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ESTIMATED CONTRIBUTIONS OF ROOT AND SHOOT TO THE NICOTINE CONTENT OF THE TOBACCO PLANT[1]

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In earlier papers (1, 3, 4), we have described patterns of alkaloid accumulation in reciprocal grafts of tobacco with tomato. The results have been interpreted to mean that the tobacco shoot possesses a low capacity for alkaloid production and that the root system is the origin of most of the alkaloid found in the intact plant. However, existing data do not permit assignment of specific values to these capacities. For this purpose, there is need for data obtained from grafted as well as intact (nongrafted) plants which have been grown under similar conditions and have exhibited similar rates of growth and development. It may then be assumed that the alkaloid content of the grafted shoot affords a reasonable estimate of the contribution of the intact shoot to its own alkaloid content. Thé present paper utilizes this assumption to provide first approximations of the relative alkaloid yielding capacities of root and shoot of 3 varieties, representing 2 species, of Nicotiana.

This approach has been extended to include the case in which the apical bud of the tobacco shoot is removed (topping) while the plant is still in the vegetative stage of development. Tso and Jeffrey (6) and Solt and Dawson (4) have shown that the alkaloid content of tobacco scions grown on tomato rootstocks may be greatly increased by topping. Such an effect is also obtained as a result of the topping of tobacco in commercial plantings.

MATERIALS AND METHODS

PLANT MATERIALS: Two species of Nicotiana were employed in these experiments, *N. tabacum* L. vars. Turkish and Connecticut Shade No. 49, and *N. rustica* L. var. gigantea. All were grown in the greenhouse during the winter and spring months of 1957 to 1958. The methods of culture, of cleft-grafting, of harvest and of preparation for assay have been described in our earlier papers (3, 4).

Tomato (*Lycopersicum esculentum* Mill. var. Marglobe) was used as rootstock. Tobacco scions were shoots cut above the 5th leaf from young plants which had grown out of the rosette stage. Non-grafted plants were stripped of the lowermost 5 leaves to compensate for similar losses by the scions. Since about 3 weeks were required to permit resumption of normal growth rates by grafted scions, the latter were harvested 3 weeks later than the non-grafted plants. The time schedule for grafting and topping is given in table I.

Plants were sampled at 2 stages of development; one just before flower bud emergence (crop 1) and the other when green seed pods were present (crop 2).

In general, 5 (sometimes 4) plants representing each type and treatment were harvested and divided separately into leaf, stem, inflorescence and, in some cases, root fractions for assay.

BASIS FOR COMPARISON: In the absence of appreciable rates of destruction the alkaloid content of an intact tobacco plant is obviously the sum of the contributions of root, stem, leaves and inflorescence, if any. The total alkaloid content of an individual plant, however, increases rapidly during growth and development, and the production of alkaloid relative to dry weight is sensitive to certain elements of the environment. For these reasons, there is some advantage to basing estimates of alkaloid yielding capacities of the different plant parts upon the total

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TABLE I

TIME SCHEDULE IN DAYS FOR GRAFTING, TOPPING AND HARVEST *

VARIETY	CROP	NONGRAFTED		GRAFTED		
		PLANTING TO TOPPING	TOPPING TO HARVEST	PLANTING TO GRAFTING	GRAFTING TO TOPPING	TOPPING TO HARVEST
Connecticut shade No. 49	1	110	22	**	**	22
	2	110	59	**	**	63
Turkish	1	115	23	87	51	27
	2	115	58	138	51	57
Rustica	1	119	31	84	58	20
	2	119	58	142	58	42

* In all cases nontopped plants were the same age at harvest as the corresponding topped plants.

** Due to premature flowering the plants were cut back near graft union and allowed to produce new shoots.

amount of alkaloid present in the individual organ, shoot or whole plant rather than upon unit dry weight.

For the purposes of the present work, therefore, the following procedure was followed: First, the total amounts of nicotine in root, stem, leaf and inflorescence of intact or topped but nongrafted plants were determined. Second, the contributions of leaves, stem and whole shoot to their own nicotine contents were estimated by assaying the corresponding parts of the grafted plants. Third, the contributions of the root system were obtained by difference between the nicotine contents of the whole plant and of the grafted shoot. Fourth, the nicotine content of leaves, stem or whole shoot of the grafted plant was divided by the nicotine content of the leaf, stem, shoot or whole plant of the non-grafted plant, respectively, in order to obtain the relative contributions of each of these parts to its own nicotine content.

It may be noted that these estimates of relative alkaloid producing capacity are not complicated by the occurrence of appreciable downward transport of alkaloid in the plant. There are, however, some relatively small errors which have been identified in the case of varieties of *N. tabacum*. The graft union is a source of quantities of alkaloid which can be only partially eliminated from the estimates by excision of the union at time of harvest. Quantities which have been transported from the union upwards to stem and leaves (4) cannot be approximated with any degree of confidence and, when included in the total alkaloid figures for these organs or for the shoot as a whole, will lead to overestimates of the alkaloid yielding capacities of these structures. In the 2nd crop of *N. tabacum* var. Turkish, a partial correction can be achieved by subtracting from the contribution of the grafted stem, the abnormally high alkaloid content (loc. cit.) of the lowermost 150 mm and substituting for this figure a quantity equal to the nicotine content of the next 150 mm section above it. Since the alkaloid contents of the 1957 (4) and 1958 (present) crops were not identical, it was assumed for purposes of making this correction that the same fraction of total alkaloid in the stem occurred in the first 150 mm above the graft union in both crops.

The data for *N. rustica* do not involve the graft union effect. It is very likely, therefore, that the estimates for *N. rustica* are more accurate than for those of the 2 varieties of *N. tabacum*. In these latter cases, however, the relative contributions of leaves, stems and shoots will be overestimated somewhat while those of the roots will be underestimated.

To ensure validity of comparison between grafted and nongrafted plants, careful attention was given to the timing of all operations (see above), to cultural treatment of the plants and to the equalizing of morphological characteristics such as number of leaves, stalk height, etc. Some of these items are detailed in tables I and II (column 5).

TABLE II

DRY WEIGHT IN G AND NUMBER OF LEAVES PER PLANT

TREATMENT	MEAN DRY WEIGHT				MEAN NUMBER OF LEAVES
	LEAVES	STEMS	INFLORESCENCE	SHOOT	
N. tabacum var Turkish (vegetative stage)					
Intact plant	29.3	22.0		51.3	30
Topped	21.4	9.0		30.4	14
Grafted	28.7	14.9		43.6	33
Grafted and topped	23.9	4.9		28.8	14
var Turkish (fruiting stage)					
Intact plant	41.4	46.7	25.4	113.0	31
Topped	43.2	20.0		63.2	13
Grafted	40.9	32.0	37.2	110.3	31
Grafted and topped	51.4	8.8		60.2	13
N tabacum var Conn No. 49 (vegetative stage)					
Intact plant	23.1	23.3		46.4	22
Topped	18.6	12.5		31.1	11
Grafted	27.4	17.3		44.7	24
Grafted and topped	22.3	12.5		34.8	10
var Conn No. 49 (fruiting stage)					
Intact plant	38.5	51.1	22.2	111.8	20
Topped	36.6	24.5		61.0	11
Grafted	48.5	56.2	43.2	147.9	21
Grafted and topped	58.2	28.9		87.0	10
N rustica var gigantea (vegetative stage)					
Intact plant	49.5	34.8		84.3	23
Topped	53.3	25.5		78.8	12
Grafted	38.3	21.7		60.0	21
Grafted and topped	43.1	21.6		64.7	12
var gigantea (fruiting stage)					
Intact plant	64.0	59.0	47.7	170.7	25
Topped	80.7	44.9		125.6	12
Grafted	38.8	34.4	41.3	114.5	22
Grafted and topped	55.1	30.0		85.1	11

STATISTICAL TREATMENT: Each figure in tables II and III represents a mean of 5 (or sometimes 4) measurements. The statistics given in table III are standard deviations. Standard errors of estimate based upon means of 5 (or 4) individual measurements were calculated and used in the following equation[2]:

$$\left[\frac{\sigma_{\bar{x}_1}}{\frac{\bar{x}_2}{\bar{X}_1}\,\frac{}{\bar{X}_2}}\right]^2 = \left[\frac{\sigma_{x_1}}{\bar{X}_1}\right]^2 + \left[\frac{\sigma_{\bar{x}_2}}{\bar{X}_2}\right]^2,$$

to calculate standard errors of estimate of the ratios described above.

[2] $\bar{x}$ = standard deviation

$\bar{X}$ = mean

CHEMICAL METHODS: Total steam-volatile pyridine alkaloid content was estimated by methods described in earlier papers (cf. 2). The minor alkaloids are incompletely distillable from magnesium oxide with steam under our conditions. Paper chromatographic examination of the distillates indicated that our measurements refer almost entirely to nicotine. The assay figures are hence calculated as nicotine. It was thought necessary, however, to examine also the alkaloid complex of the plant materials prior to distillation so that any substantial shifts in alkaloid composition associated with a given experimental treatment would be detected.

In preparation for chromatography, 10 gm of dry leaf powder was mixed thoroughly with 10 ml of *N* HCl and extracted continuously with petroleum ether for 24 hours. The extracted residue was then removed from the Soxhlet thimble and air-dried. One ml of concentrated ammonium hydroxide was then added together with enough ethyl ether to yield a slurry. This was shaken mechanically for 3 hours in a closed flask. After filtration through glass wool, the ethereal solution of alkaloids was concentrated to low volume and applied to sheets of Whatman No. 1 filter paper previously impregnated with an acetate

TABLE III

MEAN NICOTINE CONTENTS AND THEIR STANDARD DEVIATIONS IN MG PER PLANT

TREATMENT	LEAVES	STEMS	INFLORESCENCE	SHOOT	ROOTS
		N tabacum var Turkish (vegetative stage)			
Intact plant	289 ± 69	106 ± 11		395 ± 76	
Topped	675 ± 157	128 ± 19		803 ± 170	
Grafted	1.5 ± 0.1	4.7 ± 0.7		6.2 ± 0.7	
Grafted and topped	15 ± 1.2	32 ± 9.4		47 ± 9.3	
		var Turkish (fruiting stage)			
Intact plant	452 ± 62	86 ± 32	40 ± 8.6	577 ± 86	144 ± 23
Topped	2486 ± 378	241 ± 38		2727 ± 429	315 ± 63
Grafted	2.3 ± 0.9	7.7 ± 1.8	0.2 ± 0.3	11 ± 1.7	
Grafted and topped	83 ± 12	65 ± 5.5		149 ± 16	
		N tabacum var Connecticut No. 49 (vegetative stage)			
Intact plant	148 ± 17	57 ± 6		205 ± 21	
Topped	380 ± 67	97 ± 21		477 ± 88	
Grafted	0.8 ± 0.2	4.6 ± 1.2		5.3 ± 1.2	
Grafted and topped	2.5 ± 1.0	18 ± 2.9		21 ± 3.6	
		var Connecticut No. 49 (fruiting stage)			
Intact plant	327 ± 17	72 ± 14	35 ± 12	433 ± 22	123 ± 29
Topped	1617 ± 308	223 ± 29		1840 ± 335	264 ± 25
Grafted	1.3 ± 0.5	8.5 ± 4.6	0.7 ± 0.4	10 ± 5.1	
Grafted and topped	39 ± 10	96 ± 27		135 ± 33	
		N rustica var gigantea (vegetative stage)			
Intact plant	841 ± 214	183 ± 32		1024 ± 240	
Topped	2139 ± 484	301 ± 7.0		2440 ± 485	
Grafted	1.2 ± 0.5	0		1.2 ± 0.5	
Grafted and topped	0.9 ± 0.7	0.8 ± 0.5		1.7 ± 0.8	
		var gigantea (fruiting stage)			
Intact plant	1084 ± 136	194 ± 40	257 ± 26	1534 ± 145	121 ± 20
Topped	3803 ± 392	558 ± 46		4361 ± 404	304 ± 50
Grafted	1.3 ± 0.4	trace	trace	1.7 ± 0.5	
Grafted and topped	2.3 ± 0.5	3.0 ± 0.5		5.3 ± 0.9	

buffer (pH 5.6). The alkaloids were separated on this sheet by the solvent mixture of Tso and Jeffrey (5), *tert*-amyl alcohol and acetate buffer (pH 5.6). Cyanogen bromide and *p*-aminobenzoic acid were used as spot reagents.

Results

Basis for Comparison: It may be seen in table II that the requirement for equality of growth and development of grafted and nongrafted shoots is fairly well realized in both crops of the Turkish variety.

In the fruiting stage the grafted shoots of the Connecticut 49 variety were substantially heavier than nongrafted shoots. In the comparison of nontopped plants, however, the dry weight discrepancies are largely accounted for by the inflorescence which in this variety does not contain alkaloids (4). The comparison between topped plants of this variety is complicated by the higher dry weight of the latter and hence the ratio is somewhat high.

The grafted plants of *Nicotiana rustica* weighed less than the nongrafted. When pooled data relating nicotine content to plant dry weight for this species are plotted on arithmetic coordinates, however, the curve, which is quite smooth, has already become asymptotic at the vegetative stage represented in the present work. Consequently, correct yield ratios are obtained. Such is not the case in the single comparison within the Connecticut 49 variety mentioned above, because different crops of grafted plants of this variety have failed to give the same relationship between the 2 variables.

Alkaloid Content of Plants: The quantities of nicotine contained in leaves, stems, inflorescence and roots, as well as in the shoot, are given in table III.

In agreement with the earlier work, grafting Turkish tobacco scions to tomato rootstocks reduced the nicotine content of the shoots in the fruiting stage by somewhat more than 1 order of magnitude. On the other hand, topping rooted Turkish plants increased the amount of nicotine in the shoots by 1 order of magnitude. The combined effect of grafting and topping was to increase nicotine content of the shoot by 1 order of magnitude over the effect of grafting alone, but the quantities present were still only about one-third to one-fourth as great as those found in the shoots of intact plants. These observations are noteworthy in connection with the findings reported in an earlier paper (4) where a close comparison of grafted and topped plants with intact plants was not possible. A similar pattern was obtained in the case of Connecticut Shade No. 49 variety. However, the data for *Nicotiana rustica* (table III) are somewhat different. Here the nicotine content of all grafted shoots was extremely low in comparison with that of intact shoots. The increase in nicotine due to topping was no more than 2- to 3-fold.

Relative Nicotine Producing Capacities of Shoot and Leaf: The 2 varieties of *N. tabacum* do not vary significantly with respect to relative nicotine contributions of shoot and leaf, whether topped or nontopped (table IV). It is of considerable interest to note that the shoot of the intact plant very likely produces no less than 1 % and no more than 3 % of the nicotine which it normally contains. The effect of topping is to double these figures. Somewhat lower figures are obtained when the ratio employed is the proportion of nicotine in the whole plant that is produced in the shoot.

Table IV

Relative Contributions (in %) of Leaves to Nicotine Content of Leaves and of Shoot to Nicotine Content of Shoot and of Whole Plant

Proportion of nicotine	Nontopped		Topped	
	Vegetative	Fruiting	Vegetative	Fruiting
		N tabacum var Turkish		
In shoot produced in shoot	1.6 ± 0.2*	1.9 ± 0.2	5.9 ± 0.8	5.5 ± 0.5
In plant produced in shoot		1.5 ± 0.2		4.9 ± 0.4
In leaf produced in leaf	0.5 ± 0.1	0.5 ± 0.1	2.2 ± 0.2	3.3 ± 0.3
		N tabacum var Connecticut No. 49		
In shoot produced in shoot	2.6 ± 0.3	2.3 ± 0.5	4.4 ± 0.5	7.3 ± 1.0
In plant produced in shoot		1.8 ± 0.4		6.4 ± 0.9
In leaf produced in leaf	0.5 ± 0.1	0.4 ± 0.1	0.7 ± 0.1	2.4 ± 0.4
		N rustica var gigantea		
In shoot produced in shoot	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
In plant produced in shoot		0.1 ± 0.0		0.1 ± 0.0
In leaf produced in leaf	0.1 ± 0.0	0.1 ± 0.0	0.04 ± 0.02	0.06 ± 0.01

* Standard errors of estimate.

The situation in *N. tabacum* varieties is complicated (see above) by the production of alkaloid in the graft union and in the stem regions immediately above the graft union and by transport of this alkaloid to leaves higher on the same stem. For this reason ratios contained in table IV are too high by an unknown amount.

Such overestimation, however, is avoided in the case of *N. rustica*. In grafts between this species and tomato, the graft union and adjacent stem tissues do not produce and accumulate appreciable amounts of alkaloid. Hence, it may be assumed that translocation of nicotine from such sites to the leaves would be negligible or nonexistent. Therefore, the figures for relative nicotine production in the shoot are much smaller than is the case in varieties of *N. tabacum*. In all crops, whether topped or nontopped, the fraction of nicotine in the shoot, or in the entire plant which is produced in the shoot, remains rather closely around 0.1 %.

A 2nd approximation may be made of the relative nicotine producing capacity of the Turkish tobacco shoot by applying the correction for the unusually high alkaloid content of the stem immediately above the graft union. When this correction is applied to the figures for nontopped Turkish plants in the fruiting stage, the ratios and their standard errors of estimate have the following values. The fraction of nicotine in the whole plant, which was produced in the shoot, becomes 0.8 ± 0.1 %. This means that about 99.2 % of the nicotine content of the entire plant was produced in the root system. The corresponding figures for topped plants of the 2nd crop are 4.9 ± 0.4 % produced in the shoot and about 95.1 % produced in the roots. For reasons already given, both sets of figures must be regarded as maximal for the fraction produced in the shoot and minimal for the fraction produced in the root. This effect would be far more serious in the topped plants than the nontopped plants.

Estimates of relative amounts of nicotine in the leaf, which were produced in the leaf are also given in table IV. These figures represent upper limits for the reasons already given. The degree of overestimation would again be more serious in the case of the topped plants. In the nontopped plants it is quite clear, however, that the leaves produce considerably less than 1 % of their nicotine content at any given time. The figure may approach 0.1 % as calculated for *N. rustica*.

The alkaloidal composition of the 3 tobaccos was not modified qualitatively as a result of topping or grafting. Nicotine was the primary alkaloid in all cases. The Turkish and Connecticut Shade No. 49 varieties contained faint traces of nornicotine and anabasine. Topping the latter 2 varieties yielded somewhat more definite spots for nornicotine and anabasine in line with the general increase in alkaloid content as a result of topping. In general, *N. rustica* seemed to contain somewhat more of the secondary alkaloids than did the 2 varieties of *N. tabacum*. The minor alkaloids are not included in our quantitative data inasmuch as they are not distillable under our conditions of assay. A faint trace of nicotine was obtained in the tomato roots of grafted Turkish plants but the amount was too small to be measured by our routine assay procedure.

Discussion

The limitations and necessary assumptions of this work at various points above have been discussed in considerable detail. With respect to aerial parts, most of the limitations are in the direction of overestimate rather than underestimate.

In view of this situation, the data are all the more remarkable in indicating the extremely limited capacity for nicotine synthesis of the aerial organs of the tobacco plant as compared with the root system. Even when the plant is topped, no more than one-tenth of the nicotine content of the shoot, and usually much less, can be produced in the shoot. For reasons stated, the proportion is probably less than one-tenth. In the intact plant probably no more than 2 % and as little as 0.1 % of the nicotine content may be made in the shoot. The situation is made much clearer in the case of *N. rustica* by the virtual absence of transport of alkaloid from stem into leaves and from graft union into stems.

Of especial interest are the low figures for contribution of the leaf to its own nicotine content. The opinion that the leaf is a major site of nicotine production is still deeply rooted in the lore of tobacco cultivation. The weight of qualitative evidence against this idea has been increasing in recent years. The present work provides quantitative evidence of its incorrectness, and the results of the topping experiments indicate that there are not likely to be important exceptions.

These data cannot be further refined until means are found to estimate more accurately the amounts of alkaloids in the leaves, which are produced in the leaves.

Summary

The relative nicotine producing capacities in tobacco, shoot and leaf, have been estimated for intact and topped plants of 2 varieties of *N. tabacum* and 1 variety of *N. rustica*.

These estimates were based upon the assumption that the alkaloid contents of the stem and leaves of the grafted shoot, correspond to the intrinsic alkaloid producing capacities of these organs.

The limitations of this approach are discussed. It is pointed out that these limitations affect the estimates relative to nicotine production in shoot and in leaf of *N. tabacum* in the direction of overestimation as a result of some transport of alkaloid into stems and leaves of grafted plants from the graft union. This complication was not present in the case of *N. rustica*. In *N. rustica* about 0.10 % of the alkaloid contained in the shoot of the intact plant is produced in the shoot. Nearly all of this nicotine is located in the leaves. When plants of this species are topped,

these figures are not appreciably altered except that only about one-half of the total alkaloid of the shoot may occur in the leaf.

The 2 varieties of *N. tabacum* possess very similar nicotine producing capacities. In the intact plant, between 1 and 3 % of the alkaloid in the shoot was estimated to be produced in the shoot, but only about 0.5 % of that present in the leaf was estimated to be produced in the leaf. The effect of topping was to raise these figures to the level of 3 to 8 % and of 0.5 to 3 % respectively.

A partial correction of the data for Turkish tobacco indicates that substantially over 99 % of the total alkaloid in the plant is produced in the root system.

The authors are especially indebted to Mr. Joseph Stoeber of the Nevis Biological Field Station of Columbia University for growing the plants.

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A WIDE-RANGE A.C. BRIDGE FOR DETERMINING INJURY AND DEATH[1]

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Frequently in physiological and agronomical investigations it is necessary to know whether tissues are alive or dead or injured, so that a rapid method for making an appropriate diagnosis would be very useful. From the classical work of Osterhout (12) it is known that in water of high electrolyte content, the low frequency resistance of a tissue ultimately decreases with injury and falls to a low value on death. In such a medium, seriously injured or dead tissues are characterized by small values for low frequency resistance. Under other conditions, however, dead tissues are not similarly characterized. Thus in water of suitably low electrolyte content, increasing injury from a poison can result in an increasing low frequency resistance until at death a large and constant resistance value is obtained, as shown in fig 1 (for explanation see next section). In water of somewhat higher electrolyte content similar low frequency resistance values can be obtained in living and in dead sections (Greenham, unpublished). Moreover a dead and partially desiccated root can have the same low frequency resistance as a healthy root (5).

To overcome the difficulty caused by desiccation, measurements at both 1 kc/s and 100 kc/s were used (5), though 1 Mc/s would have been preferable for the higher frequency. More recently, to measure in-

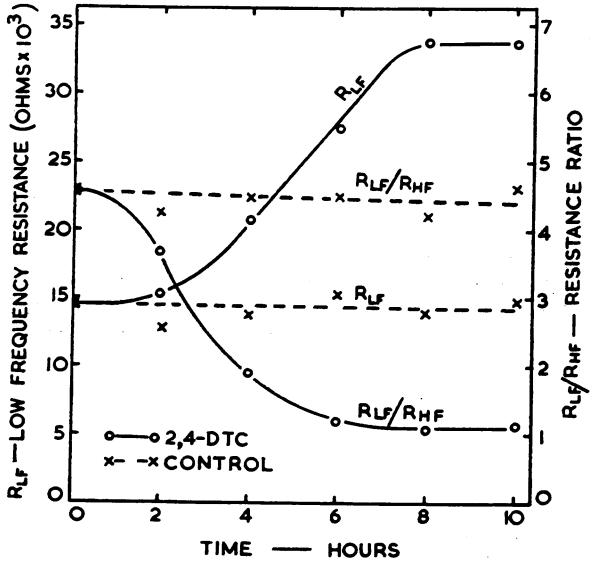

Fig. 1. Time-course of changes in electrical measurements on sections of etiolated pea stems. 2,4-DTC= 2×10^{-3} M 2,4-dichlorophenoxymethyl triethylammonium chloride; controls in distilled water. Sections equilibrated 20 hours beforehand in distilled water. Probe tips 2.5 mm apart, length exceeding diameter of sections. Measurements made with instrument described below.

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