less frequent branching to make foraging more efficient there, was not confirmed.

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Souhrn

Klonální růst osmi hermafroditních genotypů *Glechoma hederacea* sebraných na louce a v lese v jižních Čechách a na jihu Švédska byl studován ke konci vegetační sezóny ve skleníku. Záměrem práce bylo testovat: (a) zda klonální růst *G. hederacea* je geneticky determinován a (b) jaký je podíl variability na úrovni klonu

a populace (geografická oblast a louka vs. les). Pokus trval 90 dní, během nichž došlo vedle rozvoje primárních i k růstu sekundárních stolonů, jejichž počet byl až 2–6 na jednom nodu. Délka stolonů, průměrná délka internodia, průměrná šířka listové čepele a průměrná délka řapíku na primárních stolonech se lišila pro jednotlivé genotypy. Podobně rozdíly v počtu nodů na sekundárních stolonech prvního páru, v průměrné délce jejich internodií a v celkové délce stolonů prvního páru byly na úrovni genotypů statisticky průkazné. Na druhém páru sekundárních stolonů se počet nodů, počet nodů s kořeny, průměrná délka internodií, délka stolonů a počet růstových vrcholů lišil mezi jednotlivými populacemi. Tyto rozdíly však nebyly vázány na typ prostředí či geografický původ genotypů. Proto je nelze interpretovat jako výsledek ekotypické diferenciace. Oproti očekávání nebylo zjištěno, že genotypy rostoucí v prostředí s větší intenzitou světla (t.j. na louce) mají kratší internodia a větší frekvenci větvení.

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Vascular plants of Poland – a checklist

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V bohatě rozvinuté publikační činnosti polských botanických organizací vyšel nedávno výčet cévnatých rostlin území Polska, vypracovaný čtyřmi výše vyjmenovanými botaniky. Práce tohoto typu, častěji se objevující v posledních letech, dávají základní přehled o floristickém bohatství určitého území, ať jsou již nazývány jako "Checklist" (pouhý výčet či seznam rostlin) nebo jako katalog, kde vedle výčtu sem spadajících druhů (resp. i podřazených taxonů) jsou mnohdy uvedeny i další stručné údaje o příslušných rostlinách. Polský výčet cévnatých rostlin je v úvodní části a v části doplňkové (poznámky k jednotlivým vybraným taxonům) psán dvojjazyčně – polsky a anglicky, takže je tento přehled přístupný celosvětové botanické komunitě. Toto dílo vzniklo v rámci prací pro připravovaný určovací klíč polské květeny a svým obsahem navazuje na předchozí flórová zpracování polského území, jež však zachycovaly díky historickým událostem území dosti různého rozsahu. Vedle čtyřčlenného autorského kolektivu se zúčastnili práce ještě specialisté (v počtu 5), mezi nimi hlavně J. Zielinski (rody *Crataegus*, *Rosa*, *Rubus* a *Salix*), K. Rostanski (*Oenothera*) a Z. Szelag (*Hieracium*, *Potentilla*); dále spolupracovali 2 konzultanti – K. Rostanski a W. Zukowski. Po krátkém (dvojjazyčném) úvodu na 9 stranách následuje základní část díla – abecední přehled druhů a subspecií polské květeny (str. 17–215), za níž jsou uvedeny ve dvou sloupcích dvojjazyčně poznámky a vysvětlivky k vybraným taxonům (str. 217–267). Dále je kapitola s citovanou literaturou (str. 269–280) a rejstřík jmen autorů uvedených u jmen rostlin; tato informace je podána podle díla Brummitt et Powell z r. 1992 (str. 281 až 303); závěrem pak následují ještě 4 strany oprav. Uspořádání výčtu druhů je abecední a text je věcně rozlišen užitím různých typů písma (původní a zdomácnělé druhy; jejich synonyma; efemerofyta a pěstované druhy; synonyma efemerofyt). Další rozlišení je provedeno ještě použitím 9 značek. Celkem je na téměř 200 stranách seznamu uvedeno okolo 6000 vědeckých jmen rostlin a k nim je připojeno na 4000 jmen národních (polských). Základní materiál seznamu představují druhy v území původní a trvale zdomácnělé; dále jsou zařazeny i efemerofyty (podle seznamu vypracovaného Rostanskim a Sowou v r. 1986) a pěstované rostliny (tyto v počtu několika set druhů), hlavně stromy, keře a pereny. Náhodné úniky pěstovaných druhů nejsou zachyceny. Kategorie subspecie není užívána příliš často; kříženci (až na typy připomínající druhy) jsou zcela vypuštěni. V taxonomii i nomenklatuře se autoři přidržovali spíše tradičních (polských) zvyklostí; určitým vzorem jim bylo i zpracování přijaté v Rothmalerově určovacím klíči z r. 1994, jemuž dávali při rozhodování přednost před zpracováním příslušných taxonů v díle Flora Europaea. Při nomenklatorických problémech byl použit ještě Kód ICBN z r. 1988.

Nejrozsáhlejším rodem polské květeny je rod *Taraxacum* (290 druhů), po něm následuje *Hieracium* s.l. (103; z toho vlastní *Hieracium* 53 druhů a *Pilosella* 50), *Carex* s.l. (97), *Rubus* (85 přijatých druhů doprovozených zmíněním 77 lokálních biotypů), *Alchemilla* (60), *Festuca* s.l. (38), *Potentilla* s.l. (37), *Veronica* s.l. (37), *Chenopodium* s.l. (30), *Oenothera* (30), *Rosa* (30), *Salix* (30) a *Galium* (29).

Vedle výčtu druhů (a subspecií) má dílo význam i z hlediska národní nomenklatury rostlin; je zajímavé srovnat toto polské jmenosloví s jmenoslovím naším. Autoři se snažili neužívat substantiva jako druhová epiteta, ale v některých (dlouho užívaných) případech jsou taková spojení ponechána. Dosti často se jedná