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RESEARCH ARTICLE

Quantitative and qualitative analysis of alkaloids composition in the seeds of a white lupin (*Lupinus albus* L.) collection

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Abstract White lupin (*Lupinus albus* L.) has unexploited potential as a crop plant due to its high seed yield as well as protein and oil content in seeds. Well-characterized collections of gene resources are very important for breeding as a source of genetic variation. This paper presents the results of analyses for total content and qualitative composition of alkaloids in seeds of 367 *L. albus* accessions from the Polish Genebank. Accessions were divided into four classes of origin: wild collected material, land races, breeding lines, and cultivars. Apart from the expected broad variation as well as strong differentiation in the alkaloid content, a clear influence of domestication was observed. This was shown as an apparent decrease in the alkaloid content in breeding lines and cultivars classes. The total alkaloid content varies from 0.02 to 12.73% of the seed dry weight. Six major alkaloids (abundance >1%) were revealed: lupanine (28.22–94.49%, mean 76.06% in total content), 13-hydroxylupanine (0.10–32.78%, mean 8.23%), multiflorine (0.00–21.67%, mean 5.52%), albine (0.00–18.55%, mean 4.48%), angustifoline (0.24–12.14%, mean 2.07%), 11,12-seco-12,13-didehydromultiflorine (0.00–12.28%, mean 1.74%). Owing to its abundance, lupanine was found to be the most closely correlated to the total alkaloid content.

Keywords Alkaloids · Anti-nutritive compounds · Genetic resources · *Lupinus albus* · White lupin

Introduction

The genus *Lupinus* covers 275 species encompassing mostly small-seeded New World species (large-seeded *L. mutabilis* Sweet being an exception) and 13–15 large-seeded species of the Old World, including three lupin crops—*L. albus* L., *L. angustifolius* L., and *L. luteus* L. (Cardoso et al. 2013; Cowling et al. 1998a; Pascual 2004; Święcicki et al. 1996, 2001). Apart from its own environmental requirements, each lupin crop has potential benefits in feeding and farming (Brummund and Święcicki 2011).

White lupin originates from the Mediterranean area and has been cultivated since ancient times in

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Greece (Kurlovich 2002). According to Harrison and Williams (1982) the wild forms of *L. albus* contain a high level of quinolizidine alkaloids in seeds—up to 2.2% of the seed dry weight (DW), whereas cultivars with the gene reducing alkaloid content: *pauper,* possess 0.02–0.05% of the seed DW. Like other lupin crops *L. albus* plant architecture is adapted to modern cropping technologies (Górynowicz et al. 2014). Apart from the advantages common to other lupins it is also characterized by outstanding oil content in seeds (up to 14%) and the highest seed yield (Brummund and Święcicki 2011). Given these facts, white lupin has a potential as a protein plant, provided that further improvements be achieved with regard to resistance to anthracnose, earliness, and alkaloid content in seeds (Cowling et al. 1998b; Święcicki et al. 2015). Decreasing the alkaloid content in breeding as a basic requirement to use lupins as fodder has been precisely described in literature (Brummund and Święcicki 2011; Hackbarth and Troll 1956; Kamel et al. 2016).

At least five loci controlling alkaloid content are present in *L. albus* (Harrison and Williams 1982) and the one with *pauper* gene is the most effective in reducing alkaloid content and thus most frequently used in breeding (Lin et al. 2009). Cultivars possessing *pauper* gene contain 0.02–0.05% alkaloids of the seed DW (Harrison and Williams 1982; Święcicki et al. 2015) with following qualitative composition of major alkaloids (abundance >1%): lupanine—70%, albine—15%, 13-hydroxylupanine—8%, and multiflorine—3% (Wink et al. 1995). Earlier investigation on the narrow-leafed lupin collection revealed a broad variation of the total alkaloid content in seeds from 0.0005 to 2.88% of the seed DW (Kamel et al. 2016). It was stated that numerous cultivars are characterized by safely low alkaloid content (<0.02% of the seed DW) (Cowling et al. 1998a), but in genetic resources there are accessions with clearly lower content, useful for further cultivar improvement.

About 14,000 of accessions are gathered in *Lupinus* collections worldwide (Święcicki et al. 2015). Some of them are well described and characterized (Cowling et al. 1998a; Święcicki et al. 2000). To improve the value of gene resources as an initial breeding material, a precise valorization is important. Therefore, the aim of this study was to evaluate total contents and qualitative compositions of alkaloids in seeds of the Polish collection of *L. albus*.

Materials and methods

Plant material

A total of 367 accessions of white lupin from the Polish *Lupinus* Gene Bank, Wiatrowo (Poznan Plant Breeders Ltd.), were investigated. Among accessions studied, also included were cvs. Feli (Wt95 531) and Nelly (Wt95 480) as the International Union for the Protection of New Varieties of Plants (UPOV) controls for high and low alkaloid content (UPOV 2004). The investigated plant materials belong to four classes of different origins:

- CO—180 wild lines and primitive populations originated from places of natural distribution and collecting missions,
- LR—74 land races,
- XD—54 breeding lines,
- CV—59 present and old cultivars.

Accessions were sown for regeneration in the field experiment in Wiatrowo, Poland (latitude 52°45′9″N; longitude 17°8′36″E; altitude 86 m above sea level) in 2014 in a completely randomized design in two replications (plot size 1 m^2, 60 seeds per plot). Seed samples for analyses were collected from each plot after full maturity.

Total alkaloid content and individual alkaloids composition were evaluated by gas chromatography. The extraction and analyses were conducted following the procedure presented by Kamel et al. (2016).

Statistical analyses

The one-factor analysis of variance was applied for testing hypotheses concerning the differences between means from four classes of origin and significant differences between accessions inside individual characters (total and individual alkaloid contents) for each class. Testing differences between accessions were made on the basis of significance level $P = 0.01$. Moreover, for the total alkaloids content, individual alkaloids content, and four classes of origin the Gabriel procedure was used (Gabriel 1964). It divided the set of accessions in each class into three homogenous groups concerning alkaloid content (high, medium, and low) with the means significantly differentiated. As a measure of the linear dependence between the total content of alkaloids and its six

components (individual alkaloids), the correlation coefficients were calculated.

Results and discussion

The table presenting results of total alkaloid content (% of the seed DW) and qualitative composition of six major alkaloids (% of the seed DW and its % in total alkaloid content) of all investigated *L. albus* accessions is placed online at: http://www.igr.poznan.pl/uploads/resources/Lupinus%20albus.pdf.

A very broad variation was obtained for the total as well as individual alkaloid content (Table 1-I). Total alkaloid content varied from 0.016 to 12.73% of the seed DW (mean 2.47%). Thus, the maximum contents found in *L. albus* clearly exceed those reported for *L. angustifolius* (Kamel et al. 2016). A comparison of mean values as well as minimum and maximum values in CO and CV classes (Table 1-II) shows evident

Table 1 Total alkaloid contents and qualitative composition of the major alkaloids in seeds of the *L. albus* collection (I—in all classes of origin—367 accessions, II—in the CO and CV class, III—in accessions with minimum and maximum value of a given character/bold)

Part	Values	Character						
		Total alkaloid content (% of the seed DW)	Lupanine (% of total)	13-hydroxylupanine (% of total)	Multiflorine (% of total)	Albine (% of total)	Angustifoline (% of total)	11,12-seco-12,13-didehydromultiflorine (% of total)
I	Mean	2.47	76.06	8.23	5.52	4.48	2.07	1.74
	Minium	0.02	28.22	0.10	0.00	0.00	0.24	0.00
	Maximum	12.73	94.49	32.78	21.67	18.55	12.14	12.28
II	CO							
	Mean	3.05	78.91	6.04	6.01	4.43	1.72	1.50
	Minium	0.06	53.87	0.25	0.00	0.00	0.26	0.10
	Maximum	12.73	94.49	22.50	18.07	18.55	7.24	5.74
	CV							
	Mean	1.36	72.30	10.89	4.91	4.29	2.56	1.98
	Minium	0.02	28.22	2.35	1.01	0.02	0.29	0.20
	Maximum	4.91	92.82	32.78	21.67	16.41	10.15	12.28
III	Accession/class							
	Wt 95413/CV	**0.02**	59.28	24.10	2.14	3.52	4.13	0.94
	Wt 95015/CO	**12.73**	87.12	1.15	5.62	3.98	0.50	0.65
	Wt 95449/CV	0.04	**28.22**	31.72	1.99	16.41	10.15	0.63
	Wt 95099/CO	3.29	**94.49**	2.16	1.63		0.40	0.19
	Wt 95115/LR	3.44	88.58	**0.10**	2.79	6.65	0.47	0.32
	Wt 95431/CV	0.02	34.01	**32.78**	2.50	8.99	8.35	4.56
	Wt 95175/LR	0.05	31.57	32.08	**0.00**	15.66	12.14	0.00
	Wt 95531/CV (Feli)	3.14	67.45	3.99	**21.67**	0.02	1.83	3.49
	Wt 95608/CO	9.08	87.97	3.13	7.51	**0.02**	0.45	0.34
	Wt 95054/CO	2.92	60.46	6.13	6.28	**18.55**	3.32	3.91
	Wt 95090/CO	3.43	93.93	2.59	1.34	0.21	**0.26**	0.25
	Wt 95175/LR	0.05	31.57	32.08	0.00	15.66	**12.14**	**0.00**
	Wt 95480/CV (Nelly)	0.10	51.67	19.99	3.42	0.22	4.74	**12.28**

breeding successes in the white lupin. Nevertheless, it is also possible to find low alkaloid accessions in CO class and vice versa—bitter accessions in CV class. It is worth mentioning that genotypes with the lowest alkaloid content belonged not only to CV class (Kijewskij Mutant—0.016% of the seed DW), but also XD (Bialorus-1—0.016% of the seed DW) and LR (P.21525—0.017% of the seed DW) class. Overall exploitation of these results might be useful in broadening the *Lupinus albus* breeding gene pool.

In an earlier investigation of alkaloid pattern in the white lupin seeds, four major alkaloids were discovered (abundance >1% of total alkaloids): lupanine, albine, 13-hydroxylupanine, and multiflorine (Wink et al. 1995). The results of our studies revealed six major alkaloids in primitive (CO + LR) as well as improved accessions (XD + CV) (Table 1). These were lupanine (mean 76.06% of total alkaloids), 13-hydroxylupanine (8.23%), multiflorine (5.52%), albine (4.48%), angustifoline (2.07%), and 11,12-seco-12,13-didehydromultiflorine (1.74%). Additionally, a seventh alkaloid—ammodendrine—with mean content 1.01% was detected, which eventually was not considered in the analyses as it was absent in numerous accessions. Among all major alkaloids, the one always present and clearly dominating was lupanine (28.22–94.49% of total alkaloids). At the same time, other major alkaloids were found in high proportions in some accessions (e.g., maximum for 13-hydroxylupanine—32.78%, multiflorine—21.67%), while in very low proportions or absent in others (13-hydroxylupanine—0.10% and multiflorine—0.00%, respectively). This shows that a clear-cut division into major and minor alkaloids is rather difficult. In the earlier analysis of narrow-leafed lupin alkaloids, different qualitative compositions of major alkaloids were obtained (mean % of total alkaloids): lupanine—46.4%, 13-hydroxylupanine—35.6%, angustifoline—15.5%, and isolupanine—2.5% (Kamel et al. 2016).

In Table 1-III, a qualitative composition of alkaloids is presented for accessions characterized with the lowest and the highest content of total and individual alkaloids (in bold). In the accession Wt95015, distinguished with the highest total alkaloid content, lupanine dominated, and the contribution of other alkaloids was clearly low. In the case of the accession Wt95413, with the lowest total alkaloid content, a lower share of lupanine that was mainly supplemented by 13-hydroxylupanine was observed. The most apparent example of complementation was the accession Wt95431, where clearly higher share of 13-hydroxylupanine went along with decreased lupanine content; this tendency was seen in most of the accessions. No clear pattern of complementation was noticeable in the case of accessions with increased contribution of remaining alkaloids [multiflorine (Wt95531), albine (Wt95054), angustifoline (Wt95175), and 11,12-seco-12,13-didehydromultiflorine (Wt95480)]; however, in all cases lupanine or lupanine + 13-hydroxylupanine obviously dominated.

Significant differences among accessions from four classes of origin considering mean values of total and individual alkaloid content were determined by one-

Table 2 Mean values for alkaloids in four classes of origin

Character	Class of origin				
	F^2_{calc}	CO	LR	XD	CV
Total alkaloid content	73.11**	3.053a[1]	2.789a	1.316b	1.359b
Lupanine	69.30**	2.427a	2.184b	0.970c	1.074c
Multiflorine	24.90**	0.188a	0.171a	0.081b	0.090b
13-hydroxylupanine	25.46**	0.173a	0.178a	0.122b	0.084c
Albine	24.78**	0.132a	0.123a	0.065b	0.046b
Angustifoline	21.25**	0.050a	0.054a	0.032b	0.022b
11,12-seco-12,13-didehydromultiflorine	21.87**	0.044a	0.045a	0.025b	0.020b

** Significant differences $P < 0.01$

[1] Identical superscripts denote no significant ($P < 0.05$) difference between mean values in rows according to Newman–Keuls test

[2] $F_{0.05} = 2.62$, $F_{0.01} = 3.81$

Table 3 Accessions division into three homogenous groups within *L. albus* individual classes of origin for total alkaloid content and content of major alkaloids (% of the seed DW)

Alkaloid	Group[a]	Results	Class of origin			
			CO	LR	XD	CV
Total	1	Number of accessions	3	10	5	6
		Content	9.08–12.73	4.30–8.21	3.30–4.30	3.13–4.91
		Mean	10.53	5.23	3.96	3.87
	2	Number of accessions	68	38	16	23
		Content	3.15–6.45	2.31–3.96	1.45–3.08	1.21–2.73
		Mean	3.80	3.12	2.37	1.93
	3	Number of accessions	109	26	33	30
		Content	0.07–3.10	0.02–2.15	0.02–1.27	0.02–1.10
		Mean	2.29	1.37	0.40	0.42
Lupanine	1	Number of accessions	3	3	13	5
		Content	7.98–11.09	4.27–7.05	1.93–3.39	2.81–4.30
		Mean	9.20	5.49	2.44	3.36
	2	Number of accessions	64	40	10	17
		Content	2.48–5.36	1.97–3.82	0.81–1.79	1.16–2.46
		Me an	3.24	2.72	1.27	1.79
	3	Number of accessions	113	31	31	37
		Content	0.04–2.42	0.01–1.87	0.01–0.60	0.01–1.09
		Mean	1.88	1.18	0.25	0.44
13-hydroxylupanine	1	Number of accessions	18	11	2	6
		Content	0.28–0.36	0.33–0.60	0.40–0.51	0.18–0.30
		Mean	0.40	0.44	0.46	0.22
	2	Number of accessions	56	21	13	21
		Content	0.17–0.21	0.16–0.30	0.19–0.34	0.08–0.15
		Mean	0.22	0.22	0.26	0.12
	3	Number of accessions	106	42	39	32
		Content	0.01–0.14	0.00–0.15	0.00–0.14	0.00–0.07
		Mean	0.11	0.09	0.06	0.04
Multiflorine	1	Number of accessions	20	7	5	2
		Content	0.38–0.68	0.44–0.82	0.31–0.40	0.46–0.68
		Mean	0.50	0.57	0.37	0.57
	2	Number of accessions	61	23	11	11
		Content	0.18–0.31	0.16–0.37	0.11–0.22	0.14–0.34
		Mean	0.24	0.24	0.15	0.23
	3	Number of accessions	99	44	38	46
		Content	0.00–0.15	0.00–0.15	0.00–0.08	0.00–0.13
		Mean	0.09	0.07	0.02	0.03
Albine	1	Number of accessions	20	12	5	9
		Content	0.30–0.56	0.28–0.44	0.24–0.36	0.11–0.23
		Mean	0.39	0.33	0.30	0.16
	2	Number of accessions	61	17	11	21
		Content	0.12–0.20	0.12–0.25	0.07–0.17	0.03–0.10
		Mean	0.19	0.19	0.12	0.05
	3	Number of accessions	99	45	38	29
		Content	0.00–0.06	0.00–0.11	0.00–0.06	0.00–0.01
		Mean	0.05	0.04	0.02	0.00

Table 3 continued

Alkaloid	Group[a]	Results	Class of origin			
			CO	LR	XD	CV
Angustifoline	1	Number of accessions	24	14	5	9
		Content	0.09–0.20	0.10–0.19	0.11–0.19	0.05–0.10
		Mean	0.12	0.14	0.14	0.06
	2	Number of accessions	58	20	10	17
		Content	0.06–0.08	0.04–0.10	0.04–0.09	0.02–0.04
		Mean	0.07	0.07	0.06	0.03
	3	Number of accessions	98	40	39	33
		Content	0.004–0.04	0.00–0.04	0.00–0.03	0.00–0.02
		Mean	0.02	0.02	0.01	0.01
11,12-seco-12,13-didehydromultiflorine	1	Number of accessions	11	9	5	3
		Content	0.10–0.21	0.09–0.16	0.07–0.11	0.07–0.11
		Mean	0.14	0.12	0.09	0.09
	2	Number of accessions	59	35	14	18
		Content	0.04–0.10	0.03–0.08	0.03–0.06	0.02–0.05
		Mean	0.07	0.05	0.04	0.04
	3	Number of accessions	110	30	35	38
		Content	0.00–0.04	0.00–0.03	0.00–0.02	0.00–0.02
		Mean	0.02	0.01	0.01	0.01

[a] Group 1—high content of total/individual alkaloids, group 2—medium content, group 3—low content

Table 4 Correlation coefficients between total alkaloid content and the content of individual alkaloids in four classes of origin

Class of origin	Alkaloid					
	Lupanine	13-hydroxylupanine	Multiflorine	Albine	Angustifoline	11,12-seco-12,13-didehydromultiflorine
CO	0.975**	0.350**	0.664**	0.415**	0.334**	0.396**
LR	0.967**	0.498**	0.672**	0.626**	0.569**	0.533**
XD	0.987**	0.886**	0.779**	0.795**	0.839**	0.815**
CV	0.988**	0.699**	0.772**	0.493**	0.665**	0.591**

** $P < 0.01$

factor analysis of variance. Rejection of the null hypothesis (F-test) allowed us to compare a substantiality of differences between classes using the Neuman–Keuls test (Table 2). Given total alkaloid content, the CO and LR classes differed significantly from XD and CV classes. Similar pairing was observed in the case of multiflorine, albine, angustifoline, and 11,12-seco-12,13-didehydromultiflorine. This is in accordance with the domestication process affecting XD and CV classes of white lupin. In the case of other two alkaloids, different grouping was observed. Considering lupanine, a pair of XD and CV classes differed substantially from CO as well as LR class. Whereas for 13-hydroxylupanine, CO and LR classes paired and differed from XD as well as CV class.

In each class, significant differentiation of accessions was also detected considering all the investigated characters. Accessions were designated into three homogenous groups within each class of origin: group 1—high content of total/individual alkaloids, group 2—medium content, and group 3—low content (Table 3). In each class, the least populated was the group with the highest content of both total and individual alkaloids. Most of the accessions belonged to the second and third groups. Clearly, the most populated was the group with the lowest values of all analysed characters in the CO class. This shows high

potential of wild accessions as the rich source of low alkaloid material. In all classes of origin, accessions considered as bitter, in terms of food safety, were found in both groups 1 and 2. Low alkaloid accessions were present only in the third group, and this was also applied to the wild accessions of CO and LR class. Taking into consideration the mean value of total alkaloid content for each group, only the third group of XD and CV classes is clearly sweet. This fact points out the achievements of white lupin breeding. It is worth to mention that UPOV control cultivars have the following alkaloid content in the seed DW: bitter Feli (Wt95531)—3.14% and sweet Nelly (Wt95480)—0.09%.

In the case of lupanine, the main white lupin alkaloid (mean value—76.06%, Table 1), similar tendency in diversification within the classes of origin was observed (Table 3). For the remaining alkaloids characterized with clearly lower share in total alkaloid level (mean content 1.74–8.23% of the seed DW, Table 1), it is possible to observe a systematic decrease of the content in more domesticated material that is especially noticeable when comparing group 3 (low content) of CO and LR classes versus CV class.

The influence of a content of individual alkaloids on the total alkaloid content in seed dry weight was also analysed. Correlation coefficients between total and individual alkaloids content for each class were calculated. All appeared to be substantial at least on a level 0.01 (Table 4). In each class, not surprisingly, the most correlated alkaloid with the total alkaloid content was lupanine, as its contribution is always the highest. Additionally, there were examples of alkaloids with a lower share in total content also being strongly correlated (e.g., 13-hydroxylupanine, multiflorine, albine, angustifoline, and 11,12-seco-12,13-didehydromultiflorine in XD class). It can also be noticed that correlation coefficients in most cases were higher in XD and CV class in comparison to primitive CO and LR classes.

Conclusions

Conducted analysis of the total alkaloid content and a qualitative composition in seeds of the Polish collection of *L. albus* presents a very broad variation and strong differentiation of gathered accessions, much broader than hitherto described for this species and also in comparison to other lupin species (Kamel et al. 2016; Wink et al. 1995). Comparison of the results obtained in individual classes of origin showed a strong influence of domestication and breeding, which resulted in decreased content of alkaloids. Only accessions from the third group of XD and CV class can be considered as significantly low alkaloid.

Six major alkaloids (abundance >1 %) were revealed in comparison to four described earlier. The dominating alkaloid was lupanine (mean 76.06%) and the share of remaining was from 1.74 to 8.23%. To name these alkaloids as "major" was not always proper, as quite often they show very low or even trace content. Moreover, the lupanine, thanks to a very high share, appeared to be the most correlated with the total alkaloid content.

A very high contribution of lupanine (even about 95%) cannot be considered as species-specific, as its share was also high in earlier investigations on narrow-leafed lupin (about 73%). Helpful in both species discrimination could be a qualitative composition of alkaloids. Among six major alkaloids revealed in seeds of the white lupin, multiflorine, albine, and 11,12-seco-12,13-didehydromultiflorine were not present in narrow-leafed lupin.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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